



Research

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Cool echidnas survive the fire

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Fires have occurred throughout history, including those associated with the meteoroid impact at the Cretaceous–Palaeogene (K–Pg) boundary that eliminated many vertebrate species. To evaluate the recent hypothesis that the survival of the K–Pg fires by ancestral mammals was dependent on their ability to use energy-conserving torpor, we studied body temperature fluctuations and activity of an egg-laying mammal, the echidna (*Tachyglossus aculeatus*), often considered to be a ‘living fossil’, before, during and after a prescribed burn. All but one study animal survived the fire in the prescribed burn area and echidnas remained inactive during the day(s) following the fire and substantially reduced body temperature during bouts of torpor. For weeks after the fire, all individuals remained in their original territories and compensated for changes in their habitat with a decrease in mean body temperature and activity. Our data suggest that heterothermy enables mammals to outlast the conditions during and after a fire by reducing energy expenditure, permitting periods of extended inactivity. Therefore, torpor facilitates survival in a fire-scorched landscape and consequently may have been of functional significance for mammalian survival at the K–Pg boundary.

1. Introduction

The evolution of mammals has been hypothesized to be linked to the meteoroid impact at the Cretaceous–Palaeogene (K–Pg) boundary, about 65.5 million years ago (Ma), that ended the era of dinosaurs. Geological evidence suggests that the meteoroid caused global wildfires that killed all life unable to seek safe refuge [1]. After ancestral mammals had survived the fire and its aftermath, the now open niches permitted a rapid radiation of mammalian lineages [2]. Importantly, the ability to enter torpor, a substantial controlled reduction of energy expenditure and body temperature (T_b), was the likely and crucial reason why ancestral mammals survived the aftermaths of the meteorite impact, permitting these mammals to stay inactive and hidden for long periods without the need to forage [3,4].

There is growing evidence that heterothermic mammals (species that use torpor) often have an adaptive advantage over homeothermic species (that have high energy requirements related to maintenance of a constant T_b). Heterothermic species do not only use torpor to survive seasonal energetic and thermal challenges, but can also endure the consequences of unpredictable bottlenecks or natural disasters and consequently have a lower risk of becoming extinct [5–9]. Ancestral mammals were small and nocturnal and presumably had a relaxed thermoregulation, entering torpor during the colder periods of the day and possibly also undergoing bouts of long-term hibernation [10]. Many of today’s heterotherms hibernate in underground burrows [11,12] that would allow survival largely independent of the conditions on the Earth’s surface. A recent study of a small marsupial mammal demonstrated that it reduced activity and T_b after fire, thus increasing its chance of survival by reducing foraging requirements and exposure to predators in the post-fire landscape [7]. Furthermore, the hypothesis that heterothermy facilitated survival after the meteoroid impact at the K–Pg boundary is supported by anecdotal observations of short-beaked echidnas (*Tachyglossus aculeatus*; 2–4 kg), surviving fires on Kangaroo Island [13] and in the Warrumbungle National Park in Eastern Australia [14].



Figure 1. Photos of the study site (a) during the burn and (b) after the burn. Copyright of photos: J. Nowack.

Divergence of monotreme and therian mammals is estimated to have occurred at least 170 Ma [15], and the short-beaked echidna is often considered a 'living fossil' with many characteristics of ancestral mammals [10]. Although the species is now limited to the Australian continent and New Guinea, it has one of the widest geographical ranges of any native Australian mammal and occurs almost anywhere from deserts to wet forests to alpine regions [16]. Short-beaked echidnas are among the largest known deep hibernators [17] and can hibernate from a few days in warmer habitats up to several months in colder habitats, with torpor bouts of one to three weeks interrupted by short bouts of normothermia [16,18]. The wide geographical distribution and the long life expectancy (up to 45 years) of this species [19] are generally attributed to their low metabolic rate and ability to use torpor to further reduce energy expenditure [10,19]. The hypothesis that the use of torpor may also have allowed the species to outlast fires [20], therefore, seems highly plausible. To evaluate this hypothesis, we examined the activity and T_b fluctuations of free-ranging short-beaked echidnas, before, during and after a prescribed burn. We predicted that echidnas would be able to survive the fire by taking shelter in caves, underground burrows or large hollow logs, and that their response to the post-fire impact on their habitat would be an increased depth and frequency of torpor, and a reduced overall activity compared with echidnas in unburnt areas of similar habitat.

2. Material and methods

(a) Study site and prescribed fire

On 21 April 2015, a prescribed burn was conducted at Dryandra Woodland, southeast of Perth, Western Australia (31°46' S 117°10' E) by the Department of Parks and Wildlife. The prescribed burn area was 227 hectares, confined by dirt roads and tracks. The unburned woodland beyond these tracks encompassed our control site, with the home ranges of control echidnas being up to 3.2 km away from the burn area. We included a control group in the study design that was monitored concurrently with the fire-affected group and experienced the same ambient weather conditions to exclude temporal effects (such as seasonal changes in torpor use and activity) from the effect of fire. We studied 10 echidnas for 21–25 days before the fire (active burning: 21 April, 11.00–15.00 h) and for 18–31 days after the fire. Echidnas were classified as control ($n = 5$) and fire group ($n = 5$), depending on the location of their home ranges. One individual had a home range that included both fire-affected and unburnt areas, so the data for this individual was classified as belonging to the fire group

when it inhabited the burn area or to the control group when it inhabited the control area. The fire produced large amounts of smoke, and because there was little groundcover it mainly affected bushes, logs and trees, causing trees to collapse and leading to the presence of burning logs for weeks after the fire (figure 1); smoking trees were observed until the end of our study, 31 days after the burn.

