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**Nowack, J, Cooper, CE and Geiser, F (2016) Cool echidnas survive the fire. Proceedings of the Royal Society B: Biological Sciences, 283 (1828). ISSN 0962-8452**

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1 **Cool echidnas survive the fire**

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9

10 **Abstract**

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

25

26

## 27 Introduction

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

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

52 Divergence of monotreme and therian mammals is estimated to have occurred at least 170  
53 million years ago [15] and the short-beaked echidna is often considered a 'living fossil' with many  
54 characteristics of ancestral mammals [10]. Although the species is now limited to the Australian  
55 continent and New Guinea, it has one of the widest geographical ranges of any native Australian  
56 mammal and occurs almost anywhere from deserts to wet forests to alpine regions [16]. Short-  
57 beaked echidnas are amongst the largest known deep hibernators [17] and can hibernate from a few  
58 days in warmer habitats to up to several months in colder habitats, with torpor bouts of 1-3 weeks  
59 interrupted by short bouts of normothermia [16, 18]. The wide geographical distribution and the  
60 long life expectancy (up to 45y) of this species [19] are generally attributed to their low metabolic

61 rate and ability to use torpor to further reduce energy expenditure [10, 19]. The hypothesis that the  
62 use of torpor may also have allowed the species to outlast fires [20] therefore seems highly  
63 plausible. To evaluate this hypothesis, we examined the activity and  $T_b$  fluctuations of free-ranging  
64 short-beaked echidnas, before, during and after a prescribed burn. We predicted that echidnas  
65 would be able to survive the fire by taking shelter in caves, underground burrows or large hollow  
66 logs, and that their response to the post-fire impact on their habitat would be an increased depth  
67 and frequency of torpor, and a reduced overall activity compared to echidnas in unburnt areas of  
68 similar habitat.

## 69 **Material and Methods**

### 70 *Study site and prescribed fire*

71 On 21 April 2015 a prescribed burn was conducted at Dryandra Woodland, southeast of Perth,  
72 Western Australia, (31°460S 117°10E) by the Department of Parks and Wildlife. The prescribed burn  
73 area was 227 hectares, confined by dirt roads and tracks. The unburned woodland beyond these  
74 tracks encompassed our control site, with the home ranges of control echidnas being up to 3.2 km  
75 away from the burn area. We included a control group in the study design that was monitored  
76 concurrently with the fire-affected group and experienced the same ambient weather conditions to  
77 exclude temporal effects (such as seasonal changes in torpor use and activity) from the effect of fire.  
78 We studied ten echidnas for 21 to 25 days before the fire (active burning: 21<sup>st</sup> April, 1100-1500 h)  
79 and for 18 to 31 days after the fire. Echidnas were classified as control (n=5) and fire group (n=5)  
80 depending on the location of their home-ranges. One individual had a home range that included  
81 both fire-affected and unburnt areas, so the data for this individual were classified as belonging to  
82 the fire group when it inhabited the burn area or to the control group when it inhabited the control  
83 area. The fire produced large amounts of smoke and since there was little groundcover it mainly  
84 affected bushes, logs and trees, causing trees to collapse and leading to the presence of burning logs  
85 for weeks after the fire (Fig. 1); smoking trees were observed until the end of our study, 31 days  
86 after the burn.

### 87 *Procedures*

88 Echidnas were captured by hand and ten individuals were implanted with temperature data loggers  
89 ( $\pm 0.5^\circ\text{C}$ , logging interval: 15min, ~3g, iButton thermochron DS1922L, Maxim Integrated Products,  
90 Inc., Sunnyvale, California, USA) into the intraperitoneal cavity. Loggers were calibrated in a water  
91 bath (5-45°C; increments of 5°C) to the nearest 0.1°C and coated with a wax-polymer compound  
92 (Elvax, Du-point, Johannesburg, South Africa) before implantation via a small abdominal incision  
93 under oxygen/isoflurane anaesthesia (3-4% induction, 2-3% maintenance). The loggers were

94 tethered to the abdominal muscle with silk suture (to facilitate removal at the end of the study),  
95 before the skin and muscle layer were sutured separately using dissolvable suture. Analgesia was  
96 provided via a single sub-cutaneous dose of Meloxicam ( $0.2\text{mg kg}^{-1}$ ; Boehringer Ingelheim, North  
97 Ryde, Australia).

