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ORIGINAL PAPER

Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor

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Abstract Increased habitat fragmentation, global warming and other human activities have caused a rise in the frequency of wildfires worldwide. To reduce the risks of uncontrollable fires, prescribed burns are generally conducted during the colder months of the year, a time when in many mammals torpor is expressed regularly. Torpor is crucial for energy conservation, but the low body temperatures (T_b) are associated with a decreased responsiveness and torpid animals might therefore face an increased mortality risk during fires. We tested whether hibernators in deep torpor (a) can respond to the smell of smoke and (b) can climb to avoid fires at T_bs below normothermic levels. Our data show that torpid eastern pygmy-possums (*Cercartetus nanus*) are able to detect smoke and also can climb. All males aroused from torpor when the smoke stimulus was presented at an ambient temperature (T_a) of 15 °C (T_b ~18 °C), whereas females only raised their heads. The responses were less pronounced at T_a 10 °C. The first coordinated movement of possums along a branch was observed at a mean T_b of 15.6 °C, and animals were even able to climb their prehensile tail when they reached a mean T_b of 24.4 °C. Our study shows that hibernators can sense smoke and move at low T_b. However, our data also illustrate that at T_b ≤13 °C, *C. nanus* show decreased responsiveness and locomotor performance and highlight that prescribed burns during winter should be avoided on very cold days to allow torpid animals enough time to respond.

Keywords · *Cercartetus nanus* · Torpor · Locomotion · Sensory perception · Smell

Introduction

Detecting and responding to environmental stimuli is one of the defining features of living organisms. Endothermic vertebrates maximise sensory and locomotor function by maintaining a high body temperature (T_b) via combustion of fuels, but this comes at a high energetic cost especially in small species exposed to low ambient temperatures (T_a) (Tattersall et al. 2012). To deal with energetic challenges, small endotherms may enter a state of torpor during which T_b and metabolic rate are substantially reduced (Geiser 2013; Ruf and Geiser 2015). However, a disadvantage is that both sensory and locomotor function are also diminished in these heterothermic mammals during torpor (Rojas et al. 2012; Luo et al. 2014).

This reduction in sensory and locomotor function can be highly problematic during fast spreading bush fires. Global warming and other human activities have caused an increase in the frequency of wild fires, mainly during summer, all over the world (Moritz et al. 2012). Moreover, prescribed burns are conducted in the cold-season for fuel reduction and to help maintain a healthy ecosystem. These prescribed burns are lit usually between autumn and spring at a time when heterothermic animals often express deep torpor or hibernation and probably are highly vulnerable to fire. Thus, understanding and predicting behavioural and physiological responses of animals to fire and other natural disasters are

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crucial for conservation management. Although previous studies have shown that torpor facilitates post-fire survival, particularly when food availability is reduced (Stawski et al. 2015a; Nowack et al. 2016), torpor use during fires can be risky. Inhalation of toxic smoke, oxygen depletion and heat exposure during fires can cause injury or death to an animal. The length of time that an organism is exposed to high temperature or smoke is critical, and detection and avoidance of fire are essential behaviours for survival (Whelan 1995). Mobile animals are expected to either flee from the burning area or to shelter in underground burrows, caves or tree hollows (reviewed in Engstrom 2010). Previous studies on African and Australian species show that torpid terrestrial mammals are able to move at T_bs well below normothermic levels (Mzilikazi et al. 2002; Warnecke et al. 2008; Warnecke and Geiser 2010) and several small marsupials are able to run while torpid with T_bs as low as 14.8–17.9 °C (Rojas et al. 2012). However, seeking shelter might not only require the ability to run, but, especially in arboreal species, may also depend on the capacity to climb. This will not only entail coordinated locomotor capabilities on a more or less flat, horizontal surface that nevertheless are compromised by high speed (Wynn et al. 2015) but also clinging on to a surface and the challenge of moving vertically.

