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1 **Physiological and behavioral responses of an arboreal mammal to smoke and charcoal-ash**
2 **substrate**

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11

12 **Abstract**

13 The recent observation that torpor plays a key role in post-fire survival has been mainly attributed to
14 the reduced food resources after fires. However, some of these adjustments can be facilitated or
15 amplified by environmental changes associated with fires, such as the presence of a charcoal-ash
16 substrate. In a previous experiment on a small terrestrial mammal the presence of charcoal and ash
17 linked to food restriction intensified torpor use. However, whether fire cues also act as a trigger of
18 torpor use when food is available and whether they affect other species including arboreal mammals
19 remains elusive. To evaluate whether smoke, charcoal and ash can act as proximate triggers for an
20 impending period of food shortage requiring torpor for mammals, we conducted an experiment on
21 captive sugar gliders (*Petaurus breviceps*), a small, arboreal marsupial, housed in outside aviaries
22 under different food regimes and natural ambient conditions. When food was available, fire
23 simulation via exposure to smoke and charcoal-ash substrate caused a significant earlier start of
24 activity and a significant decrease in resting body temperature. In contrast, only when food was
25 withheld, did smoke and charcoal-ash exposure significantly enhance torpor depth and duration.
26 Thus, our study not only provides evidence that fire simulation does affect arboreal and terrestrial
27 species similarly, but also suggests that smoke and ash were presumably selected as cues for torpor
28 induction because they indicate an impending lack of food.

29 **Keywords:** Charcoal-ash, heterothermy, food reduction, smoke, sugar glider

30 Introduction

31 Fires have occurred throughout history and are a reoccurring seasonal event in some areas of the
32 world (Moreira et al. 2001; Pechony and Shindell 2010). Therefore, to survive, organisms must have
33 evolved adaptations to cope with the conditions during and after fires. For example, the increased
34 thickness of bark in various fire resistance plant species (Hare 1965) indicates that wildfires have
35 played an important role during their evolution. Although animals can move and avoid fires to some
36 extent, most still need to be able to deal with fires and their aftermath. Understanding how
37 organisms cope with wildfires has gained increasing importance because with climate change
38 wildfires are expected to increase in frequency and intensity worldwide (Moritz et al. 2012). As far as
39 mammals are concerned possible adaptations to post-wildfire conditions could involve the reduction
40 of metabolic processes via torpor.

41 Mammalian torpor is characterised by reductions of metabolism and body temperature (T_b)
42 often in response to acute energetic bottlenecks and often independently of season (Ruf and Geiser
43 2015; Levesque et al. 2016; Nowack et al. 2017). Indeed recent studies suggest that opportunistic
44 torpor plays a key role for survival during and after wild fires when food is generally scarce (Stawski
45 et al. 2015a; Matthews et al. 2016; Nowack et al. 2016a; Geiser et al. 2017; Stawski et al. 2017a).
46 Interestingly, although food availability is clearly an important factor, the loss of ground cover
47 creating a potentially hostile environment also appears to contribute to the observed enhanced
48 torpor use. For example, short-beaked echidnas (*Tachyglossus aculeatus*) were able to decrease
49 activity during a fire in their habitat by lowering foraging needs via the use of torpor, thereby
50 reducing the risk to get trapped in the flames (Nowack et al. 2016a). Similarly, post-fire torpor
51 expression of brown antechinus (*Antechinus stuartii*) increased with a reduction in ground cover and
52 increased predator exposure (Stawski et al. 2015a; Stawski et al. 2017a). Importantly, recent
53 experimental work has demonstrated that food-deprived antechinus exposed to smoke and a
54 charcoal-ash substrate extended torpor use by ~2-fold in comparison to periods of food deprivation
55 only, indicating that these environmental cues could also act as a proximate trigger for torpor

56 induction, likely because they signal an impending period of starvation that necessitates torpor use
57 (Stawski et al. 2017b).

58 Environmental triggers, such as barometric pressure, photoperiod or ambient temperature
59 (T_a) can be good predictors for an approaching period of low food availability. Some cues might work
60 in the long-term. For example, in Djungarian hamsters (*Phodopus sungorus*) a long darkphase (i.e.
61 short photoperiod) leads to the development of a winter-phenotype that regularly uses torpor
62 (Heldmaier and Steinlechner 1981), whereas in subtropical blossom-bats (*Syconycteris australis*) long
63 photoperiod associated with low nectar availability increases torpor expression in summer (Coburn
64 and Geiser 1998). A combination of low T_a and shortening day length induces food hoarding or
65 fattening as a preparation for hibernation in many heterothermic cold-climate species (Barry 1976;
66 Muchlinski 1980). Other environmental cues can work on a short time scale. E.g., bats use falling
67 barometric pressure as indication of food availability and modulate foraging activity and likely also
68 torpor use accordingly (Paige 1995; Czenze and Willis 2015). Furthermore, torpor use by sugar gliders
69 during a cyclonic storm was assumed to be triggered by changes in barometric pressure (Nowack et
70 al. 2015; Nowack et al. 2017).

