

Post-wildfire physiological ecology of an Australian microbat

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Abstract Historical patterns of wildfires are being altered as a result of changing climate and therefore are becoming an increasingly pressing global issue. How small mammals deal physiologically with changes in landscape and food availability due to fire remains largely unknown, although recent studies on small heterothermic terrestrial mammals have shown an increase in post-fire torpor use to reduce energy and foraging requirements. However, data on the behavioural and physiological responses of bats after fires are scarce, although potentially these volant species may differ from terrestrial mammals. Therefore, we investigated the post-fire thermal biology and activity of lesser long-eared bats (*Nyctophilus geoffroyi*) using temperature-telemetry in Warrumbungle National Park, NSW, which experienced a devastating wildfire in 2013. The study comprised two field seasons, one in 2013 within 4 months after the fire, and one in 2015 two years after the fire to identify potential changes in behaviour and physiology. Interestingly, soon after the fire, bats showed significantly shorter torpor bout duration (11.8 ± 12.5 h) and longer normothermia duration (8.7 ± 4.6 h) in comparison to those in 2015 (torpor bout duration: 24.1 ± 23.5 h; normothermia

duration: 2.5 ± 1.5 h). Insect availability was significantly (20-fold) higher in 2013 than in 2015, which was likely an important factor resulting in the short average torpor bout duration by *N. geoffroyi* after the fire. Our data indicate that volant bats appear to show the opposite post-fire behavioural and physiological responses to small terrestrial mammals, showing longer normothermic and active periods and shorter torpor bouts to capitalise on an increase in available post-fire resources.

Keywords Skin temperature · Torpor · Heterothermy · Fire

Introduction

Forest fires have been increasing in frequency and intensity and this trend is predicted to continue in the future due to climate change (Stocks et al. 1998; Westerling et al. 2006; Stephens et al. 2013; Moritz et al. 2014). While it is known that populations of terrestrial mammals usually decline immediately after a fire (Pardon et al. 2003; Recher et al. 2009), information on how individual animals cope physiologically and behaviourally during and after a fire event remains scarce (Doty et al. 2015b; Stawski et al. 2015a, b; Nowack et al. 2016). After fires, animals have to deal with environmental changes and often reduced food availability. One way to handle these environmental and energetic challenges is using torpor, a controlled reduction in metabolic rate and body temperature (T_b) often employed by microbats to minimize energy expenditure (Chruszcz and Barclay 2002; Willis et al. 2006; Stawski et al. 2014; Ruf and Geiser 2015). Torpor in heterothermic mammals is typically associated with a low ambient temperature (T_a) or decreased food or water availability (Ruf and Geiser 2015). However, in recent years new data on free-ranging animals

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have emerged to reveal that torpor is used for a variety of reasons and not only when animals are energetically stressed (Geiser and Brigham 2012) and may be expressed at mild or warm T_a s (Levin et al. 2015).

Historically, small mammals have experienced a higher rate of survival during extinction events and large-scale disturbances than larger, homeothermic mammals (Cardillo et al. 2005; Hanna and Cardillo 2014) and heterothermy appears to have been crucial to their survival (Geiser and Turbill 2009; Hanna and Cardillo 2014). The ability to express torpor may have been essential for extant microbats and other mammals not only in terms of saving energy on a short-term scale, but also in response to catastrophic events which have resulted in the extinction of some homeothermic mammalian populations (Geiser and Stawski 2011; Lovegrove et al. 2014; Nowack et al. 2016). An ecological disturbance such as wildfire may initiate torpor use due to a decrease in consumable energy and changes in T_a due to alterations in buffered microclimates (Alencar et al. 2015). Thus bats may use torpor to manage the constraints associated with food and water shortage.

However, torpor use may not always be the ideal response and can be influenced by the life history of the animal, post-fire food availability and habitat preference. Bats are the only truly volant mammals (Fenton 1983), which affords them the possibility to escape fires as an immediate response and then return if there is an increase in food availability. The incidence of wildfire significantly changes the structure of an insect community (York 1999; Swengel 2001; Moretti et al. 2004). Nevertheless, literature on the availability of edible microbat prey items immediately post-fire remains scant, with only one study known to us finding an increase in flying prey in North America between 3 and 6 months post-fire (Lacki et al. 2009). Fire can increase foraging habitat for microbats by decreasing vegetative clutter (Owen et al. 2004; Loeb and Waldrop 2008; Womack et al. 2013) and therefore results in increased activity and efficiency of insect detection. Similarly, some forest-dwelling bats prefer roosts with less canopy cover (Kalcounis-Rüppell et al. 2005; Willis and Brigham 2005) and thus, a decrease in vegetative clutter may expose roosts to solar radiation and encourage passive rewarming, a widely used strategy by heterotherms to reach a normothermic T_b (Geiser et al. 2004). However, the dense regrowth that results after time may be avoided by microbats because of the reduced effectiveness of their echolocation, or by those bats whose wing morphology is unsuitable for flying in cluttered spaces (Law and Chidel 2002). Fire can further create roosting habitat for tree-roosting species by creating hollows or increasing hollow diameter (Lunney et al. 1988; Taylor and Savva 1988; Johnson et al. 2009; Lacki et al. 2009). Conversely, fires have also been shown to destroy tree hollows and thus decrease roosting

habitat (Parnaby et al. 2010, 2011; McLean et al. 2015). Consequently, it is important to understand the progressive dynamics of the effects of fire on microbat populations and investigate the complex interactions between wildfire, insect community structure and habitat availability.