(b) Procedures

Echidnas were captured by hand, and 10 individuals were implanted with temperature data loggers ($\pm 0.5^\circ\text{C}$, logging interval: 15 min, approx. 3 g, iButton thermochron DS1922 L, Maxim Integrated Products, Inc., Sunnyvale, CA) into the intra-peritoneal cavity. Loggers were calibrated in a water bath ($5\text{--}45^\circ\text{C}$; increments of 5°C) to the nearest 0.1°C and coated with a wax-polymer compound (Elvax, Du-point, Johannesburg, South Africa) before implantation via a small abdominal incision under oxygen/isoflurane anaesthesia (3–4% induction, 2–3% maintenance). The loggers were tethered to the abdominal muscle with silk suture (to facilitate removal at the end of the study), before the skin and muscle layer were sutured separately using dissolvable suture. Analgesia was provided via a single subcutaneous dose of Meloxicam (0.2 mg kg^{-1} ; Boehringer Ingelheim, North Ryde, Australia).

A radio transmitter (Holohil RI-2C, Holohil Systems Ltd., Ontario, Canada) for locating individuals and a custom-made aluminium cradle were glued to the spines of the lower back of each echidna. The cradle was fitted with a removable GPS unit that stored location data (catalogue tracker; logging every 6 min, capacity: 4–11 days; 22 g; Catnip Technologies Ltd., Hong Kong) and a temperature data logger ($\pm 0.5^\circ\text{C}$, iButton thermochron DS1921G, logging interval: 10 min) to record external temperature. All animals weighed between 2600 and 3950 g (mean mass: 3355 ± 375 g) and were therefore considered adult. Echidnas were released at the capture location after recovery from anaesthesia, and located by radio-tracking every 5–7 days to exchange GPS units. Individuals were recaptured at the end of the study for removal of loggers as described for implantation.

(c) Ambient conditions

Ambient temperature (T_a) was measured hourly at the control and burn site using temperature data loggers placed in the shade ($\pm 0.5^\circ\text{C}$, iButton thermochron DS1921G). Precipitation data were obtained from the Bureau of Meteorology for the nearest (approx. 7 km) weather station (Caernarvon Park; 32.74° S 116.84° E). The $T_{a,s}$ for the control and fire area were strongly correlated (regression analyses; $r^2 = 0.945$, $F_{1,1156} = 20\,020$, $p < 0.001$; $T_{a(\text{control})} = T_{a(\text{fire})} \times 1.26 + 0.896$). Daily T_a ranged from a minimum of -0.5°C to a maximum of

Table 1. Mean, minimum and maximum ambient temperatures (T_a) and mean body temperatures (T_b) before and after the prescribed burn for the burn and control areas. (T_a was highly correlated for both areas ($r^2 = 0.945$, $F_{1,156} = 20\,020$, $p < 0.001$) and mean T_b s of echidnas were significantly lower in the post-fire group than in the control group after the burn (ANOVA; $F_{1,391} = 48.74$, $p < 0.001$; post hoc test results indicated by different letters.)

	burn area		control area	
	pre-fire (°C)	post-fire (°C)	pre-fire (°C)	post-fire (°C)
T_a mean	16.8 ± 2.3	14.0 ± 3.0	16.6 ± 2.3	14.6 ± 2.8
T_a minimum	3.5	-0.5	3.5	0.5
T_a maximum	34.5	30.0	31.5	26.5
T_b mean	28.0 ± 0.7^a , $n = 4$	24.1 ± 1.3^b , $n = 5$	28.2 ± 1.3^a , $n = 5$	25.6 ± 1.4^c , $n = 5$

34.5°C (table 1). During the study period, a total of 71.6 mm of rainfall was recorded on 8 days.

(d) Torpor use and activity

Normothermic echidnas typically have a body temperature (T_b) between 28 and 35°C [19] and therefore, echidnas were deemed 'normothermic' when T_b increased $> 27^\circ\text{C}$. Torpor bout durations of > 24 h ($T_b \leq 27^\circ\text{C}$) were classified as multiday torpor [18]. Echidnas in the Western Australian wheatbelt do not have a distinct hibernation season although they increase torpor use in response to cooler conditions [16].

Accuracy of the GPS units used in our study was determined by comparing the recorded locations for the loggers plotted on Google Earth with the known path of travel along a road. The measured accuracy of loggers was approximately 55 m when stationary, and 20 m when moving, and therefore comparable to GPS collars used on wildlife [21]. We used the GPS loggers to identify directional long-distance movements of animals and discarded all GPS data without clear directional movement, i.e. data points around rest shelters, as these points are likely to occur when animals were resting in tree logs, although they may potentially include foraging or basking around the shelter. We obtained the starting point and the endpoint of activity, as well as the location of shelter sites. Daily foraging areas, as well as overall home ranges (minimum convex polygon, MCP) were calculated by using a custom-written JAVA-script programme (JAVA-script version 6; G. Körtner). Overlap of individual's home ranges before and after the burn was analysed with ArcGIS v. 10 (ESRI).