71 However, current knowledge on potential short-term environmental triggers for torpor
72 induction is limited. Although a previous study has indicated that charcoal-ash substrate and smoke
73 lead to longer and deeper torpor bouts (Stawski et al. 2017b), it remains unknown whether reduced
74 food availability is the proximate cause for torpor, perhaps further enhanced by fire cues, or whether
75 torpor use after fires can be indeed triggered by exposure to smoke, charcoal and ash alone. During
76 and after fires, animals do not only have to deal with low food availability, but also with potentially
77 hostile conditions and increased predation risk due to reduced ground cover. These risks could be
78 mitigated by a sit-and-wait strategy, such as torpor. Furthermore, with the exception of one study on
79 volant bats (Doty et al. 2016), all previous studies undertaken on torpor use in response to fire and
80 its effects have been on terrestrial mammals that primarily forage and nest close to the ground.
81 Small ground-dwelling mammals as well as some bat species enter torpor beneath leaf litter on the

82 forest floor and might not be able to respond to a fast spreading fire (Perry 2012; Perry and McDaniel
83 2015). Therefore, terrestrial animals are likely to be more affected by even low intensity fires than
84 arboreal mammals, which may be out of reach of the fire in their tree hollows, unless the fire
85 scorches the canopy.

86 Our study aimed to enhance the understanding on short-term triggers for torpor induction.
87 We investigated experimentally the potential of fires cues to trigger torpor use while food is
88 available. We therefore tested whether the exposure to smoke and charcoal-ash can induce torpor
89 use in food restricted as well as fed sugar gliders (*Petaurus breviceps*), an arboreal marsupial, housed
90 in outside aviaries and subjected to natural ambient conditions. Naturally, sugar gliders feed on
91 insects, nectar, sap and *Eucalyptus* and *Acacia* gum (Smith 1982) that are likely to be reduced after a
92 high-intensity fire if the fire reaches the mid-story and/or canopy of the forest. Moreover, they
93 usually nest in massive *Angophora* and *Eucalyptus* trees (Nowack et al. 2015) that, due to their
94 circumference, are presumably resilient to low and medium intensity fires. Sugar gliders only
95 occasionally enter daily torpor during extreme adverse conditions as a last resort strategy (Körtner
96 and Geiser 2000; Christian and Geiser 2007; Nowack et al. 2015), and use torpor irregularly during
97 the cold and unproductive winter (Christian and Geiser 2007). Furthermore, this species is
98 gregarious, living in family groups throughout the year and individuals can decrease their resting
99 metabolic rate via huddling (Fleming 1980). Interestingly, torpid and normothermic individuals are
100 commonly found sharing one nest box, indicating that torpor use by one individual does not
101 necessarily promote torpor use by other individuals in the same nest (Nowack and Geiser 2016). We
102 hypothesized that exposing gliders to smoke and a charcoal-ash substrate, without a concomitant
103 food reduction, will not induce torpor, as arboreal mammals are less likely to view a charcoal-ash
104 substrate on the ground as a threat. However, we predicted that a combination of fire cues and food
105 reduction would increase torpor frequency and affect the length and depth of torpor, as gliders are
106 known to employ torpor to save energy when food is scarce and when confronted with
107 environmental challenges.

108

109 **Material and Methods**

110 *Ethical note*

111 Approval to conduct this study was granted by the University of New England Animal Ethics
112 Committee and New South Wales National Parks and Wildlife Service.

113 *Procedures*

114 Eight sugar gliders were retrieved from nest boxes at Dorrigo (30° 22'S, 152° 34'E) and Imbota Nature
115 Reserve (30° 35'S, 151° 45'E) (4 animals from one nest box at each site; 5 females, 3 males) and
116 transferred to the University of New England, where they were weighed to the nearest 0.1g, sexed,
117 aged according to Suckling (1984) and micro chipped for individual identification (Passive integrated
118 transponder tags, Destron Technologies, South St Paul, MN, USA). Because sugar gliders are social
119 animals that under natural conditions are seldom found resting on their own, animals were kept in
120 the original two capture groups and housed in adjacent outdoor enclosures (3.6 x 1.8 x 2 m) with a
121 shared a wire-mesh middle wall. Each enclosure was fitted with branches, two feeding platforms and
122 three wooden nest boxes per group. The concrete floor of the enclosures was covered with eucalypt
123 mulch. During normal holding both groups were fed daily with 80 g of a mixture of high protein baby
124 cereal, egg, honey and water, to which a high protein/vitamin supplement (Wombaroo, Glen
125 Osmond, Australia) was added. This food was supplemented by a dish of fresh fruits. Water was
126 available *ad libitum*.