Our field study therefore aimed to determine how changes in habitat structure and food availability resulting from a wildfire influence physiological and behavioural responses soon after and 2 years after a fire. We studied *Nyctophilus geoffroyi*, a small (~6 g) and widespread Australian insectivorous vespertilionid that roosts under bark, in crevices and hollows and forages both on the ground and in the air (Tidemann and Flavel 1987; Taylor and Savva 1988; Lumsden et al. 2002; Churchill 2008). This species has been shown to use torpor extensively, particularly at low T_a s (Geiser and Brigham 2000; Turbill et al. 2003), however, it will express short bouts of torpor even during summer and even in the reproductive period (Turbill and Geiser 2006). We hypothesized that (1) individual *N. geoffroyi* will respond favourably to severe wildfire in the short-term and decrease torpor use, (2) individuals increase duration of normothermia due to a decrease in vegetative clutter and (3) increase torpor use as vegetation regrowth occurs.

Methods

Our study was conducted in Warrumbungle National Park (31°17'32"S 149°00'29"E) in NSW, Australia. In January 2013, a severe wildfire burned 88 % of the 23,311 ha park and was extinguished between 20 and 28 January by heavy rain. The study was undertaken during May–June (autumn) of 2013 and May–June of 2015 to assess changes in thermal physiology and activity as a function of time since the fire. Another separate field study was conducted in October 2013, however, due to differences in climate these data were excluded from this study. However, the inclusion of October 2013 bats ($n = 2$) with autumn (May–June 2013) bats generally yielded statistically similar results and thus the data are provided separately (Supplement 1). Ambient temperature (T_a) was measured with temperature data loggers (± 0.5 °C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) in the shade 1 m above the ground. Precipitation was measured using a tipping rain gauge (TGP-9901, Tinytag, West Sussex, UK) placed 1 m above the ground on a wood pole.

Adult *N. geoffroyi* ($n = 4$ in 2013; $n = 1$ female, $n = 3$ male and $n = 7$ in 2015; $n = 1$ female, $n = 6$ male) were captured with either mist nets or harp traps placed across paths or on forest edges. Bats (mean body mass in 2013 = 7.3 ± 0.5 g and 2015 = 6.2 ± 0.8 g) were weighed using an electronic scale (0.1 g resolution, pro-Fit™, Inter-TAN Australia PTY. Limited; Cat. no. 63-9534) and fitted

with temperature-sensitive radio transmitters with individual transmitter frequencies (0.5 g, LB-2NT, Holohil Systems Inc., Carp, ON, Canada) to assess skin temperature (T_{skin}) of bats over a period of 2–25 days. Prior to attachment, transmitters were calibrated to the nearest 0.1 °C in a water bath with a precision thermometer between temperatures of 5–40 °C. After removing a small patch of fur, the transmitters were adhered to the skin of bats between the shoulder blades using a latex adhesive (B-520, Factor2, Lakeside, AZ). Due to the difficulty of implanting internal transmitters and to increase transmitter range, external transmitters were used. T_{skin} of small heterothermic mammals is usually <2.0 °C cooler than core T_{b} (Barclay et al. 1996; Körtner and Geiser 2000) and thus a reliable measurement of torpor patterns in species with large body temperature (T_{b}) fluctuations like bats. After transmitters were attached, bats were given water and kept overnight to ensure adherence of the transmitter and released at their point of capture the following evening. Bats were tracked to their roosting location daily throughout the study period.

Vegetation in 2013 was blackened by fire and contained no canopy cover, ground cover or greenery, and many trees that had survived the fire were exfoliating an outer layer of bark. In 2015, most living *Eucalyptus* trees showed signs of heavy epicormic growth along the trunk of the tree, shading known roosts comparatively more than in 2013. Ground cover had greatly recovered and the dense presence of many *Acacia* spp. (approximately 1 m high) throughout the entire study site were noted. Unlike in 2013, when roost locations were exactly established, due to thick vegetative regrowth in 2015, the exact roost locations of some bats could not be located and thus were tracked to the point of strongest radio signal. The location of each bat was marked with flagging tape as well as with a global positioning system device (GARMIN eTrex). The T_{skin} of bats was recorded in 10-min intervals using a remote receiver/logger (Körtner and Geiser 1998) set within strong reception of each individual bat. The position of the bats and reception of transmitter signal by the receiver/logger was assessed every day and, if necessary, the receiver/logger was moved to ensure data collection. Data were loaded onto a laptop computer approximately every 3–5 days.

