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

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## 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

## Introduction

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

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

**Material and Methods**

*Ethical note*

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.

*Procedures*

Eight sugar gliders were retrieved from nest boxes at Dorrigo (30° 22'S, 152° 34'E) and Imbota Nature

Reserve (30° 35'S, 151° 45'E) (4 animals from one nest box at each site; 5 females, 3 males) and

transferred to the University of New England, where they were weighed to the nearest 0.1g, sexed,

aged according to Suckling (1984) and micro chipped for individual identification (Passive integrated

transponder tags, Destron Technologies, South St Paul, MN, USA). Because sugar gliders are social

animals that under natural conditions are seldom found resting on their own, animals were kept in

the original two capture groups and housed in adjacent outdoor enclosures (3.6 x 1.8 x 2 m) with a

shared a wire-mesh middle wall. Each enclosure was fitted with branches, two feeding platforms and

three wooden nest boxes per group. The concrete floor of the enclosures was covered with eucalypt

mulch. During normal holding both groups were fed daily with 80 g of a mixture of high protein baby

cereal, egg, honey and water, to which a high protein/vitamin supplement (Wombaroo, Glen

Osmond, Australia) was added. This food was supplemented by a dish of fresh fruits. Water was

available *ad libitum*.

All individuals were implanted with temperature-sensitive radio transmitters (Sirtrack,

Havelock North, New Zealand; 2g) to remotely measure their $T_b$. Transmitters were waxed and

calibrated in a water bath to the nearest 0.1°C before being implanted intraperitoneally under

oxygen/isoflurane anaesthesia using a small abdominal incision. Individuals weighed 124.0 ± 25.0g at

capture and 117.6 ± 21.8g at the date of implantation. None of the females had pouch young at the

time of implantation or during the following experimentation. Animals were allowed to recover from

surgery for three days before the start of experiments. Some of the collected data have been

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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=0.003; rest: z≤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

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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

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 *ad libitum*** | 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) | $34.8 \pm 0.3^a$ | $33.8 \pm 1.4^b$ | $34.3 \pm 0.7^{ab}$ | $34.0 \pm 0.8^b$ |
| N | 201 | 24 | 14 | 21 |
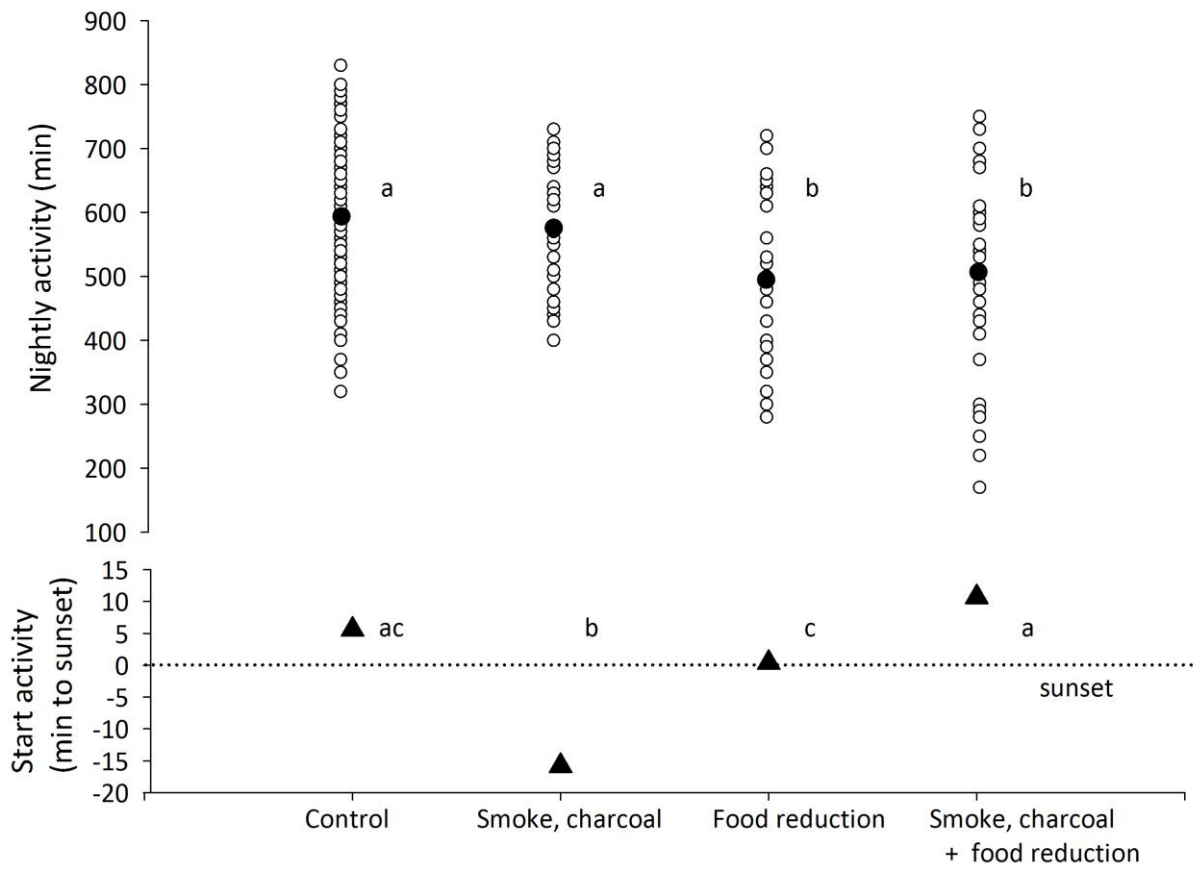
**Figures**