127 All individuals were implanted with temperature-sensitive radio transmitters (Sirtrack,
128 Havelock North, New Zealand; 2g) to remotely measure their T_b . Transmitters were waxed and
129 calibrated in a water bath to the nearest 0.1°C before being implanted intraperitoneally under
130 oxygen/isoflurane anaesthesia using a small abdominal incision. Individuals weighed 124.0 ± 25.0 g at
131 capture and 117.6 ± 21.8 g at the date of implantation. None of the females had pouch young at the
132 time of implantation or during the following experimentation. Animals were allowed to recover from
133 surgery for three days before the start of experiments. Some of the collected data have been

134 published previously in a different context (Nowack and Geiser, 2016), but in the current study we
135 present new physiological and behavioral data with an emphasis on the response to fire cues.

136 The study was conducted over 48 days between the end of June and middle of August 2014.
137 T_b was obtained at 10 min intervals using a multi-channel receiver/data logger placed outside of the
138 aviary (for detailed description of the system see: Körtner and Geiser (2000)). Body temperature in
139 normothermic resting sugar gliders is on average 34.5°C (Christian and Geiser 2007) and animals
140 were considered to be torpid when T_b fell below 30°C (see Nowack et al. 2015). For the calculation of
141 torpor bout duration (TBD) we included the time period from entry into torpor (T_b falling from 34°C),
142 to arousal from torpor (T_b increasing again above 34°C) (see Nowack et al. 2015). Large T_b variations
143 between activity ($T_b > 38$ °C) and rest phase allowed us to estimate the hours of nightly activity.
144 Conversely, a decrease in T_b below 38 °C was associated with inactivity (see Nowack et al. 2015).

145 Ambient temperature (T_a) was recorded hourly within the aviaries with data loggers placed in
146 the shade (resolution 0.5°C; Hygrochron iButton/DS1921, Maxim Integrated).

147 *Experimental protocol*

148 We tested the two different stimuli ‘fire’, consisting of smoke and charcoal-ash exposure (see below),
149 and ‘food reduction’ regarding their potential to induce torpor in sugar gliders by exposing gliders to
150 different combinations of the stimuli following the protocol below (Table 1). If food was reduced,
151 food was completely withheld the first day and partly reduced over the next two days (second day:
152 60g of protein mixture, normal amount of fruits; third day 40g of protein mixture and normal amount
153 of fruits), to resemble natural food reduction and variability after fires, when animals would not be
154 able to forage during the burn, and would have patchy, if not overall reduced, food availability for
155 the next weeks to months. Food reduction was followed by at least four nights of normal food
156 supply.

157 Fire stimuli were only provided every two weeks to reduce the risk of habituation. We
158 burned branches, wet sawdust and fresh and dried leaves for about an hour (1500-1600h) in front of
159 the enclosures on day one of the experimental treatment. The intensity of smoke was measured via

160 the concentration of smoke particles (range from 0-air to 6-thick smoke; Testo 308, Professional
161 equipment, Janesville, WI, USA) and was always between 3.2 and 4.1. Fresh and old charcoal and
162 burned branches was distributed within one section (about half of the floor) of the aviary after the
163 burn and remained there for four nights before it was removed again.

164

165 *Statistical analysis*

166 Data are presented as mean ± 1 standard deviation. If not otherwise indicated means are calculated
167 from individual mean values to account for repeated measures; n denotes the number of individuals,
168 N the number of observations. For the activity data we excluded weighing days from statistical
169 analyses when animals were removed from their next boxes for short periods, as well as one extreme
170 outlier (unexplained start of activity about 300 min later than on all other days) from one of the
171 control days. Statistical analyses were conducted using R, version 3.1.0 (R Development Core Team
172 2014). The increase of T_b after smoke introduction was tested against a control via linear mixed effect
173 models using `individual` and `group` as a random factor to account for repeated measures and the
174 fact that the animals were kept in family groups, followed by an ANOVA (*lme* in library `nlme`
175 (Pinheiro et al. 2014)). A Raleigh test was used to determine whether the start and end of the daily
176 activity period differed from random (programme by G. Körtner based on Zar (Dumonteil et al.
177 1995)). The correlation between the length of the overall daily activity period and its end (in relation
178 to sunrise) was tested via regression analyses. We employed linear mixed-effects models (*lme* in
179 library `nlme`; (Pinheiro et al. 2014)) to test for differences among the treatments (fire simulation
180 with food *ad libitum*, fire simulation with food reduction, food reduction) for the measured variables
181 (number of torpid individuals, minimum T_b during normothermic resting, minimum T_b during torpor,
182 TBD as well as nightly activity). Daily minimum T_a was included in all models as an additive effect to
183 control for differences in T_a during experimental days. We modelled repeated measures on each
184 individual as random effects and controlled for `group`. We used a residual plot to test for
185 homoscedasticity and a normal Q-Q plot to test for normal distribution. If needed, data were

