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

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11

12 **Abstract**

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

29

30 **Introduction**

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

37 both sensory and locomotor function are also diminished in these heterothermic mammals during
38 torpor (Rojas et al. 2012; Luo et al. 2014).

39 This reduction in sensory and locomotor function can be highly problematic during fast
40 spreading bush fires. Global warming and other human activities have caused an increase in the
41 frequency of wild fires, mainly during summer, all over the world (Moritz et al. 2012). Moreover,
42 prescribed burns are conducted in the cold-season for fuel reduction and to help maintain a healthy
43 ecosystem. These prescribed burns are lit usually between autumn and spring at a time when
44 heterothermic animals often express deep torpor or hibernation and probably are highly vulnerable
45 to fire. Thus understanding and predicting behavioral and physiological responses of animals to fire
46 and other natural disasters are crucial for conservation management. Although previous studies have
47 shown that torpor facilitates post-fire survival, particularly when food availability is reduced (Stawski
48 et al. 2015a; Nowack et al. 2016), torpor use during fires can be risky. Inhalation of toxic smoke,
49 oxygen depletion and heat exposure during fires can cause injury or death to an animal. The length
50 of time that an organism is exposed to high temperature or smoke is critical, and detection and
51 avoidance of fire are essential behaviors for survival (Whelan 1995). Mobile animals are expected to
52 either flee from the burning area or to shelter in underground burrows, caves or tree hollows
53 (reviewed in Engstrom 2010). Previous studies on African and Australian species show that torpid
54 terrestrial mammals are able to move at T_b s well below normothermic levels (Mzilikazi et al. 2002;
55 Warnecke et al. 2008; Warnecke and Geiser 2010) and several small marsupials are able to run while
56 torpid with T_b s as low as 14.8–17.9°C (Rojas et al. 2012). However, seeking shelter might not only
57 require the ability to run, but, especially in arboreal species, may also depend on the capacity to
58 climb. This will not only entail coordinated locomotor capabilities on a more or less flat, horizontal
59 surface that nevertheless are compromised by high speed (Wynn et al. 2015), but also clinging on to
60 a surface, and the challenge of moving vertically.

61 Since escape behavior likely is delayed due to slowed reactions of torpid animals, an early
62 detection of a fire is also of high importance, but currently few observations on escape behavior and
63 reaction to threatening stimuli during torpor are available (Grafe et al. 2002; Scesny and Robbins
64 2006). Recent studies have indicated that animals arouse from shallow torpor ($T_b \geq 25^\circ\text{C}$) when
65 exposed to high amounts of smoke (Stawski et al. 2015b). However, thick smoke is only expected
66 when the fire has already reached the animals location. For a small animal, unable to cover long
67 distances in a short time period, this may be too late to effectively respond to the fire or, if fleeing is
68 no option, seek shelter in a safe refuge.

69 The eastern pygmy-possum (*Cercartetus nanus*) is a small, nocturnal, arboreal marsupial
70 hibernator, distributed mainly along the south-east coast of Australia and commonly found in or

71 near stands of *Banksia*. The species usually shelters individually in a nest of bark and leaves in tree
72 hollows, underground or in bird nests (Menkhorst 1995). Pygmy-possums are agile climbers, have
73 prehensile tails used for climbing, and can even climb up their own tails. Although not listed as
74 endangered on the IUCN red list, eastern pygmy-possums are considered vulnerable in Australia
75 (NSW NSWP 2015). Pygmy-possums are known to enter deep, multiday torpor year-round (Geiser
76 2007; Turner et al. 2012) and are therefore not only at risk to fall victim to hazard reduction burns
77 during the colder season, but also during wildfires in summer. To survive fire animals must be able to
78 1. detect the fire and 2. get away from the fire. We therefore tested a) if torpid eastern pygmy-
79 possums can respond to the smell of smoke during torpor and b) if and at which T_b s below
80 normothermic levels they can climb.

81

82 **Material and methods**

83 *Ethics*

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

88

89 *Animal captures and housing*

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

96 Animals were housed individually in cages (40 x 12 x 9cm) in an unheated room ($T_a \geq 10^\circ\text{C}$)
97 and natural photoperiod at the University of New England, Armidale. Animals were fed daily with
98 apple and a nectar substitute consisting of high protein baby cereal, honey and a vitamin
99 supplement. Water was provided *ad libitum*.

