

# 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 can a) respond to the smell of smoke and b) can climb to avoid fires at  $T_b$ s 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 ( $T_b \sim 18^\circ\text{C}$ ), 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  $T_b \leq 13^\circ\text{C}$ , *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.

## 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 behavioral and physiological responses of animals to fire and other natural disasters are 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 behaviors 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  $T_b$ s 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  $T_b$ s 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 behavior 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 behavior 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 ( $T_b \geq 25^\circ\text{C}$ ) 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 south-east 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 NSWP 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  $T_b$ s 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-possums were retrieved from wooden nest boxes near Dorrigo (NSW, 30° 22'S, 152° 34') 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 six months. Weight of individuals varied over the duration of the study and individual weights ranged from  $25.0 \pm 4.5$  g to  $52.8 \pm 4.1$  g.

Animals were housed individually in cages (40 x 12 x 9cm) in an unheated room ( $T_a \geq 10^\circ\text{C}$ ) 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 ( $T_{\text{sub}}$ ). For small mammals,  $T_{\text{sub}}$  is closely related to  $T_b$ , particularly during torpor when  $T_b - T_a$  differentials are often  $1^\circ\text{C}$  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 anaesthetized with general isoflurane/oxygen anaesthesia. A small (~3mm) 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 ( $\pm 0.1^{\circ}\text{C}$ ) in  $5^{\circ}\text{C}$ -increments from  $5^{\circ}\text{C}$  to  $40^{\circ}\text{C}$ . All transponders continued to function below the manufacturer's recommended range of use ( $32\text{--}43^{\circ}\text{C}$ ) down to at least  $5^{\circ}\text{C}$ . 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).  $T_{\text{sub}}$  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 (500ml) 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  $T_a 10.3 \pm 0.3^{\circ}\text{C}$  or  $T_a 15.4 \pm 1.0^{\circ}\text{C}$  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  $200\text{ ml min}^{-1}$  (normothermic) and  $100\text{ ml min}^{-1}$  (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 sec). All values are presented as mass specific values ( $\text{mlO}_2\text{g}^{-1}\text{h}^{-1}$ ). Outputs of the digital thermocouple thermometer, flowmeter and oxygen analyzer were recorded using custom-written data-acquisition software onto a personal computer. Behavioral 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 11:30pm and 2pm) 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°C and 15°C as well as with a water control at 15°C. The order of experiments was randomized and spread over two to three 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 6ml 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):  $T_b - T_a = 1.9 \pm 0.9^\circ\text{C}$ .

A response to the olfactory stimulus was defined as one of the following: a visible behavioral 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 ( $MR \geq 2\text{mlO}_2 \text{ h}^{-1}\text{g}^{-1}$  only after  $\geq 60\text{min}$ ) and 'arousal' describes an immediate and fast arousal from torpor ( $MR \geq 2\text{mlO}_2 \text{ h}^{-1}\text{g}^{-1}$  within 30min).

#### *Climbing experiments*

Torpid individuals were retrieved from their nest boxes in the morning and initial body  $T_{sub}$  was recorded. For measurement at low  $T_b$ s 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 (35cm length, diameter: ~1cm) that was turned slowly and movement and behavior 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 (Tab. 1). In a second experiment individuals were held at the tip of their prehensile tail for up to one minute and  $T_{sub}$ s from which individuals were (i) 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 behavior (Tab. 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 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 ( $T_{sub} < 15^\circ\text{C}$ ) per individual for analyses.

#### *Data analyses*

Data are presented as mean  $\pm$  1 standard deviation;  $n$  denotes the number of individuals,  $N$  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 generalized 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  $T_{\text{sub}}$  for the various locomotor tasks (holding, moving, trying to climb, climbing) as well as the difference in minimal  $T_{\text{sub}}$  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:  $0.08 \pm 0.03$  ml  $O_2$   $g^{-1} h^{-1}$ ,  $N=10$  (control and experiment),  $n=5$ ;  $T_a$  10°C:  $0.07 \pm 0.04$  ml  $O_2$   $g^{-1} h^{-1}$ ,  $N=5$ ,  $n=5$ ). 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 (figure 1). Average TMR was significantly increased (on average >52-fold) between the control measurements and treatment at 15°C ( $T_b \sim 18^\circ\text{C}$ ), but not at 10°C ( $T_b \sim 13^\circ\text{C}$ ) (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 ( $T_{\text{sub}} \sim 18.3 \pm 1.4^\circ\text{C}$ ;  $n=5$ ); the three males responded with arousal (two aroused within 30 min, one male showed a delayed arousal after 43 min; example in figure 1), whereas both females only raised their heads in response to the stimulus (after 6 min 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 two hours after the presentation of the stimulus. At  $T_a$  10°C ( $T_{\text{sub}} \sim 13.3 \pm 0.3^\circ\text{C}$ ;  $n=5$ ) 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).