186 transformed using the Box-Cox function to meet statistical assumptions. Cases of variance
187 heterozygosity were accounted for. We then employed a post-hoc Tukey test (*glht* in library
188 'multcomp' (Hothorn et al. 2008)) to determine which groups differed from each other. To evaluate if
189 'torpor use' (the propensity of the animal to undergo torpor) was affected by the stimuli we used a
190 binomial model (*glmer* in library 'lme4' (Bates et al. 2014)) and accounted for repeated measures on
191 each individual as well as the two family groups as random effects.

192 **Results**

193 *Effects on activity*

194 Gliders were always found nesting in family groups and never rested solitary. Gliders were strictly
195 nocturnal during the study period and usually commenced their activity at 1715 ± 0023 hours
196 ($N=313$, $n=8$; average 03 ± 26 min after sunset; Raleigh test, $R=310.17$, $z=307.36$, $p<0.001$). Smoke
197 exposure did not cause animals to leave their nest boxes. However, during the fire simulation
198 treatment with food available, individuals started their activity on average about 20 min earlier than
199 during control days ($\chi=43.8$ $df=3$, $p<0.0001$; $z=6.2$, $p<0.001$; Fig. 1), whereas food reduction alone as
200 well as a combination of fire simulation and food reduction did not alter the start of activity
201 significantly (posthoc results in Fig.2). Length of nightly activity ranged from 170 min to 830 min and
202 was not significantly related to the start of activity ($r=0.003$, $t_{1,308}=1.39$, $p>0.05$), but highly correlated
203 with the end of activity ($r=0.98$, $t_{1,308}=120.7$, $p<0.001$; Fig.2). While food reduction caused a
204 significantly shorter nightly activity period independent of fire cues (with and without fire simulation;
205 $\chi=45.34$ $df=3$, $p<0.0001$ posthoc results presented in Fig.1), the exposure to smoke and charcoal-ash
206 alone with food being available did not significantly affect total nightly activity (Fig.1).

207

208 *Effects on normothermic resting T_b*

209 No individual was torpid at the time of smoke introduction. Smoke induced a significant increase of
210 resting T_b at the time of the exposure (smoke T_b : 37.5 ± 0.6 °C, $N=16$, $n=8$ vs. air T_b 36.9 ± 0.5 °C,

211 N=324, n=8; $F_{1,338}=42.80$, $p<.0001$; N=340, n=8). However, during the following day and irrespective
212 of food availability, fire simulation resulted in a significant decreased daily minimum normothermic
213 resting T_b by 1°C ($\chi=19.20$ $df=3$, $p=0.0003$; posthoc results presented in Table 2); in contrast, food
214 reduction alone did not significantly change resting T_b .

215

216 *Effects on torpor expression*

217 The number of animals that entered torpor per day was not significantly affected by fire simulation,
218 even when food was reduced at the same time. In contrast, significantly more animals used torpor
219 when food was reduced without fire cues ($\chi=14.023$, $df=3$, $p=0.0029$; posthoc: food reduction
220 treatment vs. control conditions: $z=3.5$, $p=0.0003$; rest: $z\leq 1.9$, $p>0.05$).

221 Torpor bouts were significantly longer and deeper when food was reduced (T_b : $\chi=21.07$ $df=3$,
222 $p=0.0001$; TBD: $\chi=30.64$ $df=3$, $p=0.000001$; posthoc tests in Fig. 3ab), and TBD was longest under the
223 combination of the fire stimuli and food restriction (on average 215min longer than on control days;
224 Fig. 3). Minimum T_b during torpor, which was also dependent on minimum T_a ($\chi=10.95$ $df=1$,
225 $p=0.0009$), did decrease significantly when food deprived, but in this case exposure to fire stimuli did
226 not result in a significant further reduction (1.2°C and 2.6°C lower than on control days; Fig.3b).
227 Under food *ad libitum* conditions fire simulation resulted in a minor shortening of TBD and elevated
228 minimum T_b during torpor slightly (Fig.3).