(e) Statistical analyses

Data are presented as mean ± 1 s.d.; n denotes the number of individuals, N the number of observations. Statistical analyses were conducted using R, v. 3.1.0 [22]. The individual that died in the fire was not included into statistical analyses owing to fire-related loss of most data. The difference in activity between the fire and control animals during the night following the burn was analysed with a t -test after testing for normality and homogeneity of variance using Shapiro–Wilk test and Bartlett's test, respectively. The relationship between T_b and ambient conditions (minimum T_a and rainfall) was determined with a linear-mixed effect model using 'individual' as a random factor to account for repeated measures, followed by an ANOVA (*lme* in library 'nlme' [23]). The same approach was used to examine mean T_b differences between the groups (pre-fire, post-fire, pre-control, post-control) as well as to test for differences in the use of multiday torpor (more than 24 h), activity (min per day; including inactive days), duration of activity (min per day; excluding inactive days), daily foraging area (MCPs) and home ranges (MCPs). For the analysis of multiday torpor use, we calculated the hours spent in multiday torpor as a percentage of the

total hours of T_b recording for each individual and then analysed arcsine-transformed data. To examine differences in the variance of mean daily T_b between treatments of the groups, we calculated a linear-mixed-effects model followed by an ANOVA, using 'day' as a random effect to account for repeated measure. Post hoc analyses were performed as Tukey tests (*glht* in library 'multcomp' [24]).

3. Results

(a) Direct impacts of the fire

Four of five echidnas at the fire site survived the burn. Three of the five tagged individuals were located in areas that actually burnt during the fire, whereas two individuals were sheltering within less than 200 m of the fire and only parts of their home ranges were affected by the burn. With the exception of one normothermic individual in the burn area that had a T_b of 28.6°C, all echidnas (in burn and control area) had a $T_b \leq 25.6^\circ\text{C}$ ($n = 9$) when the fire started. The individual that died during the burn was resting inside a log that caught fire and did not reach a normothermic T_b before it died (the echidna's iButton was retrieved after the fire; minimum T_b for that day: 23.1°C, maximum T_b : 26.6°C). A second individual resting in the same log aroused from torpor and left the log during the fire, escaping to a shelter about 160 m away. Two additional untagged echidnas that were not part of this study were also found dead in remnants of burnt logs after the fire.

Daily activity was strongly affected by the fire. Mean activity during the night immediately following the fire was significantly reduced for the post-fire group (mean activity 179 ± 125 min; range from 0 to 283 min; $n = 4$) in comparison with the control group (mean activity 474 ± 38 min; range 412–513 min; $n = 5$; t -test: $t_{3,45} = 4.53$, $p = 0.015$). All post-fire individuals remained inactive during the day(s) following the fire and three of the four individuals entered multiday torpor ranging from 51 to 123 h (example in figure 2). The fourth individual only entered short torpor bouts (interspersed with normothermic T_b s $> 27^\circ\text{C}$ for 18 h), but was inactive for 51 h after the fire. Control individuals remained active and none entered multiday torpor immediately after the burn (earliest multiday torpor bout approx. 2 days after the fire; figure 3).

(b) Post-fire adaptations

Echidnas entered short bouts of torpor almost every day during our study, with a minimum T_b of 11.6°C (figure 2);

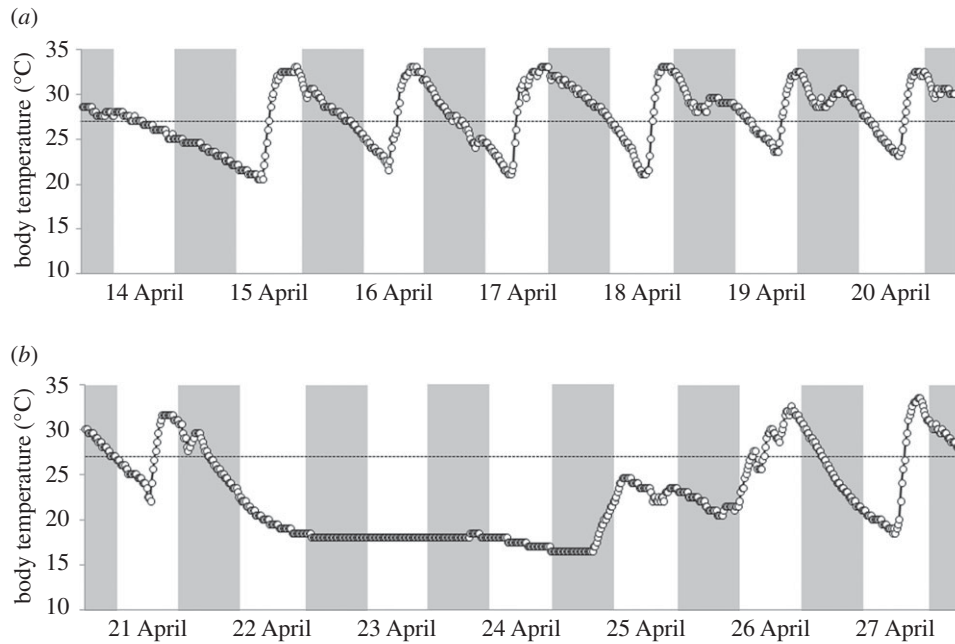


Figure 2. Body temperature traces (sampling interval every 15 min) of the same echidna (a) 7 days before and (b) 7 days after the fire on 21 April. Grey areas indicate scotophase and dashed lines mark the torpor threshold of 27°C.