100

101 *Body temperature*

102 T_b was measured as subcutaneous temperature (T_{sub}). For small mammals, T_{sub} is closely related to
103 T_b , particularly during torpor when $T_b - T_a$ differentials are often 1°C or less (Wacker et al. 2012).
104 Before the experiment, temperature-sensitive transponders (IPTT-300, Bio Medic Data Systems,

105 Delaware, USA; 0.13 g) were implanted subcutaneously. For implantation animals were
106 anaesthetized with general isoflurane/oxygen anaesthesia. A small (~3mm) incision was made in the
107 skin between the shoulder blades or in the lower ventral abdominal section for transponder
108 insertion. The insertion site was closed with a single suture (chromic gut, Ethicon, Somerville, MA,
109 USA). Prior to surgery the transponders were calibrated in a water bath against a precision mercury
110 thermometer ($\pm 0.1^\circ\text{C}$) in 5°C -increments from 5°C to 40°C . All transponders continued to function
111 below the manufacturer's recommended range of use ($32\text{--}43^\circ\text{C}$) down to at least 5°C . All
112 transponders were well within the recommended range of implanted devices of $<10\%$ of the body
113 mass of small terrestrial mammals; this recommendation was made because locomotion is not
114 negatively affected by devices of that weight (Rojas et al. 2010). T_{sub} was read from each animal with
115 a DAS-7006/7R/S Handheld Reader (Bio Medic Data Systems).

116

117 *Olfactory acuity during torpor*

118 Animals were placed in a glass respirometry chamber (500ml) situated within a temperature-
119 controlled cabinet in the early evening and metabolic rate (MR), measured as the rate of oxygen
120 consumption, was monitored overnight and throughout the following day(s) to allow animals to
121 undergo their usual daily thermal cycle. Animals were weighed before and after the experiments and
122 a linear loss of body mass during the time of measurement was assumed. Respirometry chamber T_a
123 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
124 natural photoperiod for Armidale was simulated in the climate chamber.

125 Energy expenditure of animals was determined with open flow respirometry using an
126 oxygen analyser (Sable Systems FC-1B Oxygen Analyzer, USA). The metabolic chamber was
127 connected to the oxygen analyser with airtight tubes (push mode). Flow rate was maintained
128 between 200 ml min^{-1} (normothermic) and 100 ml min^{-1} (torpid). Water vapour was scrubbed prior
129 to oxygen analysis using silica gel. We measured sample air for 15 min and then switched to outside
130 air for reference readings (4 min) using solenoid valves to account for any drift of the oxygen sensor
131 (sampling frequency every 60 sec). All values are presented as mass specific values ($\text{mlO}_2\text{g}^{-1}\text{h}^{-1}$).
132 Outputs of the digital thermocouple thermometer, flowmeter and oxygen analyzer were recorded
133 using custom-written data-acquisition software onto a personal computer. Behavioral reactions
134 were monitored via an infrared web camera and recorded with Simple Webcam Recorder
135 (AviFromWebcam, V.1.0.0.0, © 2010).

136 Experiments were performed when animals were in steady state torpor (between 11:30pm
137 and 2pm) to measure metabolic rate during torpor (TMR). For each experiment 6 ml of smoke water
138 (Regen 2000 Smokemaster, Grayson; ingredients: water, wood smoke (IMB-B9), emulsifier, food

139 colour (129)) together with 1 ml of hot water were placed into a test tube with cotton wool. The test
140 tube was inserted in between the airtight tubes of the system upstream of the animal chamber and
141 outside of the temperature-controlled cabinet for a duration of 10 min. All animals were tested with
142 the smoke stimulus at T_a 10°C and 15°C as well as with a water control at 15°C. The order of
143 experiments was randomized and spread over two to three months to ensure that the results were
144 not caused by a habituation effect. For control measurements animals were tested using the same
145 protocol as stated above, but replacing the 6ml of smoke water with water. Due to the low detection
146 range of the handheld reader we were not able to gain continuous measurements of T_{sub} during the
147 smoke experiments and instead assumed T_b to be <3°C above T_a during steady-state torpor, based
148 on Song et al. (1997): $T_b - T_a = 1.9 \pm 0.9^\circ\text{C}$.