229 **Discussion**

230 Our study tested for the first time whether physiological changes of small mammals to fires are
231 primarily related to a reduction in food availability or can also be triggered by fire cues alone. While
232 we could show that smoke and charcoal-ash exposure changed behavior and physiology of arboreal
233 sugar gliders, smoke and charcoal-ash substrate *per se* did not trigger torpor use. Nevertheless, fire
234 cues effectively lengthened torpor bouts and also decreased activity when food was withheld at the
235 same time. Our data provide the first experimental support for the hypothesis that torpor use after
236 fires is primarily related to a reduction in food availability. Furthermore, our data not only verify and

237 extend recent findings that fire stimuli in addition to food reduction intensify post-fire torpor use,
238 but indicate that this is the case for arboreal as well as terrestrial mammals (Stawski et al. 2017b).

239 Thick smoke is a clear signal for a raging fire nearby and sugar gliders reacted by increasing
240 their resting T_b , indicating raised alertness, but did not leave their nest boxes or tried to flee the fire.
241 Similar studies on terrestrial, ground-dwelling species, the fat-tailed dunnart (*Sminthopsis*
242 *crassicaudata*) and the yellow-footed antechinus (*A. flavipes*) found that individuals left the nest and
243 became active after the introduction of a smoke stimulus, perhaps as an instinctual escape
244 mechanism (Stawski et al. 2015b; Stawski et al. 2017b). These differing responses suggest that gliders
245 in their tree hollows face a lower risk from an approaching fire, but also that they are very vulnerable
246 to avian predators during daytime hours. In contrast, dunnarts and antechinus are more likely to be
247 nesting near or at ground level and if smoke is penetrating their current refuge it may be prudent to
248 escape into deep underground burrows that are more fireproof.

249 Following the fire, gliders displayed a high degree of physiological plasticity. Although fire
250 simulation did not increase torpor use, gliders slightly altered their behavior and began activity
251 significantly earlier, provided food was available. Interestingly, this effect was revoked when food
252 was withheld on the day of the fire simulation. It is likely that the gliders could smell the provided
253 food in their aviaries and modified their behavior accordingly, especially as they were already in an
254 alerted stage from the earlier smoke exposure. As such, an earlier start of activity allowed gliders to
255 exploit the “remaining” food sources, whereas reducing activity to a minimum after a fire when food
256 sources are absent or destroyed avoids non-productive foraging efforts.

257 In contrast to hibernation, i.e. multiday torpor bouts with a pronounced depression of
258 metabolic rate, daily torpor will predominantly allow species to reduce foraging needs by saving
259 energy spent during resting (Geiser 2013), but does not allow extended period of inactivity over
260 weeks or months. However, the use of daily torpor with a minimum T_b of 24°C already reduces
261 energy demands to about 20% of normothermic values (Fleming 1980) and can enable animals to
262 reduce food requirements substantially. Importantly, the abundance of terrestrial arthropods often

263 increases again in the year following a fire (Matthews et al. 2016) and ground cover and torpor use
264 usually recover within a year (Stawski et al. 2017a).

265 When only exposed to fire stimuli without food reduction, sugar gliders did not increase
266 torpor use. In fact, the few animals entering torpor under such conditions exhibited shorter and
267 shallower bouts than usual. Similarly, the exposure to smoke and charcoal had contrary effects on
268 torpor use in fat-tailed dunnarts depending on food availability: torpor use declined when food was
269 available and increased when food was withheld (Stawski et al. 2015b). Sugar gliders are known to
270 only employ torpor as a last resort strategy (Christian and Geiser 2007), but even the small decrease
271 in normothermic resting T_b and reduced activity seen after exposing gliders to fire cues without food
272 restriction, can lead to energy savings that can be of an adaptive advantage in a fire-scorched
273 landscape. As such a decline in T_b of 1.2°C by itself results in energy savings of about 6% (Christian
274 and Geiser 2007), while gliders retained the ability to respond quickly.

275 Although torpid individuals are able to move at T_b s well below normothermic levels
276 (Warnecke et al. 2008; Warnecke and Geiser 2010), T_b does affect running speed (Rojas et al. 2012),
277 climbing ability (Nowack et al. 2016b) and likely gliding ability, and would reduce survival chances
278 during a fast spreading fire. Previous studies have already shown that torpid animals arouse from
279 torpor when exposed to smoke or the smell of smoke (Scesny 2006; Stawski et al. 2015b; Nowack et
280 al. 2016b), but this response is slow.

281 Importantly, the observed responses to smoke and charcoal ash are likely not learned, but
282 genetically manifested. While sugar gliders used in this study might have experienced a fire in their
283 natural habitat, captive-bred dunnarts also respond to smoke stimuli under laboratory conditions
284 (Stawski et al. 2015b). Furthermore, short-lived antechinus (life expectancy: 1-3 years) intensify
285 torpor use in the presence of fire cues (Stawski et al. 2017b), although they were captured in a
286 habitat that had not burned for the last 20 years (pers. communication NSW National Parks to CS).