Since escape behaviour likely is delayed due to slowed reactions of torpid animals, an early detection of a fire is also of high importance, but currently few observations on escape behaviour and reaction to threatening stimuli during torpor are available (Grafe et al. 2002; Scesny and Robbins 2006). Recent studies have indicated that animals arouse from shallow torpor (T_b ≥25 °C) when exposed to high amounts of smoke (Stawski et al. 2015b). However, thick smoke is only expected when the fire has already reached the animals location. For a small animal, unable to cover long distances in a short time period, this may be too late to effectively respond to the fire or, if fleeing is no option, seek shelter in a safe refuge.

The eastern pygmy-possum (*Cercartetus nanus*) is a small, nocturnal, arboreal marsupial hibernator, distributed mainly along the southeast coast of Australia and commonly found in or near stands of *Banksia*. The species usually shelters individually in a nest of bark and leaves in tree hollows, underground or in bird nests (Menkhorst 1995). Pygmy-possums are agile climbers, have prehensile tails used for climbing, and can even climb up their own tails. Although not listed as endangered on the IUCN red list, eastern pygmy-possums are considered vulnerable in Australia (NSW NPWS 2015). Pygmy-possums are known to enter deep, multiday torpor year-round (Geiser 2007; Turner et al. 2012) and are therefore not only at risk to fall victim to hazard reduction burns during the colder season but also during wildfires in summer. To survive fire, animals must be able to (1) detect the fire and (2) get away from the fire. We therefore tested (a) if torpid eastern pygmy-possums can respond to the smell of smoke during torpor and (b) if and at which T_bs below normothermic levels they can climb.

Material and methods

Ethics

The experiments were carried out in accordance with the approved guidelines and regulations for animal care at the University of New England. Approval to conduct this study was granted by the University of New England Animal Ethics Committee and New South Wales National Parks and Wildlife Service.

Animal captures and housing

Five adult (3 males and 2 females) eastern pygmy-possums were used in the study. Pygmy-possum were retrieved from wooden nest boxes near Dorrigo (NSW, 30° 22′ S, 152° 34′ E) or captured in box aluminium traps (Elliott type A, Elliott Scientific Ltd, Upwey, Melbourne, Vic.) baited with a mixture of peanut butter and oats in Guy Fawkes National Park (30° 04′ S, 152° 20′ E). All individuals had been held in captivity for at least 6 months. Weight of individuals varied over the duration of the study and individual weights ranged from 25.0 ± 4.5 to 52.8 ± 4.1 g.

Animals were housed individually in cages (40 × 12 × 9 cm) in an unheated room ($T_a \geq 10$ °C) and natural photoperiod at the University of New England, Armidale. Animals were fed daily with apple and a nectar substitute consisting of high-protein baby cereal, honey and a vitamin supplement. Water was provided ad libitum.

Body temperature

T_b was measured as subcutaneous temperature (T_{sub}). For small mammals, T_{sub} is closely related to T_b, particularly during torpor when $T_b - T_a$ differentials are often 1 °C or less (Wacker et al. 2012). Before the experiment, temperature-sensitive transponders (IPTT-300, Bio Medic Data Systems, Delaware, USA; 0.13 g) were implanted subcutaneously. For implantation, animals were anaesthetised with general isoflurane/oxygen anaesthesia. A small (~3 mm) incision was made in the skin between the shoulder blades or in the lower ventral abdominal section for transponder insertion. The insertion site was closed with a single suture (chromic gut, Ethicon, Somerville, MA, USA). Prior to surgery the transponders were calibrated in a water bath against a precision mercury thermometer (±0.1 °C) in 5 °C-increments from 5 °C to 40 °C. All transponders continued to function below the manufacturer's recommended range of use (32–43 °C) down to at least 5 °C. All transponders were well within the recommended range of implanted devices of <10 % of the body mass of small terrestrial mammals; this recommendation was made because locomotion is not negatively affected by devices of that weight (Rojas et al. 2010). T_{sub} was read from each animal with a DAS-7006/7R/S Handheld Reader (Bio Medic Data Systems).