Entry into a torpor bout was defined as a decrease in T_{skin} below the torpor threshold of 28 °C. This definition for torpor is generally deemed appropriate because many studies use a $T_{\text{b}} < 30$ °C as a torpor threshold (Barclay et al. 1996). Torpor bout duration (TBD) was defined as the amount of time bats spent at $T_{\text{skin}} < 28$ °C for ≥ 30 min. Normothermia duration was defined as the amount of time bats spent at $T_{\text{skin}} \geq 28$ °C for ≥ 30 min. We defined the expression of normothermia after 1000 h as day normothermia because on nine occasions over both years, individuals were observed actively rewarming following passive rewarming

around 1000 h. We further defined the expression of normothermia initiated at any point from within an hour prior to dusk through the onset of dawn as night normothermia. The duration of torpor bouts that began after 1000 h were defined as day TBD. Active rewarming was defined as a marked increase in $T_{\text{skin}} \geq 28$ °C and it was only recorded if it resulted in the bat maintaining a normothermic T_{skin} for ≥ 30 min and ended with a $T_{\text{skin}} - T_{\text{a}}$ differential of at least 5 °C. Passive rewarming was defined as the tracking of T_{skin} to T_{a} during morning and afternoon warming, either followed by active rewarming near or prior to the peak of maximum day T_{a} (partial passive rewarming), or completely passively rewarming by tracking T_{skin} to a normothermic $T_{\text{a}} (\geq 28$ °C) (complete passive rewarming).

Insect abundance

To assess food availability to microbats, insects were sampled approximately every 3 days throughout the study ($N = 4$ nights 2013; $N = 5$ nights 2015) using an insect trap equipped with a 12-V ultraviolet light and dusk sensor (Turbill 2008). One insect trap was used in the study area in which bats were radio tracked, and was always deployed in the same position prior to sunset and collected the next morning. Insect samples were dried in an oven (Qualtex Solidstat, Watson Victor Ltd., Australia) at 70 °C, to reduce water weight to a minimal, stable level and weighed using an electronic scale (Resolution 0.001 g; PJ3600, Mettler-Toledo, Columbus, OH).

Statistics

Statistical software SPSS (v.22, 2013) and R (v.3.0.3, 2015) were used for all statistical analyses. An unpaired t test was used to assess differences in dry weight of insects and to compare means between the mean minimum and maximum T_{a} , average daily T_{a} , precipitation and range of T_{a} from 2013 and 2015. The times at which torpor entry and rewarming occurred were analysed using a Rayleigh test to determine if peaks were non-random, and a Watson-Williams Test to determine if similar peaks differed significantly between years. Peak times at which bats entered or rewarmed from torpor were identified by clusters of ≥ 5 entry or rewarming times within a 4-h period. In addition, the times at which bats entered torpor after sunset were only considered if the bat had maintained a normothermic T_{skin} after sunset, indicating activity. The times at which bats entered torpor at sunrise were only considered if the bat had maintained a normothermic T_{skin} during the night, again indicating activity. A mixed-effects model (LME) in R was used to examine differences in the given variable while accounting for individuals as a random effect and using average T_{a} as a covariate to offset the effect of

Table 1 Climatic variables in 2013 and 2015

	2013 <i>N</i> = 28	2015 <i>N</i> = 22	<i>T</i> test (<i>p</i> value)
Mean daily T_a (°C)	12.7 ± 3.0	10.8 ± 2.8	0.3
Min T_a (°C)	8.5 ± 3.4	6.8 ± 3.9	0.9
Max T_a (°C)	18.8 ± 4.6	16.8 ± 2.8	0.4
Range (°C)	10.3 ± 4.6	10.1 ± 4.8	0.3
Precipitation (mm/day)	2.5 ± 6.8	0.2 ± 0.63	0.5

Mean values ± SD for *N* = number of days

T_a on each variable (torpor bout duration, day torpor bout duration, night normothermia duration, day normothermia duration, duration of passive rewarming, rate of passive rewarming). To assess T_{skin} variables, analysis of variance (ANOVA) was used while accounting for individual as a random effect. We report mean ± SD for ‘*n*’ the number of individuals; ‘*N*’ is the number of observations. The null hypothesis was rejected if the significance level was $P < 0.05$. No significant difference was found between females and males when comparing any of the physiological variables ($P > 0.05$) therefore data for both sexes were pooled.

Results

Climate

The mean daily T_a , mean minimum T_a and mean maximum T_a did not significantly differ between May–June 2013 and 2015 (Table 1). Both years experienced sporadic rainfall, with a maximum of 34 mm of rain in 2013 and 21.3 mm of rain in 2015, however, mean rainfall/day did not differ significantly between years (Table 1).

Insect abundance

The average dry weight of insects was 20-fold greater in 2013 (average 0.8 ± 0.03 g per night) compared to 2015 (average 0.04 ± 0.05 g per night) ($t_{1,7} = 3.00$, $P < 0.001$). In 2013, the majority of insects collected were mosquitoes and moths from the orders Diptera (62 %) and Lepidoptera (28 %), while in 2015 most of the collected insects were moths and beetles, from the orders Lepidoptera (66 %) and Coleoptera (33 %) (Fig. 1).