149 A response to the olfactory stimulus was defined as one of the following: a visible behavioral
150 response, such as 'head raising' or an increase of torpor metabolic rate (TMR). 'Delayed arousal' was
151 defined as a slow but steady increase of the TMR that led to final arousal within the measuring
152 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
153 from torpor ($MR \geq 2\text{mlO}_2 \text{ h}^{-1}\text{g}^{-1}$ within 30min).

154

155 *Climbing experiments*

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

159 For the experiments the individuals were placed on a horizontal branch (35cm length,
160 diameter: ~1cm) that was turned slowly and movement and behavior of the animals were
161 quantified. T_{sub} was measured regularly during the experiment. We recorded T_{sub} from which an
162 animal was able to (i) hold on to the stick, and (ii) move on the stick (Tab. 1). In a second experiment
163 individuals were held at the tip of their prehensile tail for up to one minute and T_{sub} s from which
164 individuals were (i) trying to grab their tails and climb and (ii) actually were able to climb up their tail
165 were recorded to assess coordination and muscle function necessary during escape behavior (Tab.
166 1). All experiments were recorded via video camera (Canon, PowerShot SX1IS). Animals were
167 weighed after the experiments to the nearest 0.1 g with an electronic balance. Experiments were
168 repeated at least five times for each animal (range: 5-8). In order to keep data comparable we chose
169 only three measurements ($T_{sub} < 15^\circ\text{C}$) per individual for analyses.

170

171 *Data analyses*

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

183

184 **Results**

185 *Olfactory acuity during torpor*

186 All individuals were in steady-state torpor when the experiments were conducted (TMR at T_a 15°C:
187 0.08 ± 0.03 ml O_2 $g^{-1} h^{-1}$, $N=10$ (control and experiment), $n=5$; T_a 10°C: 0.07 ± 0.04 ml O_2 $g^{-1} h^{-1}$, $N=5$,
188 $n=5$). Control measurements (water) did not lead to arousal of individuals, nor to a significant
189 increase of TMR (t-test: $t_4=-2.35$, $p = 0.08$, $n=5$).

190 The response to smoke water was individual-specific and we observed a temperature effect
191 (figure 1). Average TMR was significantly increased (on average >52-fold) between the control
192 measurements and treatment at 15°C ($T_b \sim 18^\circ C$), but not at 10°C ($T_b \sim 13^\circ C$) (ANOVA: $F_{2,8}=5.07$, $p=$
193 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
194 individuals responded to the smoke stimulus at a T_a of 15°C ($T_{sub} \sim 18.3 \pm 1.4^\circ C$; $n=5$); the three males
195 responded with arousal (two aroused within 30 min, one male showed a delayed arousal after 43
196 min; example in figure 1), whereas both females only raised their heads in response to the stimulus
197 (after 6 min and 8.5 min, respectively) and only slightly increased their TMR. One of the three males
198 re-entered torpor after the arousal and again displayed minimal energy expenditure about two
199 hours after the presentation of the stimulus. At T_a 10°C ($T_{sub} \sim 13.3 \pm 0.3^\circ C$; $n=5$) only three animals (2
200 males, 1 female) responded with an marked increase of TMR that in one male eventually led to an
201 arousal within 110 min (delayed arousal).

202

203 *Climbing experiment*

204 Animals were able to hold on to the branch from the beginning of the experiment during most trials
205 ($N=12$ of 15 trials). The minimum T_{sub} for successful holding on to the branch was $10.7^\circ C$, with a

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

211 The mean minimal T_{sub} at which animals tried to climb their prehensile tail was $20.9 \pm 1.3^\circ\text{C}$
212 ($n=5$, $N=15$) and more than 90% of the attempts were observed at T_{sub} s between 19°C and 23°C .
213 Mean minimal T_{sub} at which animals were able to climb was $24.4^\circ\text{C} \pm 2.0^\circ\text{C}$. The difference between
214 T_{sub} for holding and the initial T_{sub} was not significant, while T_{sub} s of all other tasks were significantly
215 different to each other (ANOVA; $F_{4,66}=162.97$, $p < 0.001$; Tukey posthoc: holding $z=0.43$, $p=0.993$; rest
216 $z > 4.83$, $p < 0.001$).