Olfactory acuity during torpor

Animals were placed in a glass respirometry chamber (500 ml) situated within a temperature-controlled cabinet in the early evening and metabolic rate (MR), measured as the rate of oxygen consumption, was monitored overnight and throughout the following day(s) to allow animals to undergo their usual daily thermal cycle. Animals were weighed before and after the experiments and a linear loss of body mass during the time of measurement was assumed. Respirometry chamber T_a was measured with a thermocouple probe and maintained at T_a 10.3 ± 0.3 °C or T_a 15.4 ± 1.0 °C and natural photoperiod for Armidale was simulated in the climate chamber.

Energy expenditure of animals was determined with open flow respirometry using an oxygen analyser (Sable Systems FC-1B Oxygen Analyzer, USA). The metabolic chamber was connected to the oxygen analyser with airtight tubes (push mode). Flow rate was maintained between 200 ml min^{-1} (normothermic) and 100 ml min^{-1} (torpid). Water vapour was scrubbed prior to oxygen analysis using silica gel. We measured sample air for 15 min and then switched to outside air for reference readings (4 min) using solenoid valves to account for any drift of the oxygen sensor (sampling frequency every 60 s). All values are presented as mass specific values ($mlO_2\ g^{-1}\ h^{-1}$). Outputs of the digital thermocouple thermometer, flow meter and oxygen analyser were recorded using custom-written data-acquisition software onto a personal computer. Behavioural reactions were monitored via an infrared web camera and recorded with Simple Webcam Recorder (AviFromWebcam, V.1.0.0.0, © 2010).

Experiments were performed when animals were in steady-state torpor (between 11:30 p.m. and 2 p.m.) to measure metabolic rate during torpor (TMR). For each experiment 6 ml of smoke water (Regen 2000 Smokemaster, Grayson; ingredients: water, wood smoke (IMB-B9), emulsifier, food colour (129)) together with 1 ml of hot water were placed into a test tube with cotton wool. The test tube was inserted in between the airtight tubes of the system upstream of the animal chamber and outside of the temperature-controlled cabinet for a duration of 10 min. All animals were tested with the smoke stimulus at T_a 10 and 15 °C as well as with a water control at 15 °C. The order of experiments was randomised and spread over 2 to 3 months to ensure that the results were not caused by a habituation effect. For control measurements, animals were tested using the same protocol as stated above, but replacing the 6 ml of smoke water with water. Due to the low detection range of the handheld reader, we were not able to gain continuous measurements of T_{sub} during the smoke experiments and instead assumed T_b to be <3 °C above T_a during steady-state torpor, based on Song et al. (1997): $T_b - T_a = 1.9 \pm 0.9$ °C.

A response to the olfactory stimulus was defined as one of the following: a visible behavioural response, such as 'head raising' or an increase of torpor metabolic rate (TMR). 'Delayed arousal' was defined as a slow but steady increase of the TMR that led to final arousal within the measuring period ($MR \geq 2\ mlO_2\ h^{-1}\ g^{-1}$ only after ≥60 min) and 'arousal' describes an immediate and fast arousal from torpor ($MR \geq 2\ mlO_2\ h^{-1}\ g^{-1}$ within 30 min).

Climbing experiments

Torpid individuals were retrieved from their nest boxes in the morning and initial body T_{sub} was recorded. For measurement at low T_bs, animals were fasted overnight in a temperature-controlled cabinet at T_a 10 °C.

For the experiments, the individuals were placed on a horizontal branch (length 35 cm, diameter ~1 cm) that was turned slowly and movement and behaviour of the animals were quantified. T_{sub} was measured regularly during the experiment. We recorded T_{sub} from which an animal was able to (i) hold on to the stick and (ii) move on the stick (Table 1). In a second experiment, individuals were held at the tip of their prehensile tail for up to 1 min and T_{sub}s from which individuals (i) were trying to grab their tails and climb and (ii) actually were able to climb up their tail were recorded to assess coordination and muscle function necessary during escape behaviour (Table 1). All experiments were recorded via video camera (Canon, PowerShot SX1IS). Animals were weighed after the experiments to the nearest 0.1 g with an

Table 1 Ethogram of behaviours and their definitions

Behaviour	Definition
Holding	Clinging on the branch without falling off
Moving	Coordinated directed locomotor capability on the branch
Trying to climb	Twisting or bending of body to reach tail
Climbing	Successful climbing up the tail

electronic balance. Experiments were repeated at least five times for each animal (range 5–8). In order to keep data comparable, we chose only three measurements (T_{sub} <15 °C) per individual for analyses.