Torpor use and skin temperature

In 2013, bats were tracked for an average of 13.0 ± 5.6 days per individual and in 2015 for 11.8 ± 5.4 days per

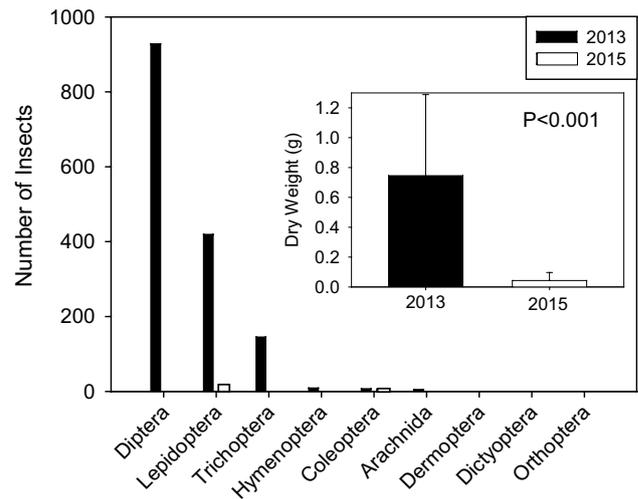


Fig. 1 Diversity, abundance and average dry weight/night of insects collected in 2013 and 2015. The majority of insects collected in 2013 were in the order Diptera, which was not detected in any samples from 2015

individual. All bats used torpor on all days, regardless of year. However, TBD was widely variable, lasting between 0.8 and 70.6 h in 2013, and 0.7–101.0 h in 2015. Multiday torpor was expressed less often in 2013 (9.3 % of all torpor bouts) than in 2015 (31.1 % of all torpor bouts). Mean TBD was 12.4 h shorter in 2013 and significantly different from 2015 ($t_{1,110} = -2.53$, $P = 0.01$) (see Table 2; Fig. 2a, b for examples; Fig. 3a). Day torpor only occasionally occurred in either year and followed a short bout of normothermia, generally during the warmest part of the day. Day torpor was only used on 25.0 % of roost days in 2013 and 15.0 % of roost days in 2015. Day TBD was shorter in 2013 but did not significantly differ from 2015 (Table 2).

In both 2013 and 2015, torpor bout duration was significantly related to average T_a per torpor bout, but the relationship was stronger in 2015 (2013: $F_{1,64} = 13.70$, $r^2 = 0.18$, $P < 0.001$, described by the equation $\text{Log}_{10} \text{TBD} = -3.5 - (0.054 \times \text{Average } T_a)$; 2015: $F_{1,45} = 26.93$, $r^2 = 0.39$, $P < 0.001$, described by the equation $\text{Log}_{10} \text{TBD} = 4.304 - (0.116 \times \text{Average } T_a)$) and the slopes differed significantly between years ($F_{1,109} = 35.14$, $P < 0.005$). Similarly, minimum T_{skin} per torpor bout was affected by the average T_a and again was stronger in 2015 (2013: $F_{1,64} = 26.7$, $r^2 = 0.30$, $P < 0.0001$, described by the equation $\text{Min } T_{skin} = -0.230 + (0.933 \times \text{Average } T_a)$; 2015: $F_{1,44} = 90.47$, $r^2 = 0.68$, $P < 0.001$, described by the equation $\text{Min } T_{skin} = -5.300 + (1.498 \times \text{Average } T_a)$), however, the slopes did not differ significantly between years.

The minimum T_{skin} in 2013 varied between 1.3 and 21.5 °C; in 2015 between 4.4 and 23.6 °C. Not accounting for T_a as an effect, mean minimum T_{skin} for all torpor bouts

Table 2 Physiological variables of free-ranging *Nyctophilous geoffroyi* from 2013 and 2015

	2013	<i>n</i>	<i>N</i>	2015	<i>n</i>	<i>N</i>	LME (<i>p</i> value)
Day TBD (h)	2.4 ± 1.0	4	13	2.7 ± 1.6	6	9	0.3
TBD (all bouts) (h)	11.8 ± 12.5	4	65	24.1 ± 23.5	6	46	<i>0.01</i>
Day normothermia duration (h)	2.6 ± 1.5	4	17	3.3 ± 1.3	6	11	0.2
Night normothermia duration (h)	8.7 ± 4.6	4	35	2.5 ± 1.5	6	26	<i>0.006</i>
Min T_{skin} per torpor bout (°C)	12.7 ± 4.8	4	65	12.3 ± 5.0	7	45	0.5
Mean T_{skin} per torpor bout (°C)	18.2 ± 4.9	4	65	16.7 ± 4.8	7	45	0.2

Mean values for all bats ± SD (for *n* = number of bats and *N* = number of observations) for listed variables in both 2013 and 2015. The *p* value denotes significant differences (italics) between 2013 and 2015 for the given variable