**Figure 1: Nightly activity during the different test treatments.** Above: Open circles represent individual values (for each treatment N=32, n=8; control N=216, n=8), *filled circles* are means. Below: *Filled triangles* show the start of activity (mean values) in relation to sunset (*dashed line*). Activity was significantly shorter in all treatments with food reduction; start of activity commenced significantly later when animals were exposed to smoke and charcoal while food was available. Significant differences are indicated by different letters (Tukey-posthoc tests).
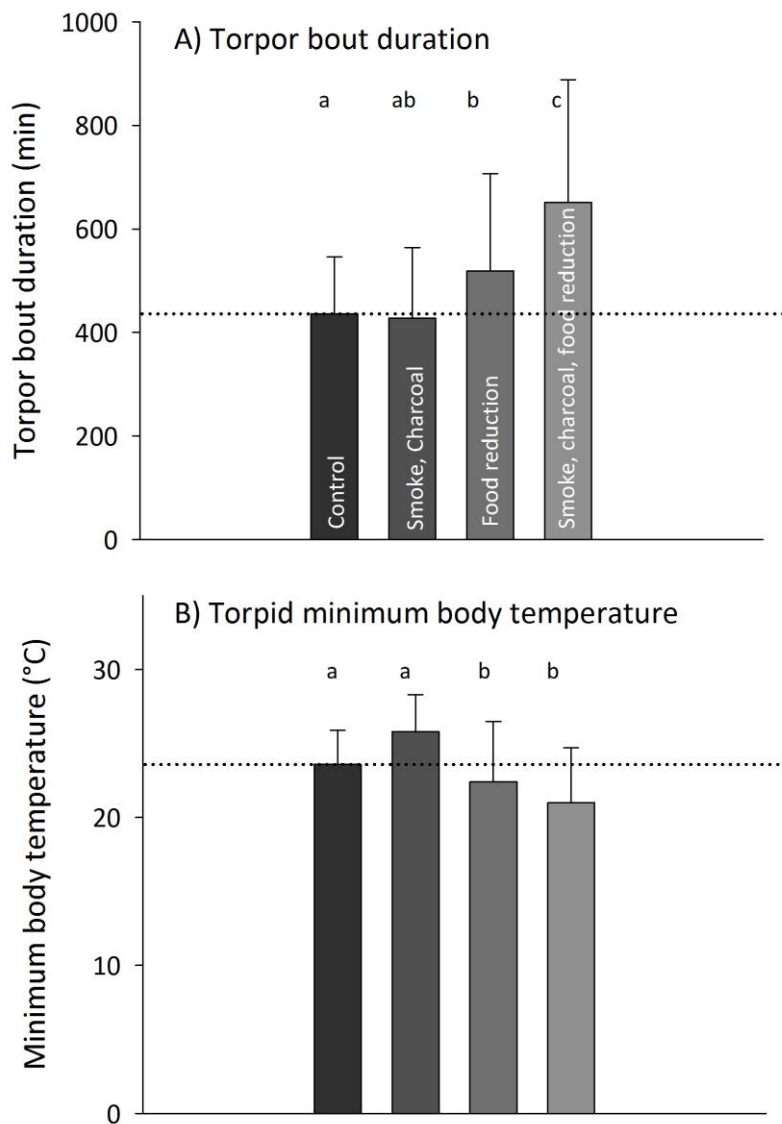