minimum T_b was positively related to a combination of minimum T_a and rainfall (ANOVA: $F_{1,412} = 4.96$, $p = 0.027$). Mean T_b s of echidnas were also significantly influenced by the fire (ANOVA: $F_{1,391} = 48.74$, $p < 0.001$; table 1). Despite a temperature-dependent decrease in T_b for all individuals (both: $z \geq 5.31$, $p < 0.001$), mean T_b s of echidnas were significantly lower for the post-fire group than the control group ($z = 10.44$, $p < 0.001$), and the pre-fire group ($z = 3.39$, $p = 0.003$). Additionally, variance of mean T_b was much higher for individuals of the post-fire group (ANOVA: $F_{3,45} = 8.49$, $p < 0.001$) than for the control ($z = 2.94$, $p = 0.017$) or pre-fire animals ($z = 4.86$, $p < 0.001$).

The fire also influenced activity of echidnas (ANOVA: $F_{3,293} = 16.59$, $p < 0.001$; table 2). Post-fire individuals were significantly less active and spent more hours in multiday torpor than individuals of control ($z = 3.61$, $p = 0.002$) or pre-fire groups ($z = 5.70$, $p < 0.001$). This difference was apparent despite a higher occurrence of multiday torpor in the control group before the fire (table 2). The use of multiday torpor was increased in the post-fire group compared with the control group, as well as in comparison with the pre-fire group (ANOVA: $F_{3,7} = 37.65$, $p = 0.001$; post hoc results: $z \geq 4.87$, $p < 0.001$ for all combinations). The duration of activity on active days was always longer for the control (mean: 458 ± 182 min, $N = 128$) than for the fire group (mean: 359 ± 164 min, $N = 107$; ANOVA: $F_{1,223} = 9.55$, $p < 0.001$; before: $z = 3.67$, $p = 0.0013$; after: $z = 2.86$, $p = 0.022$). Although overall activity was further reduced after the burn owing to more phases of inactivity (fire group: three to seven bouts of multiday torpor; control group: one to two bouts), the duration of activity on active days did not differ for both groups of echidnas before and after the fire (both: $z \geq 2.00$, $p > 0.08$).

The two echidnas with territories completely burnt increased their average daily foraging areas after the fire (8.0 ± 5.3 ha, $N = 14$ versus 16.9 ± 9.6 ha, $N = 5$ and 7.4 ± 6.0 ha, $N = 19$ versus 10.0 ± 10.2 ha, $N = 7$), presumably as a result of destroyed shelter sites and impact on foraging areas. However, overall, there was no significant difference in daily foraging areas between the fire and the control group after the

fire ($z = 0.18$; $p = 0.998$). Interestingly, whereas the daily foraging areas of the control group decreased over the time of the study from 11.0 ± 2.9 ha ($N = 71$) to 8.7 ± 1.1 ha ($N = 59$; $z = 2.68$, $p = 0.037$; ANOVA: $F_{3,224} = 3.39$, $p = 0.019$), the daily foraging areas of the fire groups remained constant (8.7 ± 2.1 ha, $N = 71$ versus 8.9 ± 4.9 ha, $N = 36$; $z = 0.44$, $p = 0.972$).

Habitat use of the post-fire individuals was not notably affected by the fire (fire animals: 55.2 ± 6.7 ha, $N = 75$, $n = 4$ versus 51.0 ± 10.6 ha, $N = 47$, $n = 4$; control animals: 61.2 ± 28.9 ha, $N = 71$, $n = 5$ versus 39.9 ± 17.6 ha, $N = 60$, $n = 5$; ANOVA: $F_{3,6} = 2.81$, $p = 0.131$) and no individual left its territory (figure 4). Although echidnas were mostly found in unburned patches between the burned areas, we observed three of the four surviving tagged echidnas of the fire group in heavily burnt patches. We also observed a change of shelter sites for the post-fire group to new, unburnt shelters, presumably owing to the destruction of logs that were the main shelters used by echidnas in the burn area (eight of 14 known shelter logs were damaged or destroyed by the fire).