Data analyses

Data are presented as mean ± 1 standard deviation; *n* denotes the number of individuals and *N* the number of observations. Statistical analyses were conducted in R, version 3.2.2 (R Development Core Team 2014). The increase of metabolic rate in response to the water stimulus during control measurements was analysed with a paired *t* test after testing for normality and homogeneity of variance using Shapiro–Wilk test and Bartlett's test, respectively. The metabolic response to smoke water at the different temperatures was analysed with generalised linear mixed effect models using 'individual' as a random factor to account for repeated measures, followed by an ANOVA (*lme* in library 'nlme' (Pinheiro et al. 2014)). The same approach was used to define the relationship between body mass and minimal T_{sub} for the various locomotor tasks (holding, moving, trying to climb, climbing) as well as the difference in minimal T_{sub} between the tasks. Post hoc analyses were performed as Tukey tests (*glht* in library 'multcomp' (Hothorn et al. 2008)).

Results

Olfactory acuity during torpor

All individuals were in steady-state torpor when the experiments were conducted (TMR at T_a 15 °C: 0.08 ± 0.03 $mlO_2\ g^{-1}\ h^{-1}$, $N = 10$ (control and experiment), $n = 5$; T_a 10 °C: 0.07 ± 0.04 $mlO_2\ g^{-1}\ h^{-1}$, $N = 5$, $n = 5$). Control measurements (water) did not lead to arousal of individuals nor to a significant increase of TMR (*t* test: $t_4 = -2.35$, $p = 0.08$, $n = 5$).

The response to smoke water was individual specific and we observed a temperature effect (Fig. 1). Average TMR was significantly increased (on average >52-fold) between the control measurements and treatment at T_a 15 °C (T_b ~18 °C), but not at T_a 10 °C (T_b ~13 °C) (ANOVA: $F_{2,8} = 5.07$, $p = 0.04$; post hoc: 10–15 °C and control-15 °C: $z \geq 2.50$, $p \leq 0.03$; control-10 °C: $z = 0.45$, $p = 0.89$). All individuals responded to the smoke stimulus at a T_a of 15 °C (T_{sub} ~18.3 ± 1.4 °C; $n = 5$); the three males responded with arousal (two aroused within 30 min, one male showed a delayed arousal after 43 min; example in Fig. 1), whereas both females only raised their heads in response to the stimulus (after 6 and 8.5 min, respectively) and only slightly increased their TMR. One of the three males re-entered torpor after the arousal and again displayed minimal energy expenditure about 2 h after the presentation of the stimulus. At T_a 10 °C (T_{sub} ~13.3 ± 0.3 °C; $n = 5$), only three animals (2 males, 1 female) responded with an marked increase of TMR that in one male eventually led to an arousal within 110 min (delayed arousal).