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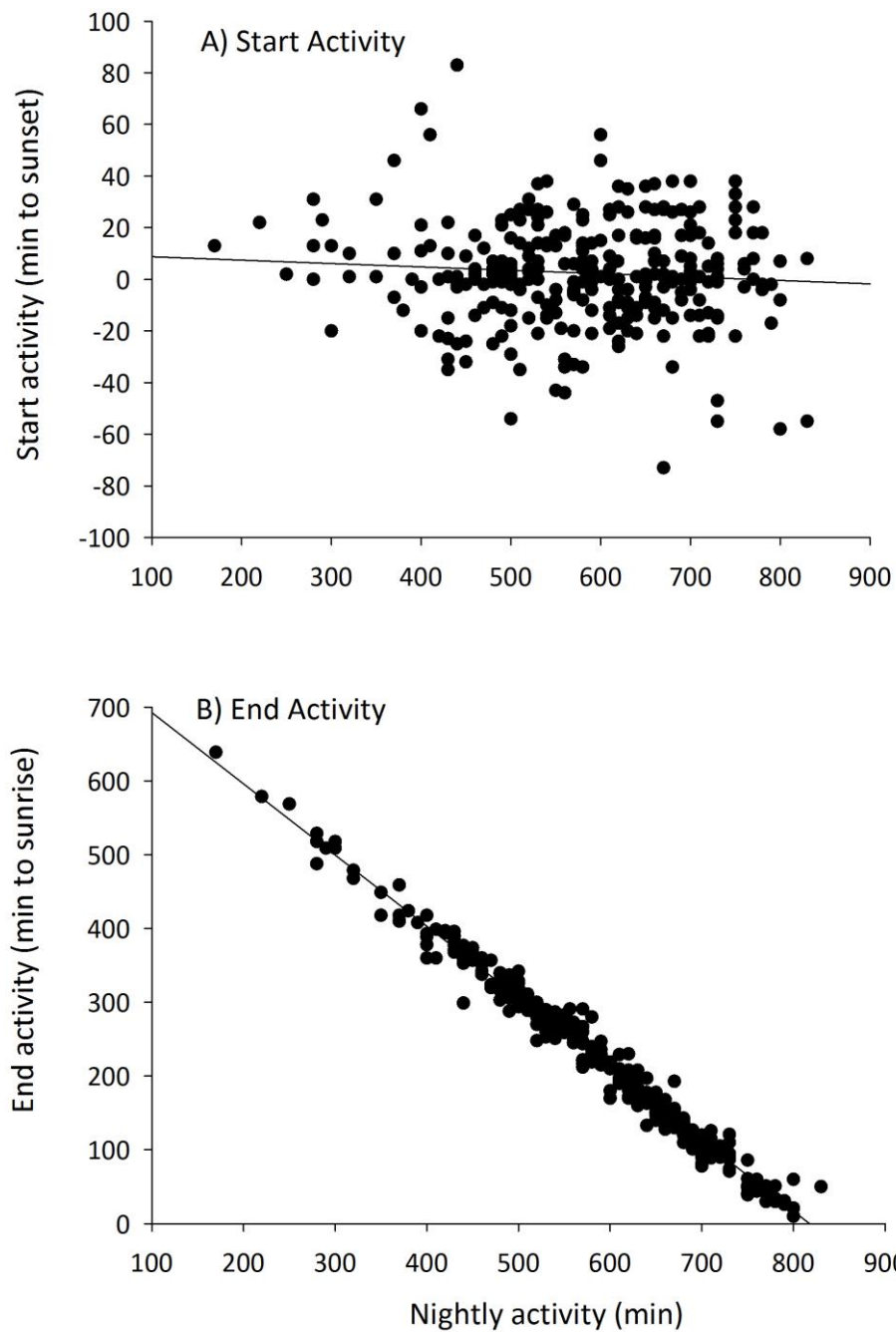
**Figure 2:** Correlation between the nightly activity and a) the start of activity (Start of activity= -0.013 * nightly activity + 10.088; r=0.003) and b) the end of activity (end of activity= -0.965 * nightly activity + 789.294; r=0.9811). Circles represent individual values (N=308, n=8).

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

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