

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

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Abstract

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

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 worldwide (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

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

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

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

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

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

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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

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

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

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

Experimental protocol

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

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

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

Statistical analysis

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

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

Results

Effects on activity

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

Effects on normothermic resting T_b

No individual was torpid at the time of smoke introduction. Smoke induced a significant increase of 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,

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

Effects on torpor expression

The number of animals that entered torpor per day was not significantly affected by fire simulation, even when food was reduced at the same time. In contrast, significantly more animals used torpor when food was reduced without fire cues ($\chi=14.023$, df=3, $p=0.0029$; posthoc: food reduction treatment vs. control conditions: $z=3.5$, $p=0.003$; rest: $z\leq 1.9$, $p>0.05$).

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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Author contributions

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

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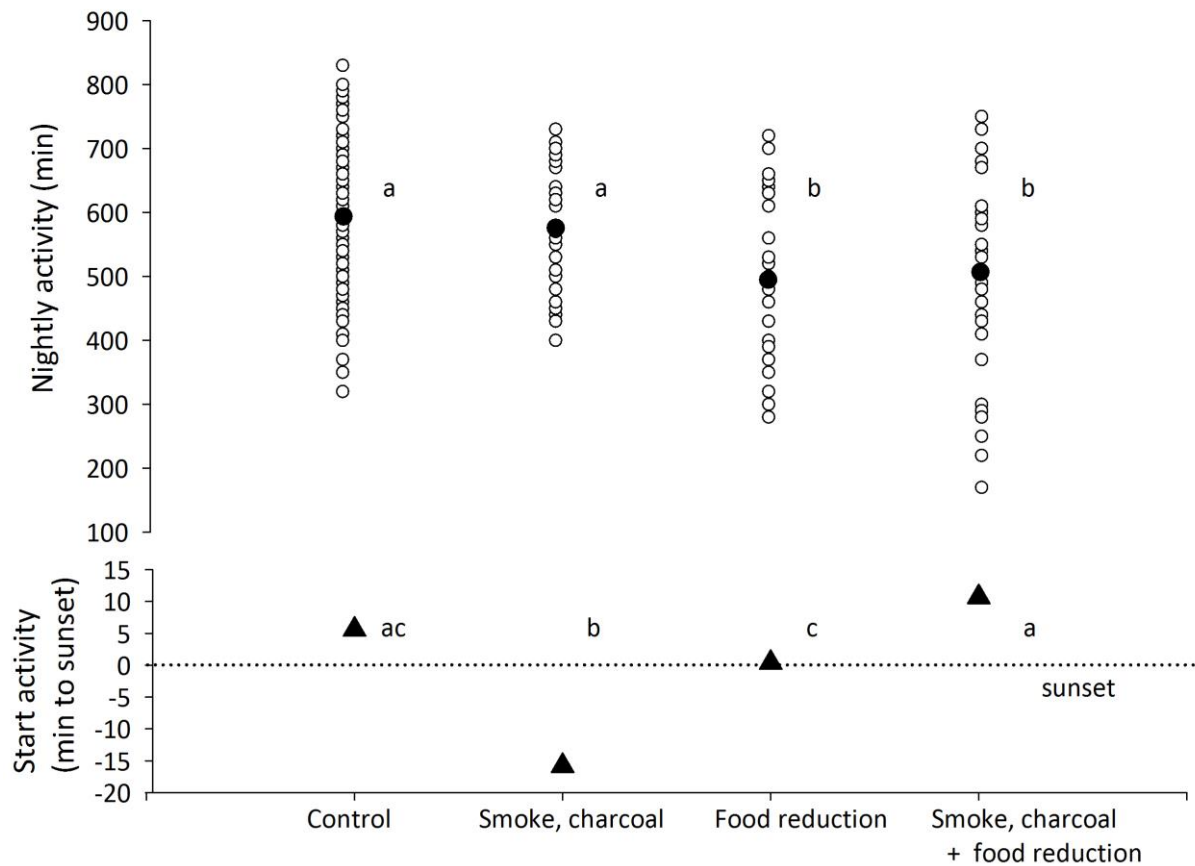
Table 1: Experimental protocol

	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).