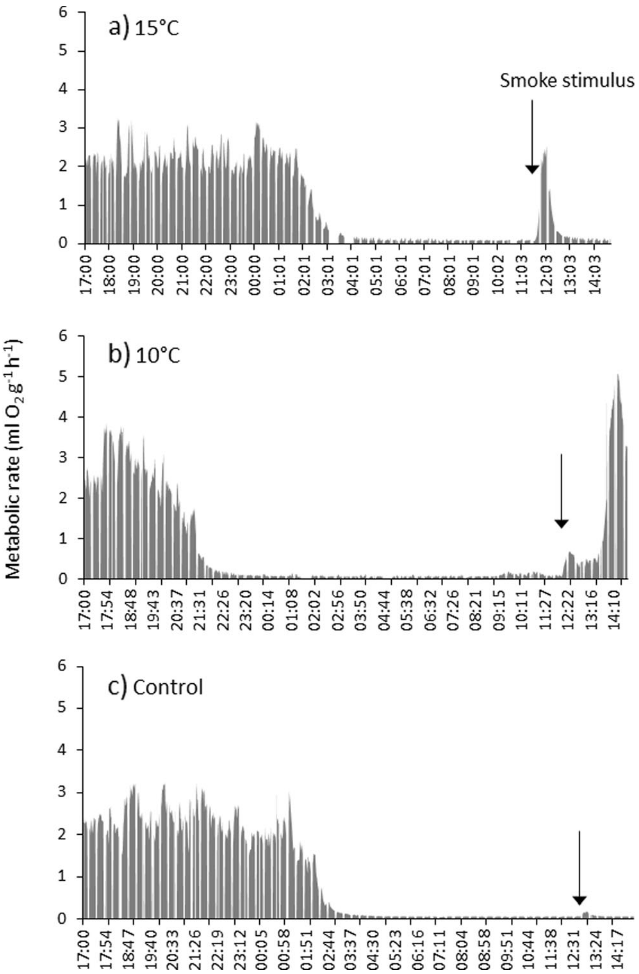

Fig. 1 Metabolic response of a male pygmy-possum (*Cercartetus nanus*) to **a** smoke stimulus at T_a 15 °C (arousal, within 30 min), **b** smoke stimulus at T_a 10 °C (delayed arousal, after 110 min) and **c** control (water stimulus) at T_a 15 °C. The *arrow* marks the moment the stimulus was presented to the individual. The depicted individual was the only one that re-entered torpor after the arousal

Climbing experiment

Animals were able to hold on to the branch from the beginning of the experiment during most trials ($N = 12$ of 15 trials). The minimum T_{sub} for successful holding on to the branch was 10.7 °C, with a mean of 12.7 ± 1.6 °C ($N = 15$, $n = 5$) (Fig. 2). While the T_{sub} at which animals were able to hold on to the branch was similar among individuals, locomotor capability for moving and climbing differed among individuals (Fig. 3). The first coordinated movement on the turning horizontal branch ('moving') was observed at 13.4 °C and all

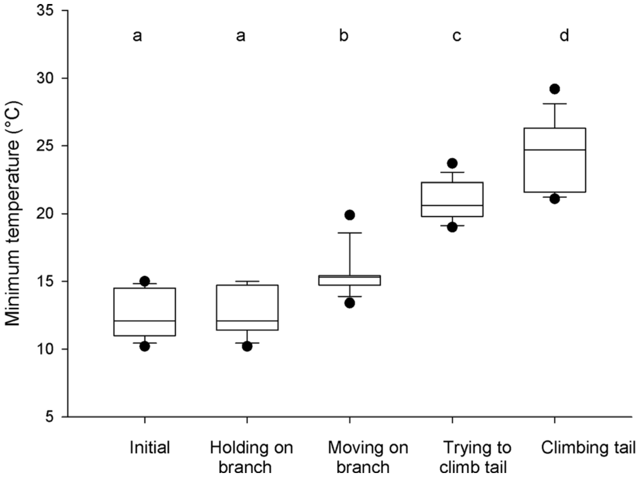

Fig. 2 Locomotor performance of pygmy-possums (*Cercartetus nanus*) for different tasks in regard to subcutaneous temperature. *Box plots* represent median, as well as 5-, 25-, 75- and 95-percentiles. Outliners are depicted as *black dots*. Animals were able to hold on to the branch from the beginning of the experiment; T_{sub}s of all other tasks were significantly different from each other. Significant differences are indicated by *different letters*

but one individual, which only started moving at ~18 °C, moved at $T_{\mathrm{sub}} \leq 15.4$ °C (mean 15.6 ± 1.1 °C, $n = 5$, $N = 15$).