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

#### 107 *Ambient conditions*

108 Ambient temperature ( $T_a$ ) was measured hourly at the control and burn site using temperature data  
109 loggers placed in the shade ( $\pm 0.5^\circ\text{C}$ , iButton thermochron DS1921G). Precipitation data were  
110 obtained from the Bureau of Meteorology for the nearest ( $\sim 7\text{km}$ ) weather station (Caernarvon Park;  
111  $32.74^\circ\text{S}$   $116.84^\circ\text{E}$ ). The  $T_{a\text{s}}$  for the control and fire area were strongly correlated (regression  
112 analyses;  $r^2=0.945$ ,  $F_{1,1156}= 20020$ ,  $p<0.0001$ ;  $T_{a(\text{control})}= T_{a(\text{fire})}*1.26 + 0.896$ ). Daily  $T_a$  ranged from  
113 a minimum of  $-0.5^\circ\text{C}$  to a maximum of  $34.5^\circ\text{C}$  (Tab. 1). During the study period a total of 71.6mm of  
114 rainfall was recorded on eight days.

#### 115 *Torpor use and activity*

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

120 Accuracy of the GPS units used in our study was determined by comparing the recorded  
121 locations for the loggers plotted on Google Earth with the known path of travel along a road. The  
122 measured accuracy of loggers was approximately 55m when stationary, and 20m when moving and  
123 therefore comparable to GPS collars used on wildlife [21]. We used the GPS loggers to identify  
124 directional long distance movements of animals and discarded all GPS data without clear directional  
125 movement, i.e. data points around rest shelters, as these points are likely to occur when animals  
126 were resting in tree logs, although they may potentially include foraging or basking around the  
127 shelter. We obtained the starting point and the end point of activity, as well as the location of

128 shelter sites. Daily foraging areas, as well as overall home ranges (minimum convex polygon; MCP)  
129 were calculated by using a custom-written Java-script programme (Java script version 6; G. Körtner).  
130 Overlap of individual's home ranges before and after the burn were analysed with ArcGIS 10 (ESRI).

### 131 *Statistical analyses*

132 Data are presented as mean  $\pm 1$  standard deviation;  $n$  denotes the number of individuals,  $N$  the  
133 number of observations. Statistical analyses were conducted using R, version 3.1.0 [22]. The  
134 individual that died in the fire was not included into statistical analyses due to fire-related loss of  
135 most data. The difference in activity between the fire and control animals during the night following  
136 the burn was analysed with a t-test after testing for normality and homogeneity of variance using  
137 Shapiro-Wilk test and Bartlett's test, respectively. The relationship between  $T_b$  and ambient  
138 conditions (minimum  $T_a$  and rainfall) was determined with a linear mixed effect model using  
139 'individual' as a random factor to account for repeated measures, followed by an ANOVA (*lme* in  
140 library 'nlme' [23]). The same approach was used to examine mean  $T_b$  differences between the  
141 groups (pre-fire, post-fire, pre-control, post-control) as well as to test for differences in the use of  
142 multiday-torpor (>24 hours), activity (min/day; including inactive days), duration of activity  
143 (min/day; excluding inactive days), daily foraging area (MCPs) and home ranges (MCPs). For the  
144 analysis of multiday torpor use we calculated the hours spent in multiday-torpor as a percentage of  
145 the total hours of  $T_b$  recording for each individual and then analysed arcsine transformed data. To  
146 examine differences in the variance of mean daily  $T_b$  between treatments of the groups we  
147 calculated a linear mixed effects model followed by an ANOVA, using 'day' as a random effect to  
148 account for repeated measure. Post-hoc analyses were performed as Tukey tests (*glht* in library  
149 'multcomp' [24]).

## 150 **Results**

### 151 *Direct impacts of the fire*

152 Four of five echidnas at the fire site survived the burn. Three of the five tagged individuals were  
153 located in areas that actually burnt during the fire, while two individuals were sheltering within  
154 <200m of the fire and only parts of their home ranges were affected by the burn. With the exception  
155 of one normothermic individual in the burn area that had a  $T_b$  of 28.6°C, all echidnas (in burn and  
156 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  
157 was resting inside a log that caught fire and did not reach a normothermic  $T_b$  before it died (the  
158 echidna's iButton was retrieved after the fire; minimum  $T_b$  for that day: 23.1°C, maximum  $T_b$ : 26.6°C).  
159 A second individual resting in the same log aroused from torpor and left the log during the fire,  
160 escaping to a shelter about 160m away. Two additional untagged echidnas that were not part of this  
161 study were also found dead in remnants of burnt logs after the fire.