217 Although some individuals were significantly heavier than others the T_{sub} and body mass of
218 the individuals for any of the tasks were not correlated (ANOVA; holding: $F_{1,9}= 4.67$, $p= 0.06$; moving;
219 $F_{1,9}= 1.08$, $p= 0.33$; trying to climb: $F_{1,9}= 0.02$ $p=0.88$, $p=0.33$, climbing: $F_{1,9}= 0.45$, $p= 0.52$).

220

221 Discussion

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

229 In the past torpor was often viewed as a risky state because it had been assumed that torpid
230 individuals are easy prey for predators. More recently, this dogma has been challenged because
231 survival rates of individuals during the hibernation season are higher than during the active season
232 (Turbill et al. 2011). Moreover, it appears that heterothermic species are at a lower risk of becoming
233 extinct than homeothermic species that are unable to express torpor (Geiser and Turbill 2009;
234 Hanna and Cardillo 2014). A reason for the better survival rate seems to be that torpid mammals are
235 less likely to be discovered by predators as they are typically hiding in a sealed burrow or other
236 protected shelters while being motionless and cold, therefore emitting less stimuli detectable by
237 predators (Turbill et al. 2011). On the other hand, impaired locomotion during torpor is a
238 disadvantage when it comes to threats that require an active response, such as wildfires. A torpid
239 individual most likely cannot respond very quickly when its hibernaculum/resting site is on the

240 threat of burning. Dunnarts, small insectivorous marsupials, responded immediately to high
241 amounts of smoke and aroused from shallow torpor ($T_b \sim 25^\circ\text{C}$) (Stawski et al. 2015b). However, it
242 was not clear from that study whether the response was triggered by the smell or rather by the
243 smoke particles or the high concentration of CO. Our study confirms that the presentation of the
244 smoke stimulus alone can be perceived by torpid pygmy-possums with a body temperature as low as
245 13°C . Our data are in line with another study that has previously shown that torpid bats ($\sim 18^\circ\text{C}$)
246 respond to noise stimuli with an increase of T_b (Luo et al. 2014) and suggests that sensory signals,
247 other than mainly tactile stimuli (Speakman et al. 1991), can be perceived and processed during
248 deep torpor.

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

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

267 Arousal from torpor in response to the smell of smoke does not suffice and will not
268 guarantee the survival of the individual when the animal cannot also move quickly enough to evade
269 the danger. It is well known that running speed in ectothermic lizards is a negative function of T_b and
270 similar relationships have been established recently in two species of ground-dwelling heterothermic
271 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°C did not
272 seem to not visibly affect running speeds of heterothermic ground squirrels (Wooden and Walsberg
273 2003). Our data show that pygmy-possums are able to move on a horizontal branch at T_{sub} of about

274 15°C, which is in the same range as found for movements on the ground for terrestrial species (14.8–
275 17.9°C (Rojas et al. 2012)), although the movement on the branch is likely more difficult than on a
276 straight smooth surface. However, our experiment also indicates that co-ordinated flight behavior,
277 i.e. climbing required to evade fires in arboreal species, can only be performed by pygmy-possums
278 from about T_b 20°C and above. At a T_b of about 20°C individuals were trying to climb their tails, which
279 requires the involvement of main abdominal muscles and entails bending and stretching.
280 Interestingly, pygmy-possums seem to be able to cling on the branch from the beginning of the
281 experiment and therefore perhaps even at lower T_b during torpor. That advanced locomotor
282 performance can only be performed at higher T_b s is also shown by a study on bats that found that
283 although bats were able to crawl at a T_b of 8°C, flapping of wings only occurred at 22°C and aerial
284 flight was only possible at temperatures around 28°C (Choi et al. 1998).

285 In conclusion, our data show that pygmy-possums can perceive and respond to olfactory
286 stimuli during torpor and perform advanced locomotor skills with T_b s well below normothermic
287 values, but show decreased responsiveness and locomotor performance at T_b s \leq 13°C. Wildfires are
288 usually related to high T_a in summer and even prescribed burns are usually conducted on cool (16-
289 25°C, pers communication NSWNP) rather than cold days in Australia. Therefore, we can assume
290 that if torpid animals are present in an area of a burn they are able to arouse before the fire has
291 reached their nest location and have the chance to seek a safe refuge during the fire. However, if
292 deaths of small mammals due to fires are to be minimised prescribed burns should not be conducted
293 during the coldest part of winter.