The mean minimal T_{sub} at which animals tried to climb their prehensile tail was 20.9 ± 1.3 °C ($n = 5$, $N = 15$) and more than 90 % of the attempts were observed at T_{sub}s between 19 and 23 °C. Mean minimal T_{sub} at which animals were able to climb was 24.4 °C ± 2.0 °C. The difference between T_{sub} for holding and the initial T_{sub} was not significant, while T_{subs} of all other tasks were significantly different to each other (ANOVA; $F_{4,66} = 162.97$, $p < 0.001$; Tukey post hoc: holding $z = 0.43$, $p = 0.993$; rest $z > 4.83$, $p < 0.001$).

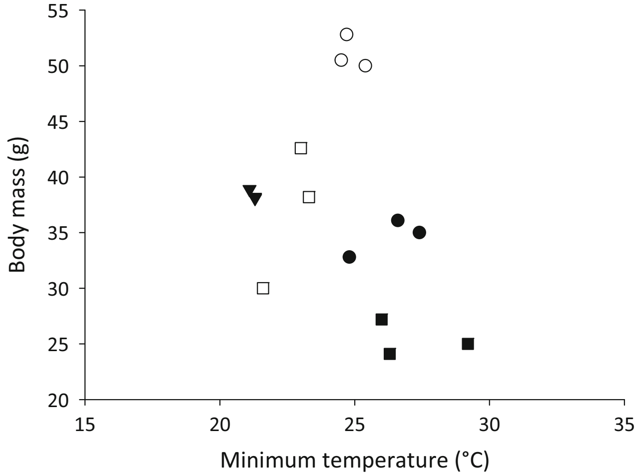

Fig. 3 Individual locomotor performance for successful tail climbing performance of pygmy-possums (*Cercartetus nanus*). Depicted are the three trials with the lowest subcutaneous temperatures for all five individuals in regard to body mass. Individuals are represented by *different symbols*; males are indicated as *filled symbols*; females are represented by *open symbols*

Although some individuals were substantially heavier than others the T_{sub} and body mass of the individuals for any of the tasks were not correlated (ANOVA; holding: $F_{1,9} = 4.67$, $p = 0.06$; moving: $F_{1,9} = 1.08$, $p = 0.33$; trying to climb: $F_{1,9} = 0.02$ p = 0.88, $p = 0.33$; climbing: $F_{1,9} = 0.45$, $p = 0.52$).

Discussion

Our data reveal that pygmy-possums can perceive and respond to olfactory stimuli during torpor and perform advanced locomotor tasks with T_{b}s well below normothermic values, but show decreased responsiveness and locomotor performance at lower T_{sub}s. Furthermore, we illustrate that slow locomotion is possible at T_{b}s as low as 13.4 °C, climbing along a horizontal branch at T_{b} ~15.4 °C, whereas advanced locomotor tasks, such as climbing up the tail, can only successfully be performed with a T_{b} ~24 °C. Our study shows that hibernators can sense olfactory stimuli, such as smoke and move at low T_{b}s.

In the past, torpor was often viewed as a risky state because it had been assumed that torpid individuals are easy prey for predators. More recently, this dogma has been challenged because survival rates of individuals during the hibernation season are higher than during the active season (Turbill et al. 2011). Moreover, it appears that heterothermic species are at a lower risk of becoming extinct than homeothermic species that are unable to express torpor (Geiser and Turbill 2009; Hanna and Cardillo 2014). A reason for the better survival rate seems to be that torpid mammals are less likely to be discovered by predators as they are typically hiding in a sealed burrow or other protected shelters while being motionless and cold, therefore emitting less stimuli detectable by predators (Turbill et al. 2011). On the other hand, impaired locomotion during torpor is a disadvantage when it comes to threats that require an active response, such as wildfires. A torpid individual most likely cannot respond very quickly when its hibernaculum/resting site is on the threat of burning. Dunnarts, small insectivorous marsupials, responded immediately to high amounts of smoke and aroused from shallow torpor (T_{b} ~25 °C) (Stawski et al. 2015b). However, it was not clear from that study whether the response was triggered by the smell or rather by the smoke particles or the high concentration of CO. Our study confirms that the presentation of the smoke stimulus alone can be perceived by torpid pygmy-possums with a $\mathrm{T_b}$ as low as 13 °C. Our data are in line with another study that has previously shown that torpid bats ($\mathrm{T_b}$~18 °C) respond to noise stimuli with an increase of T_{b} (Luo et al. 2014) and suggests that sensory signals, other than mainly tactile stimuli (Speakman et al. 1991), can be perceived and processed during deep torpor.