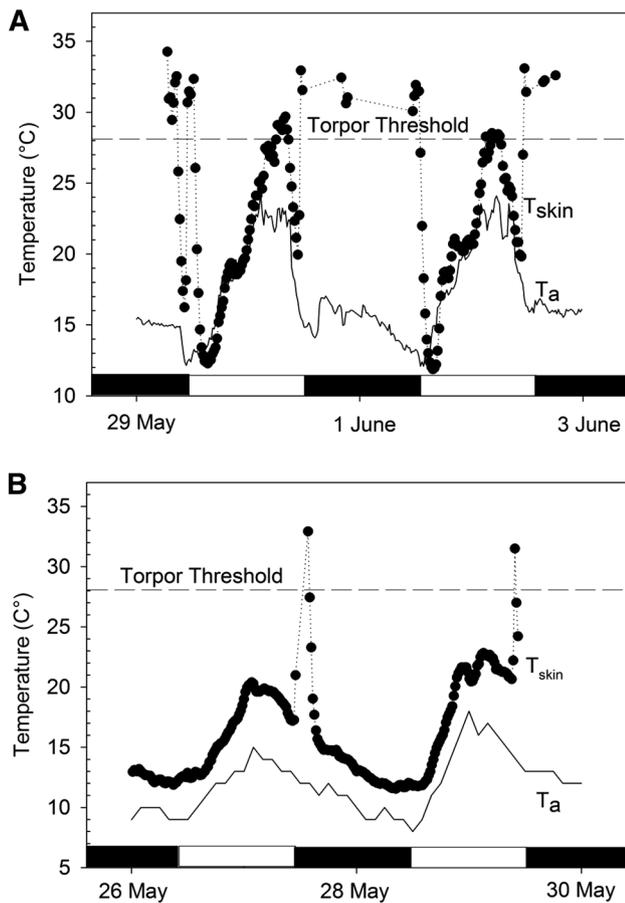


Fig. 2 T_{skin} trace over 2 days in 2013 and in 2015 of **a** a single male bat in 2013 and **b** a single male bat in 2015

in 2013 did not significantly differ from 2015. Although mean T_{skin} for all torpor bouts was 1.5 °C greater in 2013, it did not differ significantly from 2015.

Normothermia and passive rewarming

Night normothermia duration fluctuated widely and ranged between 1.0 and 16.1 h in 2013 and 0.5–7.0 h in

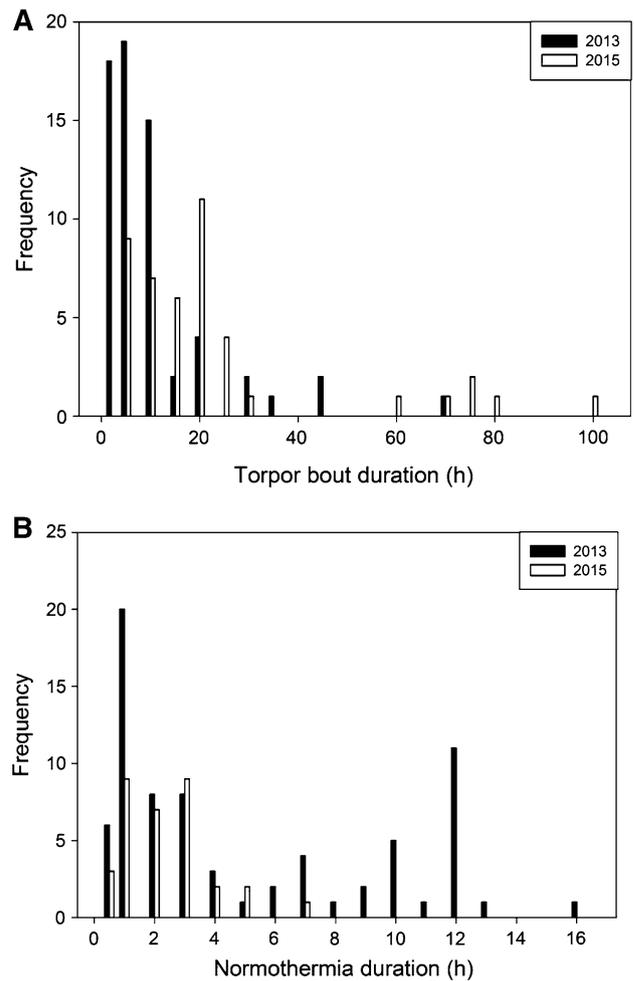


Fig. 3 Frequency distributions for free-ranging *Nyctophilus geoffroyi* in 2013 and 2015 of **a** torpor bout duration (bin width = 5 h) and **b** normothermia duration (bin width = 1 h)

2015 (Fig. 3b). Night normothermia duration was over threefold longer in 2013 and differed significantly from 2015 ($t_{1,59} = -4.10, P < 0.01$), however, day normothermia duration was not significantly different between years (Table 2).