4. Discussion

Our study demonstrates that the short-beaked echidna responds to the short- and medium-term impacts of fire (i.e. during fire and up to three weeks after fire) in its habitat by increasing torpor use. Echidnas also reduced their activity as a direct response to the burn and expressed more and longer phases of multiday torpor after the fire than the control group, apparently to compensate for reduced foraging opportunities while the surrounding area was still burning. Importantly, no individual left its burnt home range after the fire, and instead responded by varying T_b ; in general, fire-affected echidnas decreased mean T_b and increased periods of inactivity for weeks after the fire in the post-fire landscape. This response was not simply a seasonal effect, as control echidnas that were monitored concurrently and subject to the same ambient conditions in an unburnt area

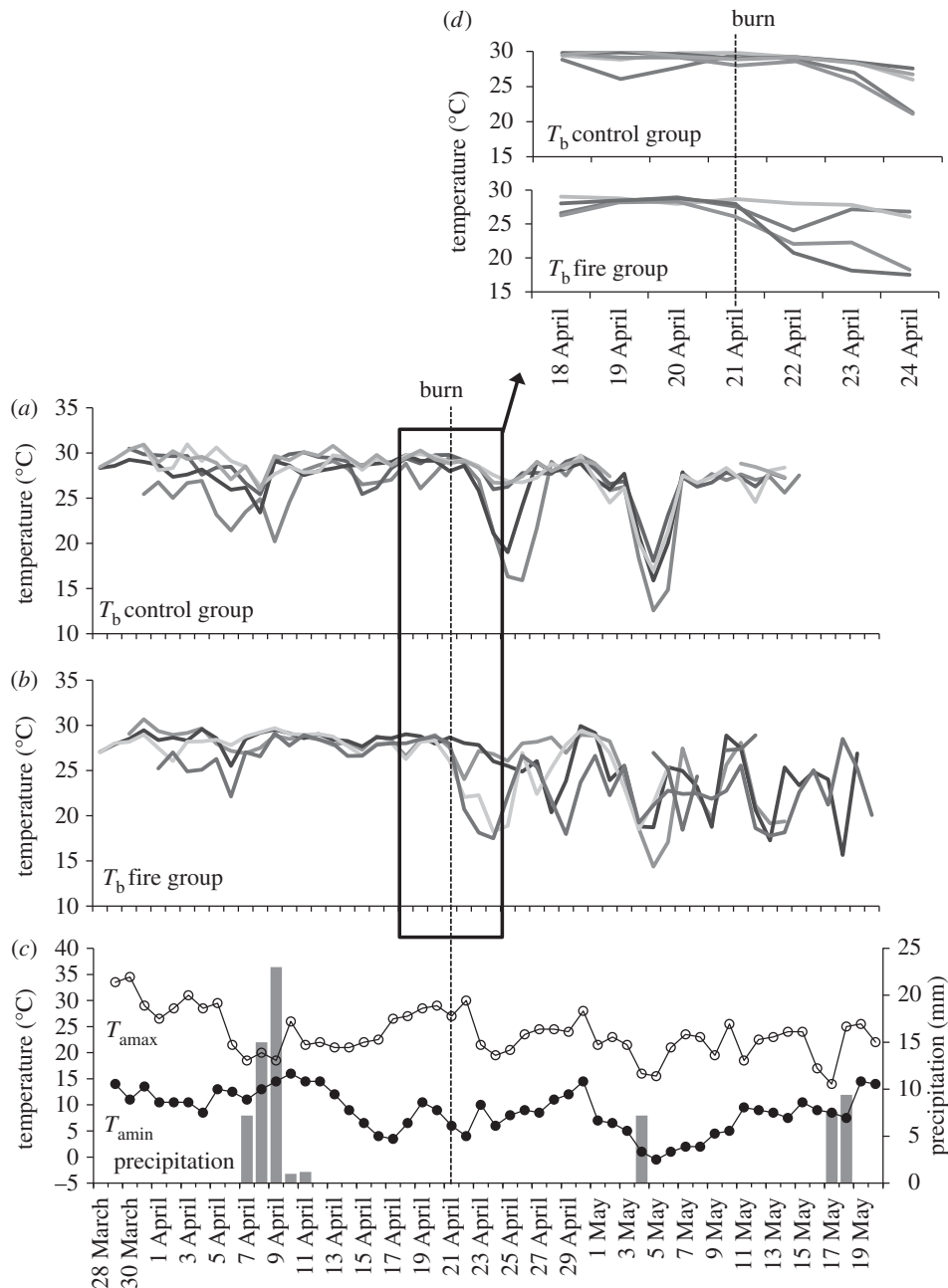


Figure 3. Mean body temperatures (T_b) before and after the burn for (a) the control echidnas ($n = 5$) and (b) the fire animals ($n = 5$; individual that died in the fire not shown; individual that spent only six days in the burn area depicted) in relation to (c) ambient conditions (maximum ambient temperature, T_{amax} ; minimum ambient temperature, T_{amin} ; precipitation, grey bars). The inset (d) shows the T_b traces for the 3 days before and after the fire. Note that the fire-affected animals entered torpor sooner after the burn than the control animals, and there was greater inter-individual T_b variation for fire-affected echidnas after the burn.

did not change patterns of torpor use in the same way as the fire-affected echidnas.

In addition to explaining how this successful and widely distributed species may withstand periodic environmental disturbance, our findings add more general support to the hypothesis that the ability to enter torpor was crucial in allowing ancestral mammals to survive the aftermath of the catastrophic meteorite impact at the K–Pg boundary [3]. Reduced light levels and reoccurring fires continued for a year or more and must have affected animal survival for a long period [25]. Although the torpor bouts observed in our study only lasted a few days, previous studies have shown that echidnas can hibernate for months (seven months hibernation with bouts of less than or equal to three weeks) [10]. Furthermore, some mammals, such as eastern pygmy-

possums (*Cercartetus nanus*) can hibernate up to 12 months under laboratory conditions [26] and edible dormice (*Glis glis*) more than 10 months in the wild [27]. Therefore, opportunistic long-term hibernation would probably have enabled heterothermic ancestral mammals to outlast the effects of the meteoroid for months.