294

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376

Table 1: Ethogramm of behaviors and their definitions

Behavior	Definition
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

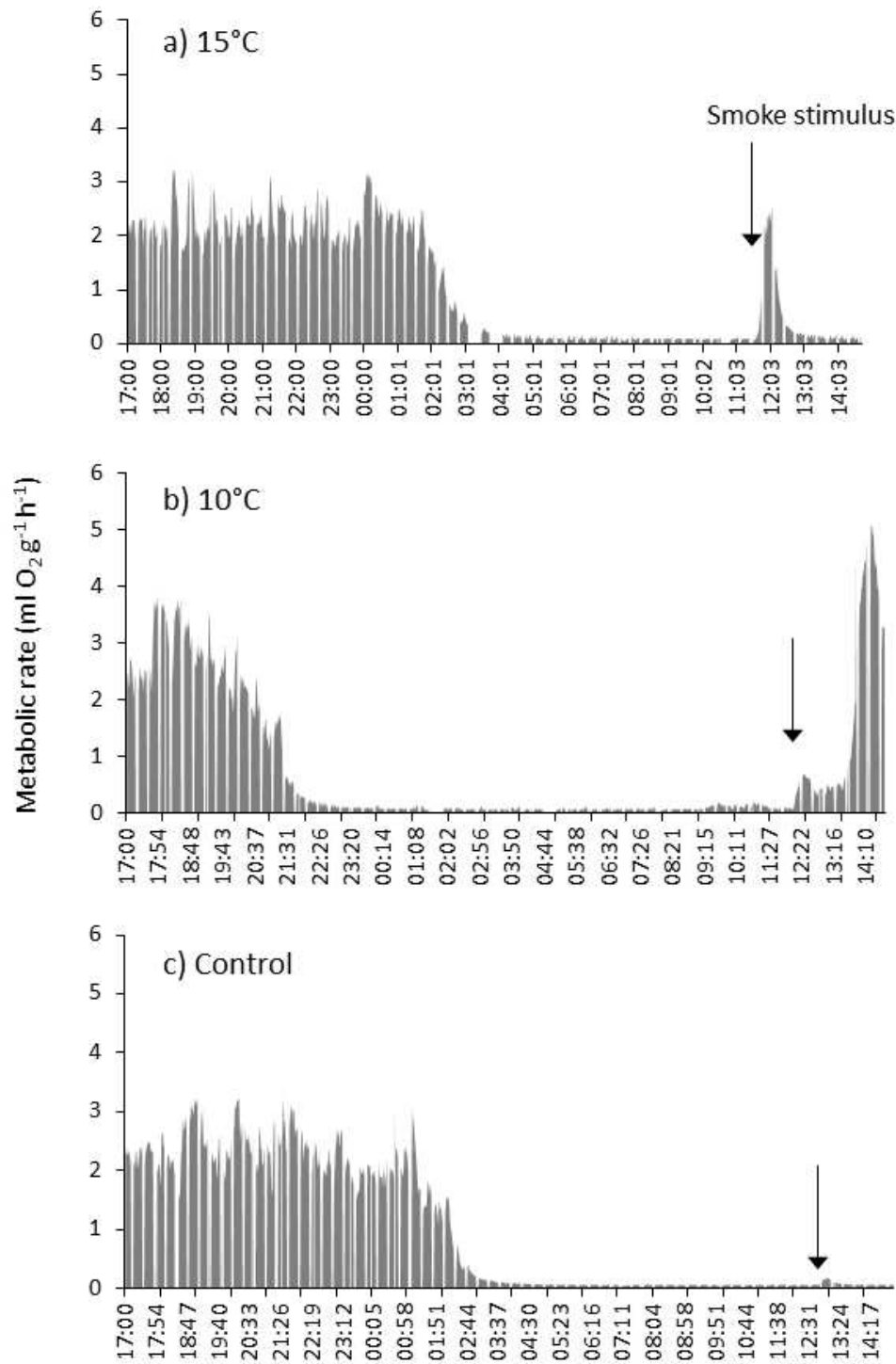


Figure 1abc: Metabolic response of a male individual to a) smoke stimulus at 15°C (arousal, within 30 min), b) smoke stimulus at 10°C (delayed arousal, after 110 min), and c) control (water stimulus) at 15°C. The arrow marks the moment the stimulus was presented to the individual. The depicted individual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