However, while all pygmy-possums showed a clear response at a T_{b} of about 18 °C, individuals only responded with delayed arousal or a slight increase of TMR at low T_bs, indicating a diminished responsiveness to sensory cues. Neurobiological studies have shown that the brain becomes less responsive with declining T_b (Larkin and Heller 1996) and it is likely that responsiveness to external stimuli diminishes at even lower T_bs than tested in this study. This is also emphasised by the fact that at a core T_b of below 11 °C, the electroencephalogram of the brain appears as a flat line and activity can only be observed in deeper brain areas responsible for thermoregulation (Larkin and Heller 1999).

While a previous study of dunnarts exposed to high amounts of smoke, entailing not only the smell but also irritating particles and high levels of CO, showed that animals increased activity and acted alarmed for a few hours (Stawski et al. 2015b), this response was not observed in the pygmy-possums. Although all pygmy-possums responded to the smoke stimulus at the higher T_a, one animal re-entered torpor immediately after the arousal, while the females did not arouse at all and only showed a behavioural response. This indicates that more cues than just the smell of smoke are necessary to mimic an approaching fire. It is also conceivable that the response was only triggered by the unfamiliar smell but not identified as a potential threat. More work is needed to investigate if torpid animals can differentiate between threatening stimuli, such as the smell of a predator or a fire, and harmless cues.

Arousal from torpor in response to the smell of smoke does not suffice and will not guarantee the survival of the individual when the animal cannot also move quickly enough to evade the danger. It is well known that running speed in ectothermic lizards is a negative function of T_b and similar relationships have been established recently in three species of ground-dwelling heterothermic marsupials (Rojas et al. 2012). In contrast, a decrease of T_b by 7–8 °C to just above a T_b of 30 °C did not seem to visibly affect running speeds of heterothermic ground squirrels (Wooden and Walsberg 2003). Our data show that pygmy-possums are able to move on a horizontal branch at T_{sub} of about 15 °C, which is in the same range as found for movements on the ground for terrestrial species (14.8–17.9 °C (Rojas et al. 2012)), although the movement on the branch is likely more difficult than on a straight smooth surface. However, our experiment also indicates that coordinated flight behaviour, i.e. climbing required to evade fires in arboreal species, can only be performed by pygmy-possums from about T_b 20 °C and above. At a T_b of about 20 °C, individuals were trying to climb their tails, which requires the involvement of main abdominal muscles and entails bending and stretching. Interestingly, pygmy-possums seem to be able to cling on the branch from the beginning of the experiment and therefore perhaps even at lower T_b during torpor. That advanced locomotor performance can only be performed at higher T_bs is also shown by a study on bats that found that although bats were able to crawl at a T_b of 8 °C, flapping of wings only occurred at 22 °C and aerial flight was only possible at temperatures around 28 °C (Choi et al. 1998).

In conclusion, our data show that pygmy-possums can perceive and respond to olfactory stimuli during torpor and perform advanced locomotor skills with T_bs well below normothermic values, but show decreased responsiveness and locomotor performance at $T_b\text{s} \leq 13$ °C. Wildfires are usually related to high T_a in summer and even prescribed burns are usually conducted on cool (16–25 °C, pers communication NSW NPWS) rather than cold days in Australia. Therefore, we can assume that if torpid animals are present in an area of a burn, they are able to arouse before the fire has reached their nest location and have the chance to seek a safe refuge during the fire. However, if deaths of small mammals due to fires are to be minimised, prescribed burns should not be conducted during the coldest part of winter.

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