Table 3 Torpor entry and rewarming times of free-ranging *Nyctophilous geoffroyi* from 2013 and 2015

		Torpor entry						Torpor rewarming					
		<i>n</i>	<i>N</i>	Average time (h)	<i>z</i>	<i>r</i>	<i>P</i>	Average time (h)	<i>n</i>	<i>N</i>	<i>z</i>	<i>r</i>	<i>p</i>
2013	Peak 1	4	36	5:56 ± 2:14	0.020	0.84	<0.01	5:08 ± 0:56	4	13	1.12	0.99	<0.01
	Peak 2	4	14	15:19 ± 1:00	0.87	0.97	<0.01	12:55 ± 1:47	4	16	2.05	0.99	<0.01
	Peak 3	4	16	19:27 ± 1:59	1.35	0.88	<0.01	17:41 ± 1:02	4	37	2.3	0.99	<0.01
2015	Peak 1	7	13	13:12 ± 2:00	0.34	0.88	<0.01	11:54 ± 2:11	7	14	1.59	0.86	<0.01
	Peak 2	7	28	19:52 ± 1:31	0.64	0.93	<0.01	17:52 ± 1:34	7	26	0.61	0.92	<0.01

Mean values for all bats ± SD (for *n* = number of bats and *N* = number of observations) for listed variables in both 2013 and 2015. Significance of torpor entry and rewarming times were calculated using a Rayleigh test, and the *p* value denotes if the arousal or rewarming times were significantly clustered (italics). Differences in entry and rewarming times between years were evaluated using a Watson–Williams test. For torpor entry times, peak 2 from 2013 and peak 1 from 2015 significantly differed, however peak 3 from 2013 and peak 2 from 2015 did not differ significantly. For torpor rewarming times, peak 2 from 2013 and peak 1 from 2015, and peak 3 from 2013 and peak 2 from 2015 did not differ significantly (statistical details provided in-text)

Prior to day normothermia, the T_{skin} of bats either passively tracked T_a and then bats actively rewarmed once T_a began to increase rapidly (partial passive rewarming), or completely passively rewarmed to a normothermic T_{skin} (complete passive rewarming). In 2013, bats completely passively rewarmed on eight occasions, accounting for 67 % of all passive rewarming bouts, whereas bats in 2015 only expressed complete passive arousals on only two separate occasions, accounting for 40 % of all passive rewarmings. Bats used passive rewarming (both partial passive and complete passive) 12 times in 2013 (23.1 % of roost days), but only 5 times in 2015 (on 8.3 % of roost days). The duration and rate of passive rewarming was similar in 2013 (duration 4.9 ± 2.3 h at an average rate of 0.08 ± 0.1 °C/min) and 2015 (duration 3.0 ± 0.9 h at an average rate of 0.07 ± 0.03 °C/min), and neither of these variables differed significantly (duration: $t_{1,15} = -1.85$, $P > 0.05$; rate: $t_{1,15} = -0.29$, $P > 0.05$).

Temporal organization of entry and rewarming

The times at which torpor entries occurred expressed one major peak around sunrise and two minor peaks in the late morning/afternoon and after sunset and significantly differed from random variation (Table 3) (Fig. 4a). In 2015, bats only entered torpor around sunrise twice, rather they more often entered torpor in the late morning/afternoon or around sunset, and these times significantly differed from random variation (Table 3) (Fig. 4a). The times at which bats entered torpor at midday were significantly later in 2013 than in 2015 ($F_{1,25} = 9.07$, $P < 0.01$). However, the times at which bats entered torpor at sunset did not differ significantly between years.

In 2013, the times at which rewarming from torpor occurred again expressed one major peak at sunset and two minor peaks a few hours prior to sunrise and in the late morning/afternoon and significantly differed from random

variation (Table 3). Similar to the times at which torpor entries occurred, bats in 2015 only displayed two distinct rewarming peaks, either in the late morning/afternoon and sunset, and these times significantly differed from random variation (Fig. 4b). However, the times at which midday and sunset torpor rewarming occurred did not significantly differ between 2013 and 2015 (Table 3).

Discussion

Our study reveals that surviving microbats respond favourably to a post-wildfire resource pulse and (1) express shorter torpor bout duration and (2) longer normothermia duration in the short-term after a fire in comparison to 2 years post-fire. This is the first study to quantify the thermal physiology and activity of microbats in response to a catastrophic wildfire, and the first study to show a positive thermo-energetic response from a heterothermic mammal to a severe wildfire.

Previous echolocation studies in Australia and North America have found a positive relationship between bat activity in the short-term after both wildfire (Buchalski et al. 2013) and prescribed fire (Armitage and Ober 2012; Inkster-Draper et al. 2013; Loeb and Waldrop 2008), potentially due to more efficient foraging when canopy cover is reduced (Perry 2012). Some studies have radio tracked microbats during a prescribed fire, finding that bats indeed move away from smoke (Dickinson et al. 2009), but soon after are attracted back to recently burnt sites due to an increase in insect and roost availability (Lacki et al. 2009). Our study species is a slow-flying and highly manoeuvrable microbat that can move >10 km per day (Lumsden et al. 2002). *N. geoffroyi* consume insects both mid-air, and importantly, on the forest floor, both in forest clutter and also low-clutter spaces near tree trunks (Brigham et al. 1997a). In dry forest types, they have been found