### *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  $T_{\text{sub}}$  for successful holding on to the branch was  $10.7^\circ\text{C}$ , with a

mean of  $12.7 \pm 1.6^{\circ}\text{C}$  ( $N=15$ ,  $n=5$ ) (figure 2). While the  $T_{\text{sub}}$  at which animals were able to hold on to the branch was similar among individuals, locomotor capability for moving and climbing differed among individuals (figure 3). The first coordinated movement on the turning horizontal branch ('moving') was observed at  $13.4^{\circ}\text{C}$  and all but one individual, which only started moving  $\sim 18^{\circ}\text{C}$ , moved at  $T_{\text{sub}} \leq 15.4^{\circ}\text{C}$  (mean:  $15.6 \pm 1.1^{\circ}\text{C}$ ,  $n=5$ ,  $N=15$ ).

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

Although some individuals were significantly heavier than others the  $T_{\text{sub}}$  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  $T_{\text{b}}$ s well below normothermic values, but show decreased responsiveness and locomotor performance at lower  $T_{\text{sub}}$ s. Furthermore, we illustrate that slow locomotion is possible at  $T_{\text{b}}$ s as low as  $13.4^{\circ}\text{C}$ , climbing along a horizontal branch at  $T_{\text{b}} \sim 15.4^{\circ}\text{C}$ , whereas advanced locomotor tasks, such as climbing up the tail, can only successfully be performed with a  $T_{\text{b}} \sim 24^{\circ}\text{C}$ . Our study shows that hibernators can sense olfactory stimuli, such as smoke and move at low  $T_{\text{b}}$ 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 ( $T_b \sim 25^\circ\text{C}$ ) (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 body temperature as low as  $13^\circ\text{C}$ . Our data are in line with another study that has previously shown that torpid bats ( $\sim 18^\circ\text{C}$ ) 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  $18^\circ\text{C}$ , individuals only responded with delayed arousal or a slight increase of TMR at low  $T_b$ s, 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  $T_b$ s than tested in this study. This is also emphasised by the fact that at a core  $T_b$  of below  $11^\circ\text{C}$ , 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 2015), 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 behavioral 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 two species of ground-dwelling heterothermic marsupials (Rojas et al. 2012). In contrast, a decrease of  $T_b$  by  $7\text{--}8^\circ\text{C}$  to just above a  $T_b$  of  $30^\circ\text{C}$  did not seem to not 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  $T_{\text{sub}}$  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 co-ordinated flight behavior, 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  $T_b$ s 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  $T_b$ s well below normothermic values, but show decreased responsiveness and locomotor performance at  $T_b$ 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 NSWNP) 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.

## Acknowledgements

We thank Arne Müller and Chris Wacker for assistance in animal maintenance. The project was supported by grants from the German Academic Exchange Service and the A.F.W. Schimper Stiftung für ökologische Forschung to JN, a University of New England Postdoctoral Research Fellowship to CS, by the Australian Research Council and the University of New England to FG and by the French Ministry of Agriculture, Agrifood and Forestry and by the Region Auvergne (France) to MD.