Torpor during natural disasters has previously been reported for sugar gliders (*Petaurus breviceps*), which remained inactive during a cyclone and used torpor to compensate for lost foraging opportunities during heavy rainfall and strong winds [6]. Although torpor can increase an animal's probability of survival by allowing it to remain hidden and inactive in its hibernaculum or shelter, it can also be detrimental under certain circumstances owing to reduced reaction times and locomotory performance at low T_b [28]. One echidna, known to be torpid at

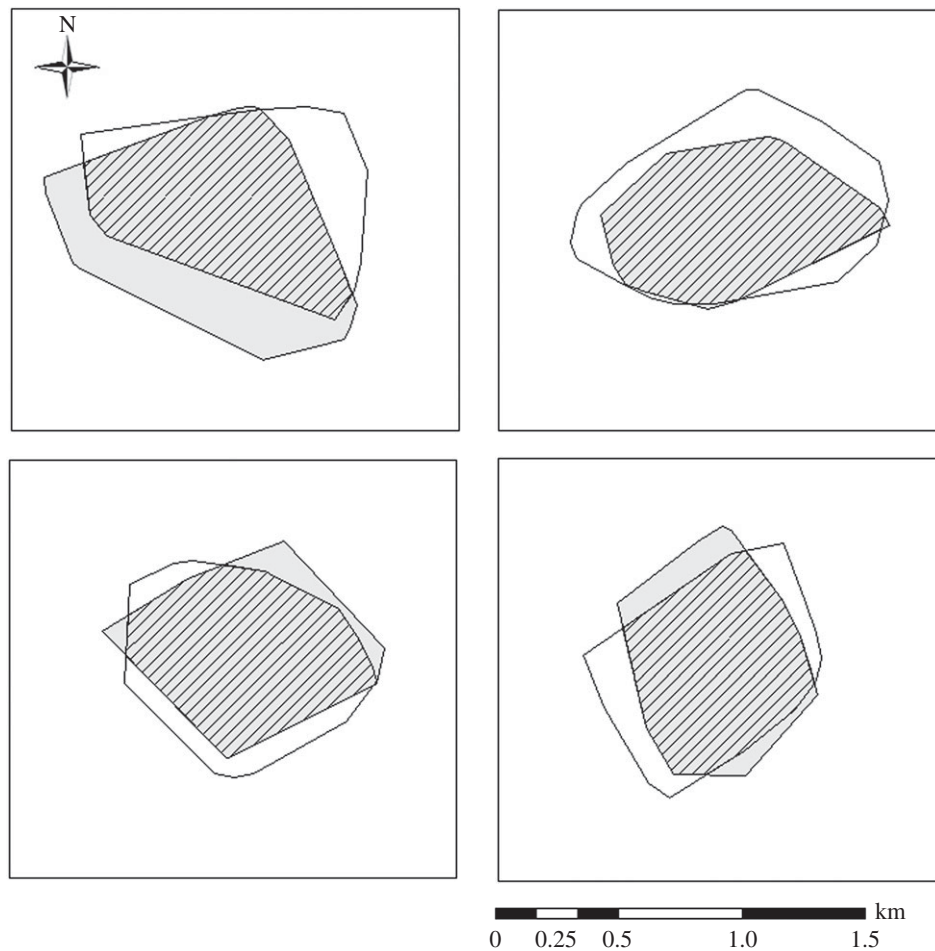


Figure 4. Comparison of home ranges for individuals of the fire group before (unfilled polygon) and after the fire (grey polygon). Home ranges were calculated as MCPs; overlap areas are indicated as dashed areas.

Table 2. Total duration of multiday torpor (h) for both fire and control animals before and after the fire. (One individual was only observed resting in the fire area after the burn ($N = 6$) and was considered a control animal during all other days of observation. The duration of multiday torpor was significantly increased in the post-fire group in comparison to the pre-fire and control groups (ANOVA; $F_{3,7} = 37.65$, $p < 0.001$; post hoc test results indicated by different letters.)

	total duration of multiday torpor (h)	
	pre-fire	post-fire
<i>burn area</i>		
no. 1	0	220.5
no. 2	43.5	422
no. 3	0	217.5
no. 4	0	288.5
no. 5	—	43.5
	10.9 ± 21.7^a	238.4 ± 136.9^b
<i>control area</i>		
no. 1	0	64
no. 2	129	138
no. 3	60	142.5
no. 4	0	68
no. 5	0	0
	37.8 ± 57.2^a	82.5 ± 59.2^a

the time of the fire, died in the burn when the log it was sheltering in caught fire. However, it is unlikely that it was unable to respond quickly enough to the fire owing to a low T_b of 23.1°C, because echidnas were observed to move with similar low T_b s of around 23°C in this and other studies ([29] and J. Nowack 2015, personal observation), and another individual with the same minimum T_b was able to flee from the same log. Furthermore, it has been shown experimentally that animals terminate torpor bouts when exposed to smoke [30]. In comparison with logs, seeking refuge in deep underground burrows at the time of a fire would probably allow survival even during severe fires that destroy all ground cover. Although echidnas are considered to be sensitive to heat stress, and burrow temperature will increase during a high impact wildfire, echidnas can tolerate temperatures of 35–40°C in shelters for up to 10 h [31].