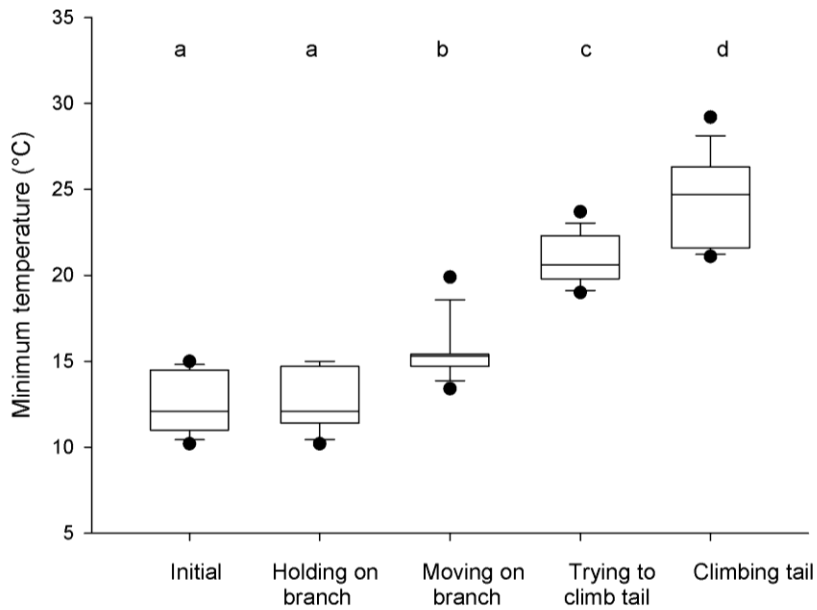


Figure 2: Locomotor performance for different tasks in regard to body temperature. Boxplots represent median, as well as 5-, 25-, 75- and 95-percentiles. Outliers are depicted as black dots. Animals were able to hold on to the branch from the beginning of the experiment; T_{subs} of all other tasks were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

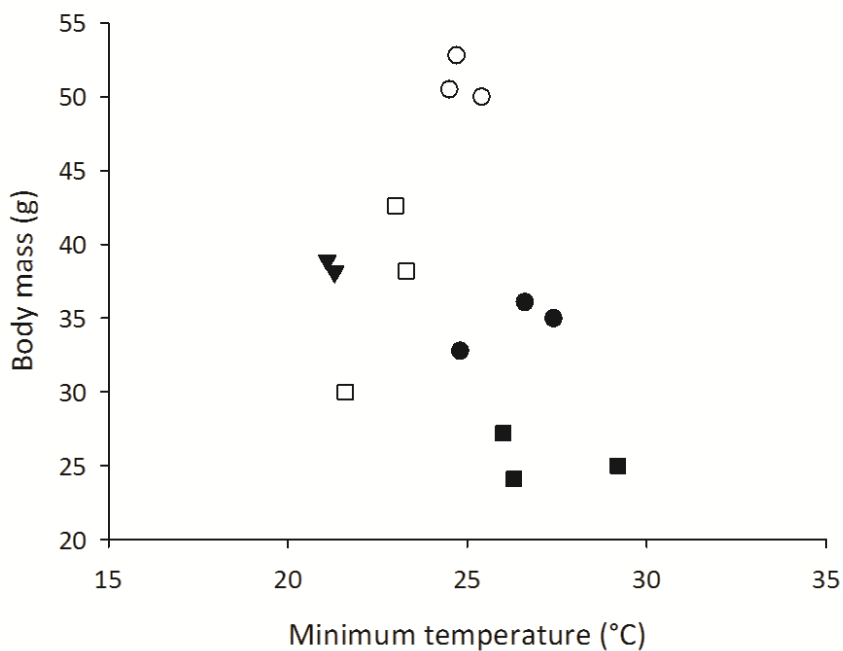


Figure 3: Individual locomotor performance for successful tail climbing performance. Depicted are the three trials with the lowest subcutaneous temperatures (T_{sub}) for all five individuals in regard to body mass. Individuals are represented by different symbols; males are indicated as filled symbols;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