162 Daily activity was strongly affected by the fire. Mean activity during the night immediately  
163 following the fire was significantly reduced for the post-fire group (mean activity  $179 \pm 125$ min;  
164 range from 0 to 283min;  $n=4$ ) in comparison to the control group (mean activity  $474 \pm 38$ min; range  
165 412 to 513min;  $n=5$ ; t-test:  $t=4.53$ ,  $df=3.45$   $p=0.015$ ). All post-fire individuals remained inactive  
166 during the day(s) following the fire and three of the four individuals entered multiday torpor ranging  
167 from 51h to 123h (example in Fig.2). The fourth individual only entered short torpor bouts  
168 (interspersed with normothermic  $T_b$ s  $>27^\circ\text{C}$  for 18h) but was inactive for 51h after the fire. Control  
169 individuals remained active and none entered multiday torpor immediately after the burn (earliest  
170 multiday torpor bout  $\sim 2$  days after the fire; Fig.3).

### 171 *Post-fire adaptations*

172 Echidnas entered short bouts of torpor almost every day during our study, with a minimum  $T_b$  of  
173  $11.6^\circ\text{C}$  (Fig.2); minimum  $T_b$  was positively related to a combination of minimum  $T_a$  and rainfall  
174 (ANOVA:  $F_{1,412}=4.96$ ,  $p=0.0265$ ). Mean  $T_b$ s of echidnas were also significantly influenced by the fire  
175 (ANOVA:  $F_{1,391}=48.74$ ,  $p<0.001$ ; Tab.1). Despite a temperature-dependent decrease in  $T_b$  for all  
176 individuals (both:  $z\geq 5.31$ ,  $p<0.001$ ), mean  $T_b$ s of echidnas were significantly lower for the post-fire  
177 group than the control group ( $z=10.44$ ,  $p<0.001$ ), and the pre-fire group ( $z=3.39$ ,  $p=0.003$ ).  
178 Additionally, variance of mean  $T_b$  was much higher for individuals of the post-fire group (ANOVA:  
179  $F_{3,45}=8.49$ ,  $p<0.001$ ) than for the control ( $z=2.94$ ,  $p=0.017$ ) or pre-fire animals ( $z=4.86$ ,  $p<0.001$ ).

180 The fire also influenced activity of echidnas (ANOVA:  $F_{3,293}=16.59$ ,  $p<0.0001$ ; Tab. 2). Post-  
181 fire individuals were significantly less active and spent more hours in multiday torpor than  
182 individuals of control ( $z=3.61$ ,  $p=0.002$ ) or pre-fire groups ( $z=5.70$ ,  $p<0.001$ ). This difference was  
183 apparent despite a higher occurrence of multiday torpor in the control group before the fire (Tab.2).  
184 The use of multiday torpor was increased in the post-fire group compared to the control group, as  
185 well as in comparison to the pre-fire group (ANOVA:  $F_{3,7}=37.65$ ,  $p=0.001$ ; post-hoc results:  $z\geq 4.87$ ,  
186  $p<0.001$  for all combinations). The duration of activity on active days was always longer for the  
187 control (mean:  $458 \pm 182$ min,  $N=128$ ) than for the fire group (mean:  $359 \pm 164$ min,  $N=107$ ; ANOVA:  
188  $F_{1,223}=9.55$ ,  $p<0.001$ ; before:  $z=3.67$ ,  $p=0.0013$ ; after:  $z=2.86$ ,  $p=0.022$ ). Although overall activity of  
189 the fire animals was further reduced after the burn due to more phases of inactivity (fire group: 3-7  
190 bouts of multiday torpor; control group: 1-2 bouts), the duration of activity on active days did not  
191 differ for echidnas before and after the fire for neither the control nor the fire animals (both:  $z\geq 2.00$ ,  
192  $p>0.08$ ).