Echidnas not only reduced activity immediately after the burn, but they also reduced activity and T_b for at least three weeks after the fire. Interestingly, the post-fire group had a higher variance in mean T_b than the other groups, in which individuals used multiday torpor synchronously in response to ambient conditions. This indicates that post-fire individuals adjusted T_b flexibly, presumably in response to varying resource disturbance resulting from the patchy burn, and not just as a reaction to T_a or rainfall (as observed for the control echidnas). This individual plasticity in thermoregulatory response presumably allows individual echidnas to match energy use to resource availability at fine spatial and temporal scales, and is probably an important aspect of the species' ability to persist in varied and changing landscapes.

The small marsupial antechinus, *Antechinus stuartii* (approx. 20 g), uses shallow daily torpor and reduces activity after fires to compensate for reduced food availability and to cope with increased exposure to predators owing to reduction in ground cover [7]. For the rather large (approx. 4 kg) and heavily armoured echidna reduced activity for predator avoidance seems less likely [19]. However, reduced food availability, presence of smoke and environmental changes such as a reduction in vegetation or availability of shelter could all have contributed to the observed post-fire changes in thermoregulation and activity. We hypothesize that changes in food availability are the most likely to impact on this species. Although the fire destroyed logs that were used as shelters, echidnas were able to find alternate nesting sites when their pre-fire shelters had burnt. Furthermore, there was little undergrowth in the study site before the fire, so changes in sun exposure of echidnas during diurnal activity are unlikely. Smoke might act as a cue for fire avoidance strategies, but avoidance of smoke *per se*, especially low to the ground, is not a likely reason for the observed changes, especially several weeks after the fire. Therefore, we hypothesize that the observed medium-term reduction in T_b and activity was to a large extent a response to reduced food availability. Echidnas mainly feed on ants and termites [19] and previous studies on the effect of fire on arthropods suggest that the abundance of subterranean ants and termites would not have been severely reduced by the burn [32]. However, the fire destroyed woody debris and leaf litter containing termites, ants and other small arthropods and subterranean arthropods might have moved deeper into cooler soil, resulting in a relatively increased foraging effort in comparison with the control group.

Echidnas have many characteristics of ancestral mammals, and their low metabolic rate and ability to enter torpor are viewed as crucial traits for the species' success. The ability to

stay hidden and sheltered during wildfires is not only a trait that most likely allowed early mammals to survive beyond the K–Pg extinction event and to withstand seasonal wildfires in the past, but will also facilitate species' survival during current and future natural disasters. Increased habitat fragmentation and destruction, global warming and other human activities have caused an increase in the frequency and intensity of natural disasters, particularly wild fires. Fires are now recognized as a major disturbance affecting many parts of the world, and a further increase in the frequency and severity of wildfires is anticipated for the future [33], highlighting the importance of predicting responses of animals to fire and other natural disasters.

Ethics. All experiments were performed according to the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, and were approved by the Curtin University and UNE animal ethics committees. The study was carried out under Regulation 17 and Regulation 4 licences from the West Australian Department of Parks and Wildlife (SF010202 and CE004766).

Data accessibility. Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rf8th>.

Author contributions. All authors designed and planned the study; J.N. and C.E.C. conducted the fieldwork; J.N. analysed the data and wrote the manuscript. C.E.C. and F.G. edited the manuscript and provided logistical support.

Competing interests. We have no competing interests.