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Table 1: Ethogramm of behaviors and their definitions

<b>Behavior</b>	<b>Definition</b>
Holding	Clinging on the branch without falling off
Moving	Co-ordinated directed locomotor capability on the branch
Trying to climb	Twisting or bending of body to reach tail
Climbing	Successful climbing up the tail

## Figures

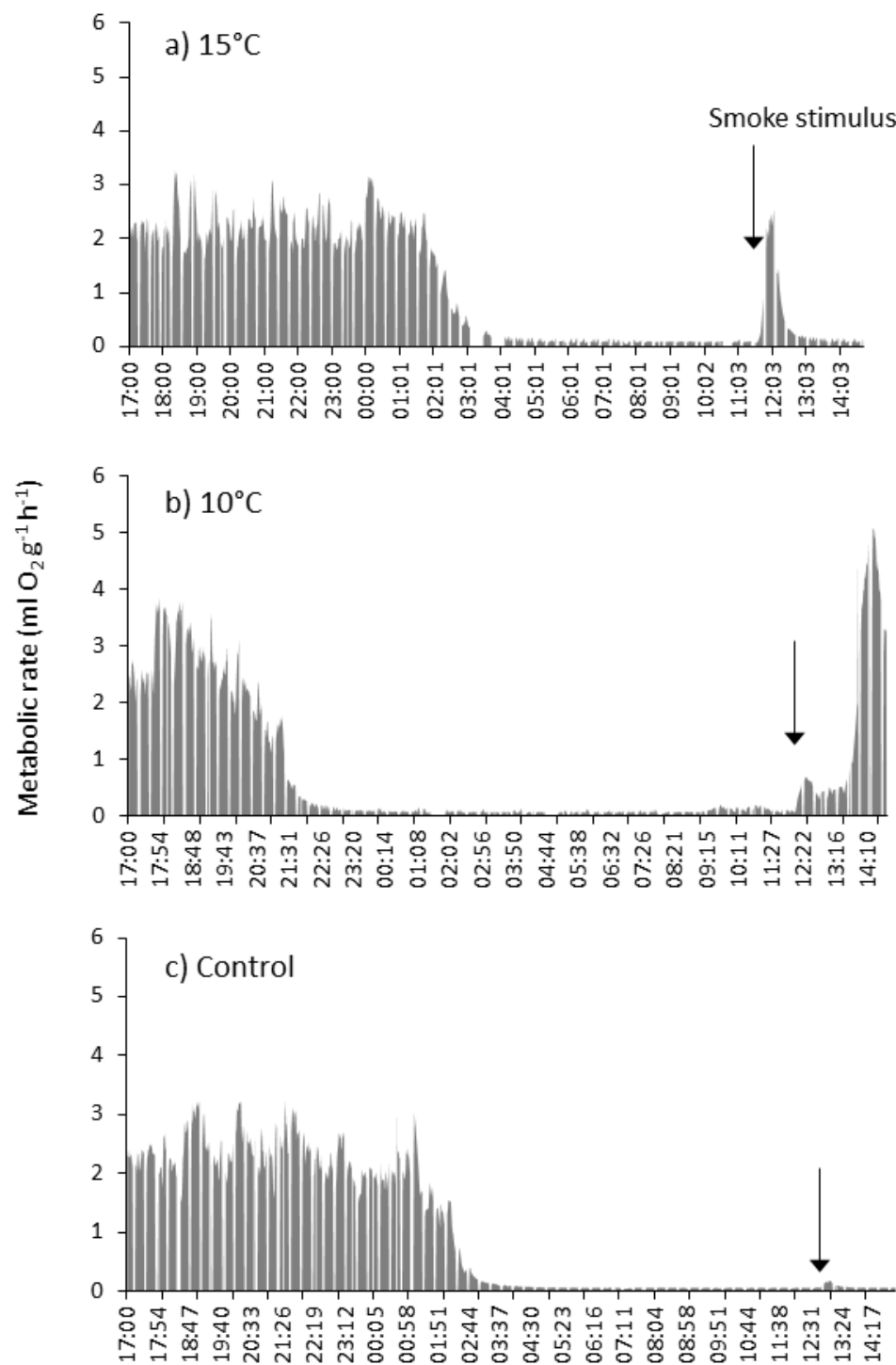


Figure 1abc: Metabolic response of a male individual to a) smoke stimulus at 15°C (arousal, within 30 min), b) smoke stimulus at 10°C (delayed arousal, after 110 min), and c) control (water stimulus) at 15°C. The arrow marks the moment the stimulus was presented to the individual. The depicted individual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