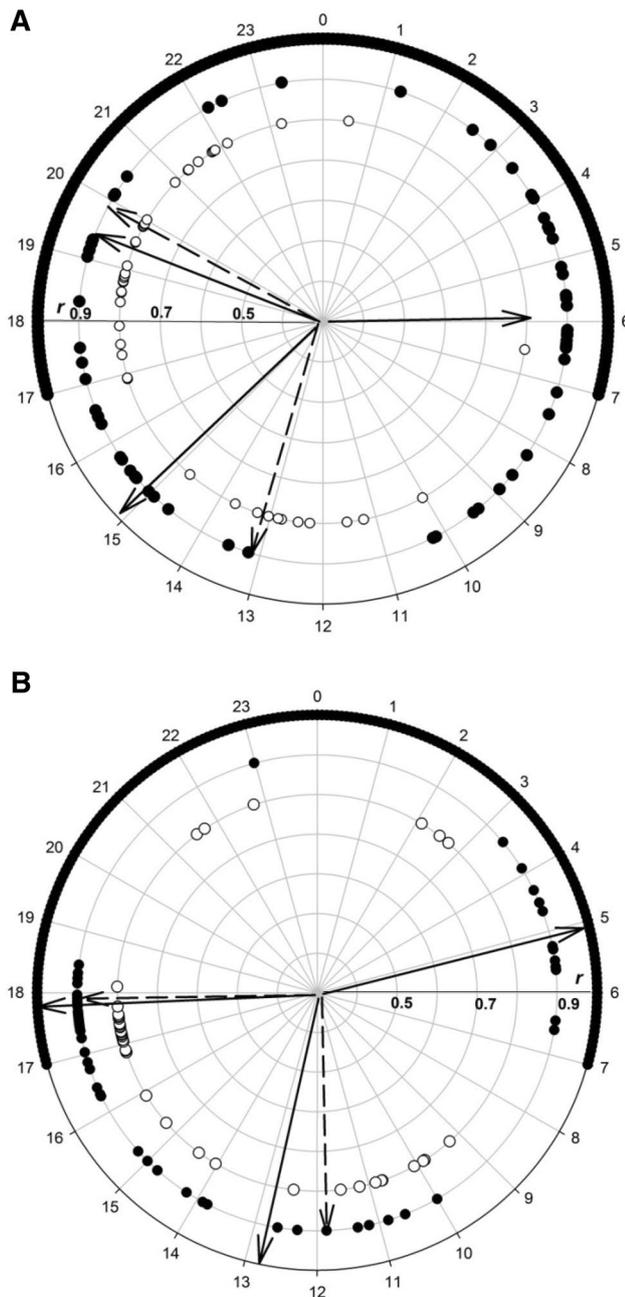


Fig. 4 The circular distribution over 24 h of **a** peak torpor entry times and **b** peak torpor rewarming times in 2013 (black circles, solid arrow) and 2015 (white circles, dashed arrow). A longer arrow length indicates a stronger grouping per peak. Night is indicated by a black solid line on the outer circle

to be more active over narrow open spaces, such as dry stream beds, where foraging is potentially more efficient (Law et al. 2011). Therefore, even though *N. geoffroyi* forage well in a cluttered habitat, an absence of ground cover and sparse canopy cover after fire could have allowed them to more easily detect moving insects. This could potentially increase the benefits of foraging and explain

the longer normothermia duration and thus a decrease in average TBD. The main prey items of the study species are moths and beetles (Churchill 2008), both of which were collected in large numbers in 2013, but had greatly decreased in 2015. Because of the significant increase in available food in 2013 compared to 2015, *N. geoffroyi* may have been more inclined to stay normothermic and active longer at night to hunt and feed. Bats in 2013 were indeed on average 1.1 g heavier than bats in 2015, supporting our hypothesis that insect availability will affect normothermia duration; heavier bats may be more willing to increase MR and T_b for more time to forage longer. Some recolonizing insects prefer post-fire vegetation or increase in abundance post-fire (Swengel 2001). Lacki et al. (2009) found a 34 % increase in microbat prey items 3 months following a prescribed fire, similar to our finding of increased post-wildfire microbat prey abundance. However, in 2015 when ground and canopy cover had extensively recovered, foraging, especially on the ground or mid-canopy which was almost impossible to penetrate due to the vast number of seedlings, would have become considerably more difficult and could have resulted in the decrease in normothermia duration and increase in TBD. This is supported by bats commonly expressing multiday torpor bouts (~1/3 of all recorded torpor bouts) in 2015, and often only using short bouts of normothermia at night (sometimes for <30 min). Bats in 2015 may have aroused from torpor at night to assess foraging potential and quickly returned to a torpid state when unable to efficiently manoeuvre or locate insects within the cluttered area.