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References

- Morgan J, Artemieva N, Goldin T. 2013 Revisiting wildfires at the K–Pg boundary. *J. Geophys. Res.* **118**, 1508–1520. (doi:10.1002/2013jg002428)
- O'Leary MA *et al.* 2013 The placental mammal ancestor and the post-K–Pg radiation of placentals. *Science* **339**, 662–667. (doi:10.1126/science.1229237)
- Lovegrove BG, Lobban KD, Levesque DL. 2014 Mammal survival at the Cretaceous–Palaeogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs. *Proc. R. Soc. B* **281**, 20141304. (doi:10.1098/rspb.2014.1304)
- Turbill C, Bieber C, Ruf T. 2011 Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc. R. Soc. B* **278**, 3355–3363. (doi:10.1098/rspb.2011.0190)
- Nowack J, Dausmann KH. 2015 Can heterothermy facilitate the colonization of new habitats? *Mammal Rev.* **45**, 117–127. (doi:10.1111/mam.12037)
- Nowack J, Rojas AD, Körtner G, Geiser F. 2015 Snoozing through the storm: torpor use during a natural disaster. *Sci. Rep.* **5**, 11243. (doi:10.1038/srep11243)
- Stawski C, Körtner G, Nowack J, Geiser F. 2015 The importance of mammalian torpor for survival in a post-fire landscape. *Biol. Lett.* **11**, 20150134. (doi:10.1098/rsbl.2015.0134)
- Geiser F, Brigham RM. 2012 The other functions of torpor. In *Living in a seasonal world* (eds T Ruf, C Bieber, W Arnold, E Milesi), pp. 109–121. Berlin, Heidelberg, Germany: Springer.
- Geiser F, Turbill C. 2009 Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* **96**, 1235–1240. (doi:10.1007/s00114-009-0583-0)
- Grigg G, Beard L, Augee M. 2004 The evolution of endothermy and its diversity in mammals and birds. *Physiol. Biochem. Zool.* **77**, 982–997. (doi:10.1086/425188)
- Blanco MB, Dausmann KH, Ranaivoarisoa JF, Yoder AD. 2013 Underground hibernation in a primate. *Sci. Rep.* **3**, 1768. (doi:10.1038/srep01768)
- Arnold W, Heldmaier G, Ortman S, Pohl H, Ruf T, Steinlechner S. 1991 Ambient temperatures in hibernacula and their energetic consequences for alpine marmots *Marmota marmota*. *J. Therm. Biol.* **16**, 223–226. (doi:10.1016/0306-4565(91)90029-2)
- Roberts J. 1995 *Echidna: the survivor*. Melbourne, Australia: Piper Films Pty Ltd.
- Stawski C, Körtner G, Geiser F. 2014 Specialist survey report: Warrumbungle National Park post-fire fauna survey. New South Wales National Parks and Wildlife Service, Australia.
- Belov K, Hellman L, Cooper DW. 2002 Characterisation of echidna IgM provides insights into the time of divergence of extant mammals. *Dev. Comp. Immunol.* **26**, 831–839. (doi:10.1016/S0145-305X(02)00030-7)
- Nicol SC, Andersen NA. 1996 Hibernation in the echidna: not an adaptation to cold? In *Adaptations to the cold: Tenth International Hibernation Symposium* (eds F Geiser, AJ Hulbert, SC Nicol), pp. 7–12. Armidale, Australia: University of New England Press.
- Geiser F. 2004 Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239–274. (doi:10.1146/annurev.physiol.66.032102.115105)
- Ruf T, Geiser F. 2015 Daily torpor and hibernation in birds and mammals. *Biol. Rev.* **90**, 891–926. (doi:10.1111/brv.12137)
- Nicol S, Andersen NA. 2007 The life history of an egg-laying mammal, the echidna (*Tachyglossus aculeatus*). *Ecoscience* **14**, 275–285. (doi:10.2980/1195-6860(2007)14275:tlhoae]2.0.co;2)

20. Abensperg-Traun M. 1991 Survival strategies of the echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae). *Biol. Conserv.* **58**, 317–328. (doi:10.1016/0006-3207(91)90098-T)
21. Forin-Wiart M-A, Hubert P, Sirguy P, Poulle M-L. 2015 Performance and accuracy of lightweight and low-cost GPS data loggers according to antenna positions, fix intervals, habitats and animal movements. *PLoS ONE* **10**, e0129271. (doi:10.1371/journal.pone.0129271)
22. R Development Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
23. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2016 Linear and nonlinear mixed effects models. R package version 3.1-126. See <http://cran.r-project.org/package=nlme>.
24. Hothorn T, Bretz F, Westfall P. 2008 Simultaneous inference in general parametric models. *Biometr. J.* **50**, 346–363. (doi:10.1002/bimj.200810425)
25. Robertson DS, McKenna MC, Toon OB, Hope S, Lillegraven JA. 2004 Survival in the first hours of the Cenozoic. *Geol. Soc. Am. Bull.* **116**, 760–768. (doi:10.1130/b25402.1)
26. Geiser F. 2007 Yearlong hibernation in a marsupial mammal. *Naturwissenschaften* **94**, 941–944. (doi:10.1007/s00114-007-0274-7)
27. Bieber C, Ruf T. 2009 Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* **96**, 165–171. (doi:10.1007/s00114-008-0471-z)
28. Rojas AD, Körtner G, Geiser F. 2012 Cool running: locomotor performance at low body temperature in mammals. *Biol. Lett.* **8**, 868–870. (doi:10.1098/rsbl.2012.0269)
29. Brice PH, Grigg GC, Beard LA, Donovan JA. 2002 Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Aust. J. Zool.* **50**, 461–475. (doi:10.1071/Z001080)
30. Stawski C, Matthews JK, Körtner G, Geiser F. 2015 Physiological and behavioural responses of a small heterothermic mammal to fire stimuli. *Physiol. Behav.* **151**, 617–622. (doi:10.1016/j.physbeh.2015.09.002)
31. Brice PH, Grigg GC, Beard LA, Donovan JA. 2002 Heat tolerance of short-beaked echidnas (*Tachyglossus aculeatus*) in the field. *J. Therm. Biol.* **27**, 449–457. (doi:10.1016/S0306-4565(02)00015-3)
32. Coleman TW, Rieske LK. 2006 Arthropod response to prescription burning at the soil–litter interface in oak–pine forests. *Forest Ecol. Manage.* **233**, 52–60. (doi:10.1016/j.foreco.2006.06.001)
33. Moritz MA, Parisien M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K. 2012 Climate change and disruptions to global fire activity. *Ecosphere* **3**, 49. (doi:10.1890/es11-00345.1)