



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.

1. Introduction

Fires have occurred throughout history and are a reoccurring seasonal event in some areas of the world [24,33]. 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-resistant plant species [16] 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 [25]. 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 [21,31,39]. Indeed recent studies

suggest that opportunistic torpor plays a key role for survival during and after wild fires when food is generally scarce [13,23,27,42,43]. Interestingly, although food availability is clearly an important factor, the loss of ground cover as well as the hostile environment also appear 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 [27]. Similarly, post-fire torpor expression of brown antechinus (*Antechinus stuartii*) increased with a reduction in ground cover and increased predator exposure [42,43]. 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 [45].

Environmental triggers, such as barometric pressure, photoperiod or

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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 dark-phase (i.e. short photoperiod) leads to the development of a winter-phenotype that regularly uses torpor [17], whereas in subtropical blossom-bats (*Syconycteris australis*) long photoperiod associated with low nectar availability increases torpor expression in summer [5]. 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 [1,26]. Other environmental cues can work on a short time scale. For example, bats use falling barometric pressure as an indication of food availability and modulate foraging activity and likely also torpor use accordingly [8,32]. Furthermore, torpor use by sugar gliders during a cyclonic storm was assumed to be triggered by changes in barometric pressure [30,31].

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 [45], 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 [9], 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 [34,35]. 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 [41] 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 [30] 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 [4,20,30], and use torpor irregularly during the cold and unproductive winter [4]. Furthermore, this species is gregarious, living in family groups throughout the year and individuals can decrease their resting metabolic rate via huddling [11]. 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 [29]. 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.

2. Material and methods

2.1. 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.

2.2. 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 0.1 g, sexed, aged according to Suckling [47] 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 × 1.8 × 2 m) with a shared 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; 2 g) 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 ± 25.0 g at capture and 117.6 ± 21.8 g 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 published previously in a different context [29], 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: [20]). Body temperature in normothermic resting sugar gliders is on average 34.5 °C [4] and animals were considered to be torpid when T_b fell below 30 °C (see [30]). 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 [30]). Large T_b variations between activity ($T_b > 38$ °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 [30]).

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

2.3. 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: 60 g of protein mixture, normal amount of fruits; third day 40 g of protein

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