193 The two echidnas with territories completely burnt ( $n=2$ ) increased their average daily  
194 foraging areas after the fire ( $8.0 \pm 5.3$ ha,  $N=14$  vs.  $16.9 \pm 9.6$ ha,  $N=5$  and  $7.4 \pm 6.0$ ha,  $N=19$  vs.  $10.0 \pm$   
195  $10.2$ ha,  $N=7$ ), presumably as a result of destroyed shelter sites and impact on foraging areas.

196 However, overall there was no significant difference in daily foraging areas between the fire and the  
197 control group after the fire ( $z=0.18$ ;  $p=0.9980$ ). Interestingly, whereas the daily foraging areas of the  
198 control group decreased over the time of the study from  $11.0 \pm 2.9\text{ha}$  ( $N=71$ ) to  $8.7 \pm 1.1\text{ha}$  ( $N=59$ ;  
199  $z=2.68$ ,  $p=0.037$ ; ANOVA:  $F_{3,224}=3.39$   $p=0.019$ ), the daily foraging areas of the fire groups remained  
200 constant ( $8.7 \pm 2.1\text{ha}$ ,  $N=71$  vs  $8.9 \pm 4.9\text{ha}$ ,  $N=36$ ;  $z=0.44$ ,  $p=0.9716$ ).

201 Habitat use of the post-fire individuals was not notably affected by the fire (fire animals:  
202  $55.2 \pm 6.7\text{ha}$ ,  $N=75$ ,  $n=4$  vs.  $51.0 \pm 10.6\text{ha}$ ,  $N=47$ ,  $n=4$ ; control animals:  $61.2 \pm 28.9\text{ha}$   $N=71$ ,  $n=5$  vs.  
203  $39.9 \pm 17.6\text{ha}$   $N=60$ ,  $n=5$ ; ANOVA:  $F_{3,6}=2.81$ ,  $p=0.1305$ ) and no individual left its territory (Fig.4).  
204 Although echidnas were mostly found in unburned patches between the burned areas, we observed  
205 three of the four surviving tagged echidnas of the fire group in heavily burnt patches. We also  
206 observed a change of shelter sites for the post-fire group to new, unburnt shelters, presumably due  
207 to the destruction of logs that were the main shelters used by echidnas in the burn area (eight of 14  
208 known shelter logs were damaged or destroyed by the fire).

## 209 Discussion

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

220 In addition to explaining how this successful and widely-distributed species may withstand  
221 periodic environmental disturbance, our findings add more general support to the hypothesis that  
222 the ability to enter torpor was crucial in allowing ancestral mammals to survive the aftermath of the  
223 catastrophic meteorite impact at the K-Pg boundary [3]. Reduced light levels and reoccurring fires  
224 continued for a year or more and must have affected animal survival for a long period [25]. Although  
225 the torpor bouts observed in our study only lasted a few days, previous studies have shown that  
226 echidnas can hibernate for months (7-months hibernation with bouts of  $\leq 3$  weeks) [10].  
227 Furthermore, some mammals, such as eastern pygmy-possums (*Cercartetus nanus*) can hibernate up  
228 to 12 months under laboratory conditions [26] and edible dormice (*Glis glis*) more than 10 months in



229 the wild [27]. Therefore, opportunistic long-term hibernation would likely have enabled  
230 heterothermic ancestral mammals to outlast the effects of the meteoroid for months.

231 Torpor during natural disasters has previously been reported for sugar gliders (*Petaurus*  
232 *breviceps*), which remained inactive during a cyclone and used torpor to compensate for lost  
233 foraging opportunities during heavy rainfall and strong winds [6]. Although torpor can increase an  
234 animal's probability of survival by allowing it to remain hidden and inactive in its hibernaculum or  
235 shelter, it can also be detrimental under certain circumstances due to reduced reaction times and  
236 locomotory performance at low  $T_b$  [28]. One echidna, known to be torpid at the time of the fire, died  
237 in the burn when the log it was sheltering in caught fire. However, it is unlikely that it was unable to  
238 respond quickly enough to the fire due to a low  $T_b$  of 23.1°C, since echidnas were observed to move  
239 with similar low  $T_b$ s of around 23°C in this and other studies [29 and pers. observation JN], and  
240 another individual with the same minimum  $T_b$  was able to flee from the same log. Furthermore, it  
241 has been shown experimentally that animals terminate torpor bouts when exposed to smoke [30]. In  
242 comparison to logs, seeking refuge in deep underground burrows at the time of a fire would likely  
243 allow survival even during severe fires that destroy all ground cover. Although echidnas are  
244 considered to be sensitive to heat stress, and burrow temperature will increase during a high impact  
245 wildfire, echidnas can tolerate temperatures of 35-40°C in shelters for up to 10 hours [31].