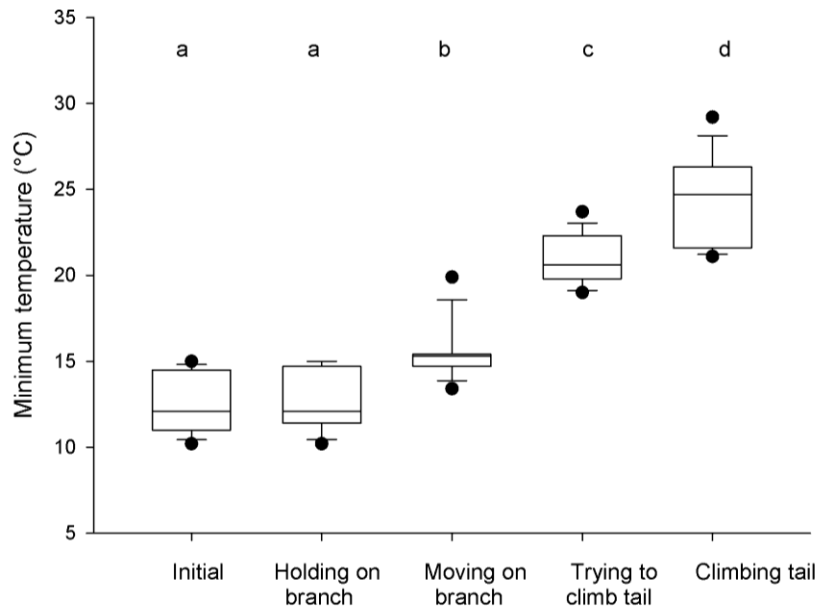


Figure 2: Locomotor performance for different tasks in regard to body temperature. Boxplots represent median, as well as 5-, 25-, 75- and 95-percentiles. Outliners are depicted as black dots. Animals were able to hold on to the branch from the beginning of the experiment;  $T_{\text{sub}}$  of all other tasks were significantly different from each other. Significant differences are indicated by different letters.

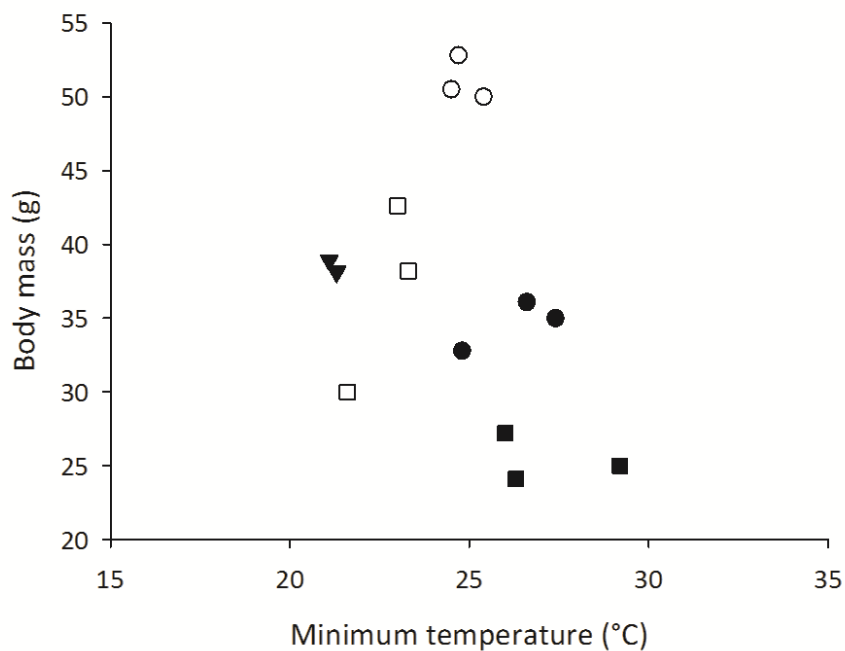


Figure 3: Individual locomotor performance for successful tail climbing performance. Depicted are the three trials with the lowest subcutaneous temperatures ( $T_{\text{sub}}$ ) for all five individuals in regard to body mass. Individuals are represented by different symbols; males are indicated as filled symbols; females are represented by open symbols.