287 In summary, our study supports the view that an increase in torpor use after fires is mainly
288 driven by the reduction of food availability and that food availability is a primary ecological

289 determinant of torpor use. However, our data also show that fire stimuli on their own can act as a
290 signal that leads to changes in behavior and physiology. Since the observed physiological plasticity in
291 response to charcoal-ash exposure was dependent on food availability this response probably further
292 increases their chances of survival. Reoccurring wildfires have a long history on earth and fire cues
293 may have evolved as important triggers for torpor induction because they indicate a lack of food and
294 potentially also reduced cover. It has previously been shown that heterothermic mammals often
295 have a lower risk of becoming extinct and likely cope better with catastrophic events than
296 homeothermic species (Geiser and Turbill 2009; Hanna and Cardillo 2014; Lovegrove et al. 2014;
297 Geiser et al. 2017; Nowack et al. 2017). Torpor use in response to reduced food availability after fires
298 seems highly advantageous as it allows the surviving terrestrial and arboreal species to remain in the
299 fire-scorched landscape without the need to migrate to unburnt sites. Understanding how animals
300 respond to cues of natural disasters, such as bush fires, droughts or storms, is all the more important
301 in the light of climate change and the anticipated increase in the frequency and intensity of
302 catastrophic environmental events (Christensen and Christensen 2003; CSIRO 2011; Moritz et al.
303 2012).

304

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311 University of New England to FG.

312 **Author contributions**

313 JN and FG designed the study, JN collected and analysed the data and wrote the first draft of the
314 manuscript. All authors commented on the manuscript.

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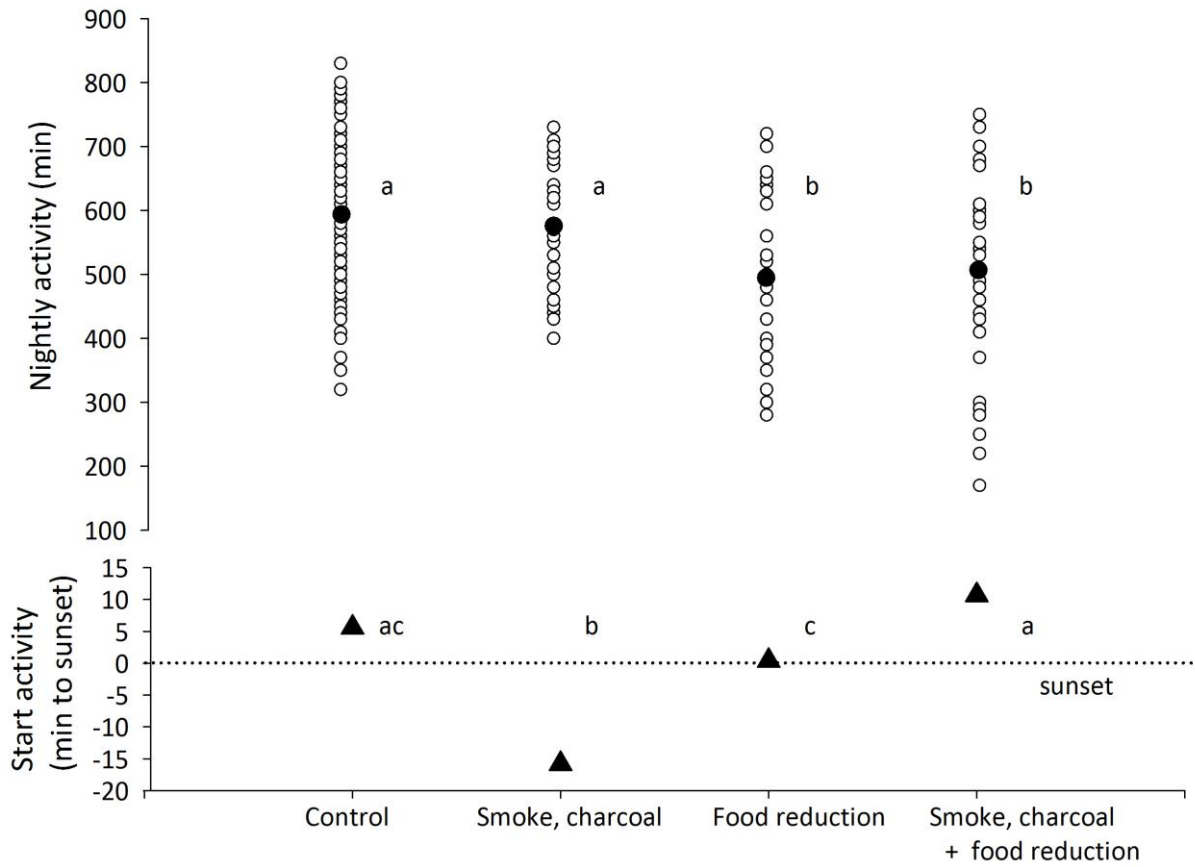
Table 1: Experimental protocol