439

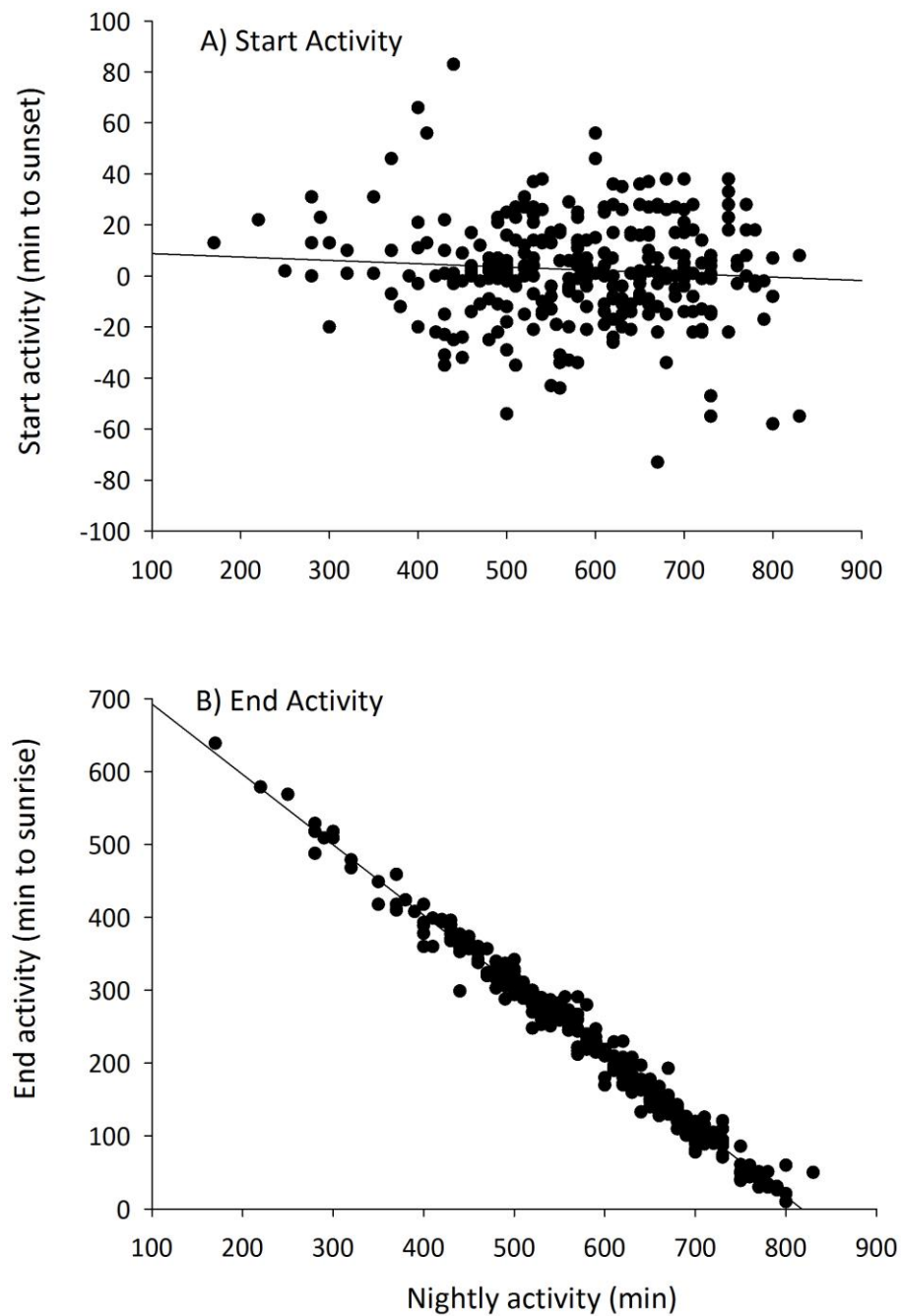


Figure 2: Correlation between the nightly activity and a) the start of activity (Start of activity= $-0.013 \times \text{nightly activity} + 10.088$; $r=0.003$) and b) the end of activity (end of activity= $-0.965 \times \text{nightly activity} + 789.294$; $r=0.9811$). Circles represent individual values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

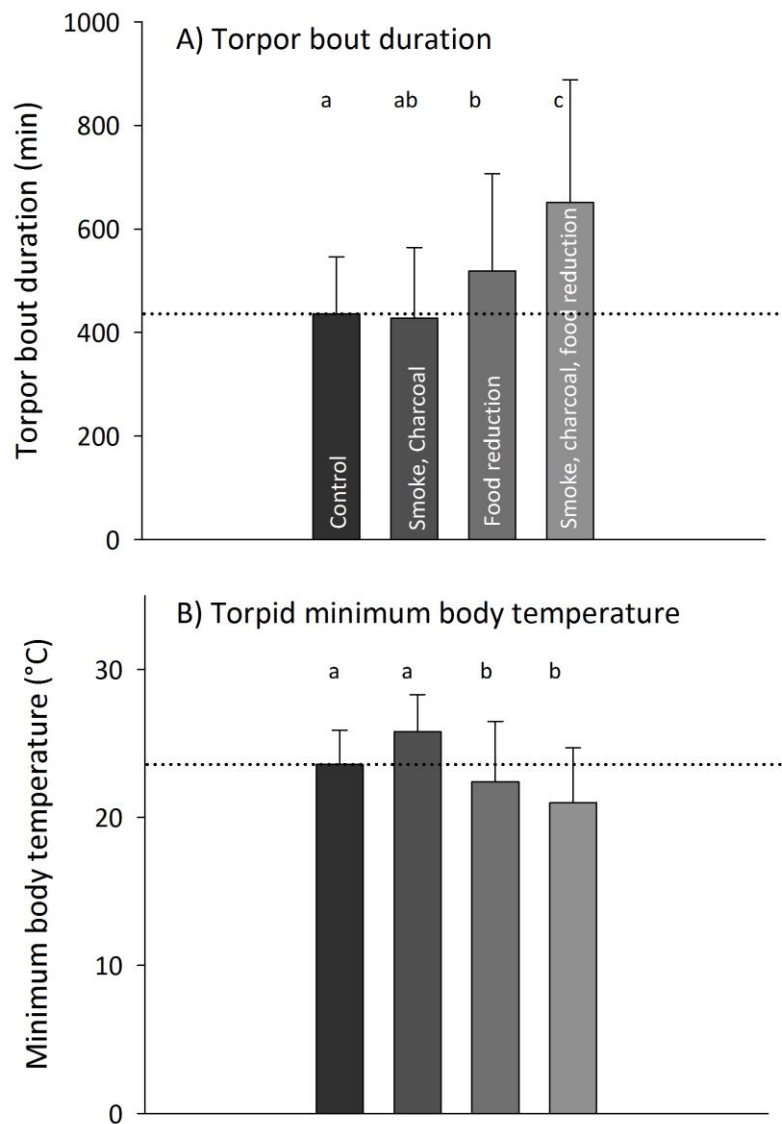


Figure 3: Torpor depth and duration during the different test treatments. A) Torpor bout duration, B) Minimum body temperature during torpor. The *dashed lines* represent the mean TBD/ T_b under control conditions (N=33, n=7). Letters represent results of posthoc Tukey test. Different letters represent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