Microbats in Australia use torpor often, even if they are in good body condition (Stawski and Geiser 2010), live in the tropics and subtropics where temperature is mild, and when food is generally available (Stawski et al. 2008; Geiser and Stawski 2011), and even in the arid zone during extreme heat waves (Bondarenko et al. 2014). Because microbats have a high surface area to volume ratio, they experience high heat loss at low T_a s and thus are highly affected by fluctuations in T_a . The less pronounced use of torpor in 2013, even at low T_a s, supports our hypothesis that a change in habitat structure and food availability would be beneficial to microbats and facilitate longer normothermia duration, which otherwise increases energetic demands. Bats were thus likely influenced by the positive changes in resource availability and habitat structure immediately after the fire and were more likely or willing to forego longer and deeper bouts of torpor. This is further supported by a more highly correlated relationship between T_a and TBD in 2015; whereas despite fluctuations in T_a , bats in 2013 were attracted to an increase in resources and forwent longer bouts of torpor even if T_a was low. Bats were also more inclined to enter and rewarm from torpor throughout the day and night in 2013 than bats in 2015. This is likely

because in 2015 bats saved energy to rewarm from torpor either late afternoon or at sunset to forage or assess foraging potential. Consequently, normothermia duration in 2015 was short and bats entered torpor on average 2:15 h after initial rewarming, most often entering torpor between sunset and midnight (67 % of all entries). Conversely, bats in 2013 most often entered torpor at sunrise ± 3 h (55 % of all entries) after foraging throughout the night.

Interestingly, passive rewarming did not seem to be a frequently used strategy in either year, although it was expressed more often in 2013 (23.1 % of roost days) than in 2015 (8.4 % of roost days). Passive rewarming is an important thermal strategy to achieve a high midday T_b to cut the costs of active rewarming (Turbill et al. 2003; Currie et al. 2015). It is possible that passive rewarming was used more often in 2013 due to a higher roost temperature (T_{roost}). Although T_{roost} s were not directly measured, we can estimate differences in T_{roost} by assessing mean and minimum T_{skin} during torpor bouts. As mean and minimum T_{skin} were somewhat higher in 2013, T_{roost} s may have indeed been higher due to greater light penetration with an absence of canopy cover/epicormic growth. The lack of canopy cover coupled with the severely blackened state of roosting trees would have allowed for a higher midday roost temperature from solar radiation (Lourenço and Palmerim 2004), thus facilitating a higher number of passive arousals in 2013. Microbats have been shown to prefer darker coloured bat boxes, potentially to facilitate a greater number of passive midday arousals to achieve normothermia (Doty et al. 2015a). Consequently, the infrequent use of passive rewarming in 2015 may not simply be a product of decreased solar radiation, but also a facultative strategy to increase TBD and save more energy.

An increase in post-fire night normothermia duration by *N. geoffroyi* differs considerably from the strategies of other heterothermic mammals, such as the marsupial yellow-footed antechinus (*Antechinus flavipes*). *A. flavipes* increased torpor use to survive after the fire in Warrumbungle National Park when food availability on the ground was low (the majority of insects found in the light trap in 2013 were not typical antechinus prey items) and visual detection by predators is high (Stawski et al. 2015a) when compared to previous field and laboratory studies (Rojas et al. 2014). Similarly, brown antechinus (*A. stuartii*) were found to decrease activity following a light prescribed fire in Guy Fawkes National Park, NSW (Stawski et al. 2015b). Brown antechinus remained within their original pre-fire home range and responded to the prescribed fire by increasing TBD two-fold and increasing torpor frequency from 52 to 92 % of the day. A decrease in ground and canopy cover may have increased perceived predation risk in these terrestrial mammals (observations of feral foxes, cats and pigs were noted throughout both study periods) and the observed decrease in activity and increase in torpor use would help to ameliorate this risk. Interestingly,

superb lyrebirds (*Menura novaehollandiae*) increased foraging activity for a short period immediately after a prescribed fire potentially to capitalise on an increase in dead, visible prey items in areas where ground cover had been burnt (Doty et al. 2015b). Similar to bats, lyrebirds are afforded the ability to easily escape prescribed fire by flight, return to their home-range and exploit an available post-fire energetic resource pulse. The structure of a post-fire landscape and mode of foraging and resource availability for the species in question are, therefore, important factors determining the increase or decrease of torpor use or activity after fire.

Although torpor can be a useful tool for individuals faced with energetic constraints, such as low T_a or reduction in consumable energy, it is not necessarily always beneficial in a post-fire environment. Unlike antechinus that use torpor reluctantly (Rojas et al. 2014), microbats appear to use torpor often as a “default” mechanism to balance energy supply and demand (Stawski et al. 2014) and also forage in the air and use echolocation to locate prey and this sensory system is highly constrained by vegetation structure (Broders et al. 2004). Therefore, an increase in resources and a low-clutter foraging environment with maintenance of standing trunks (Brigham et al. 1997b) would have granted bats the opportunity for maximal food intake. Our study highlights the importance of understanding the specific life histories and habitat use of animals in response to natural disasters. As results from one taxon cannot be extrapolated to another, empirical data from diverse species are required for scientifically informed management decisions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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