	Atmosphere	Ground cover	Food
Control	Air	Normal	Normal food supply
Fire simulation & food reduction	Smoke	Charcoal-ash	Food reduction
Fire simulation, food <i>ad libitum</i>	Smoke	Charcoal-ash	Normal food supply
Food reduction	Air	Normal	Food reduction

Table 2: Average minimum normothermic body temperature (T_b) during the different treatments (torpor bouts excluded). Mean with SD and sample sizes (N) are shown (number of animals represented always n=8). Exposure to smoke and charcoal-ash reduced minimum T_b during resting (see Table 2). Significant differences are indicated by different letters (Tukey-posthoc tests).

	Control	Smoke- charcoal-ash	Food reduction	Smoke, charcoal-ash + food reduction
Minimum T_b (°C)	34.8 ± 0.3 ^a	33.8 ± 1.4 ^b	34.3 ± 0.7 ^{ab}	34.0 ± 0.8 ^b
N	201	24	14	21

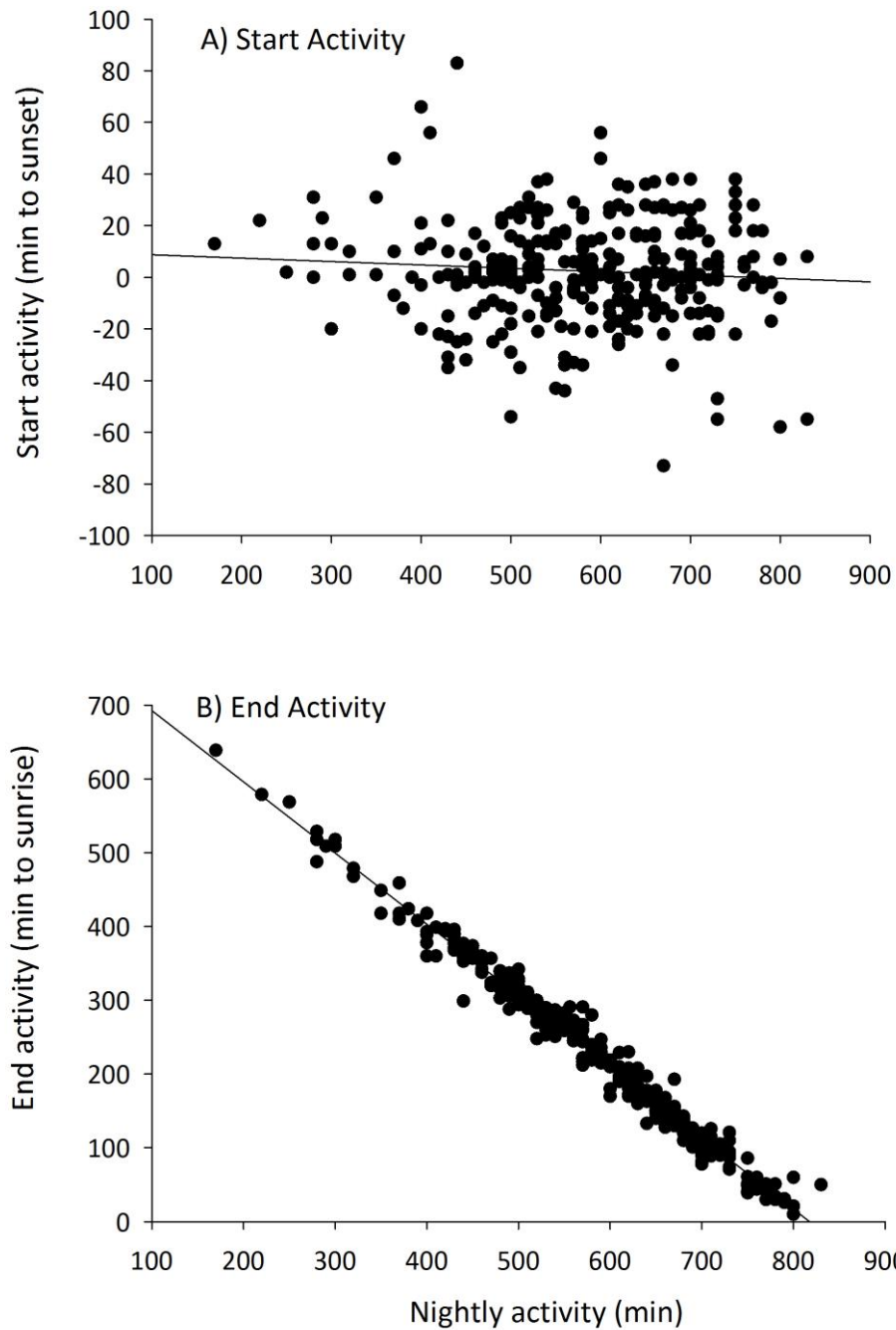
431 **Figures**



432

433 **Figure 1: Nightly activity during the different test treatments.** Above: Open circles represent
 434 individual values (for each treatment N=32, n=8; control N=216, n=8), *filled circles* are means. Below:
 435 *Filled triangles* show the start of activity (mean values) in relation to sunset (*dashed line*). Activity
 436 was significantly shorter in all treatments with food reduction; start of activity commenced
 437 significantly later when animals were exposed to smoke and charcoal while food was available.
 438 Significant differences are indicated by different letters (Tukey-posthoc tests).

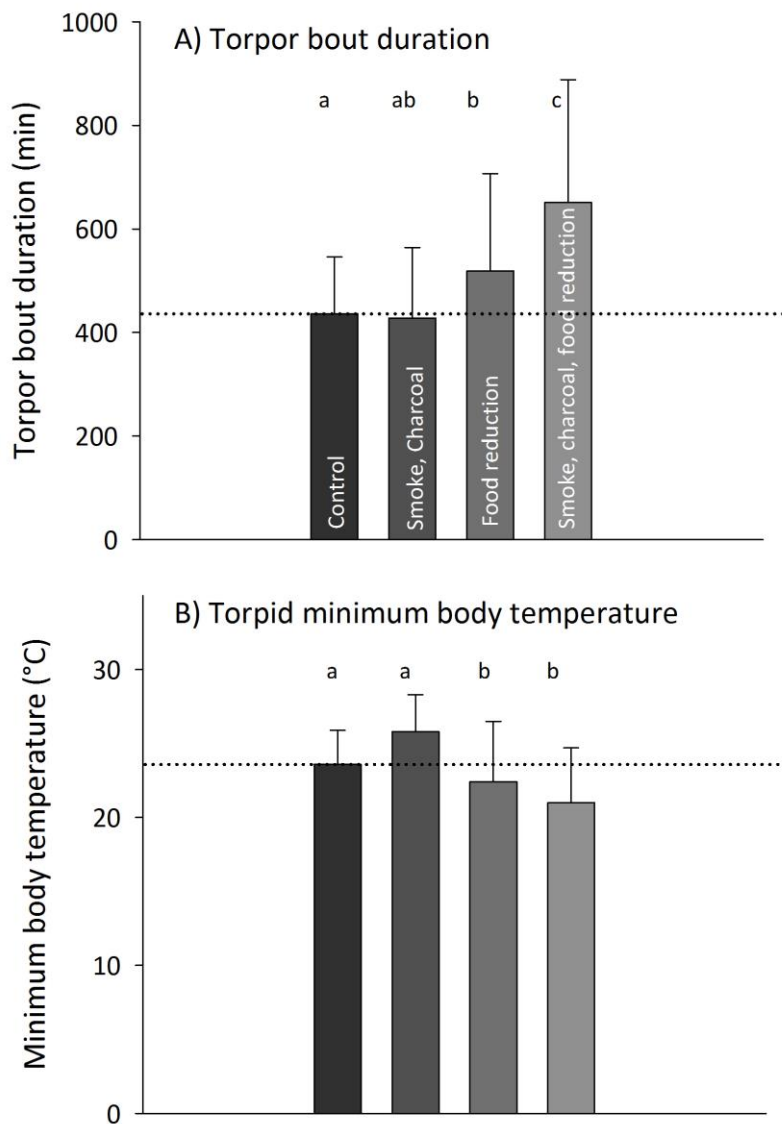
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440

441 **Figure 2:** Correlation between the nightly activity and a) the start of activity (Start of activity= -0.013
 442 * nightly activity + 10.088; $r=0.003$) and b) the end of activity (end of activity= -0.965 * nightly activity
 443 + 789.294; $r=0.9811$). Circles represent individual values (N=308, n=8).

444



445
 446 **Figure 3: Torpor depth and duration during the different test treatments.** A) Torpor bout duration,
 447 B) Minimum body temperature during torpor. The *dashed lines* represent the mean TBD/T_b under
 448 control conditions (N=33, n=7). Letters represent results of posthoc Tukey test. Different letters
 449 represent significant differences.

450