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

255 The small marsupial antechinus, *Antechinus stuartii* (~20g), uses shallow daily torpor and  
256 reduces activity after fires to compensate for reduced food availability and to cope with increased  
257 exposure to predators due to reduction in ground cover [7]. For the rather large (~4kg) and heavily  
258 armoured echidna reduced activity for predator avoidance seems less likely [19]. However, reduced  
259 food availability, presence of smoke, and environmental changes such as a reduction in vegetation  
260 or availability of shelter could all have contributed to the observed post-fire changes in  
261 thermoregulation and activity. We hypothesise that changes in food availability are the most likely  
262 to impact on this species. Although the fire destroyed logs that were used as shelters, echidnas were

263 able to find alternate nesting sites when their pre-fire shelters had burnt. Furthermore, there was  
264 little undergrowth in the study site before the fire, so changes in sun exposure of echidnas during  
265 diurnal activity are unlikely. Smoke might act as a cue for fire avoidance strategies, but avoidance of  
266 smoke *per se*, especially low to the ground, is not a likely reason for the observed changes, especially  
267 several weeks after the fire. Therefore, we hypothesise that the observed medium-term reduction in  
268  $T_b$  and activity was to a large extent a response to reduced food availability. Echidnas mainly feed on  
269 ants and termites [19] and previous studies on the effect of fire on arthropods suggest that the  
270 abundance of subterranean ants and termites would not have been severely reduced by the burn  
271 [32]. However, the fire destroyed woody debris and leaf litter containing termites, ants and other  
272 small arthropods and subterranean arthropods might have moved deeper into cooler soil, resulting  
273 in a relatively increased foraging effort in comparison to the control group.

274 Echidnas have many characteristics of ancestral mammals, and their low metabolic rate and  
275 ability to enter torpor are viewed as crucial traits for the species' success. The ability to stay hidden  
276 and sheltered during wildfires is not only a trait that most likely allowed early mammals to survive  
277 beyond the K-Pg extinction event and to withstand seasonal wildfires in the past, but will also  
278 facilitate species' survival during current and future natural disasters. Increased habitat  
279 fragmentation and destruction, global warming and other human activities have caused an increase  
280 in the frequency and intensity of natural disasters, particularly wild fires. Fires are now recognised as  
281 a major disturbance affecting many parts of the world, and a further increase in the frequency and  
282 severity of wildfires is anticipated for the future [33], highlighting the importance of predicting  
283 responses of animals to fire and other natural disasters.

#### 284 **Ethics Statement**

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

#### 289 **Data accessibility**

290 Data available from the Dryad Digital Repository: doi:10.5061/dryad.rf8th

#### 291 **Competing interests**

292 We have no competing interests.

#### 293 **Funding Statement**

294 The project was financially supported by grants from the DAAD and the A.F.W. Schimper Stiftung to  
295 JN, by the Australian Research Council and the UNE to FG and Curtin University and a UWA-UQ  
296 Bilateral Research Collaboration Award to CEC.

297 **Author contributions**

298 All authors designed and planned the study; JN and CEC conducted the fieldwork; JN analysed the  
299 data and wrote the manuscript. CEC and FG edited the manuscript and provided logistical support.

300 **Acknowledgements**

301 We thank the staff of the Western Australian Department of Parks and Wildlife, particularly Mitchell  
302 Davis, for supporting the project and Arne Müller, Phil Withers, Bill Bateman, Lauren Gilson, John  
303 Lawson, Lisa Richards, Gerhard Körtner, Charles Lacoste and Stewart Nicol for their help during the  
304 study.

## Literature

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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 ( $r^2=0.3365$ ,  $F_{1,445}=227.2$ ,  $p<0.001$ ) 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 <sup>a</sup> , n=4 | 24.1 ± 1.3 <sup>b</sup> , n=5 | 28.2 ± 1.3 <sup>a</sup> n=5 | 25.6 ± 1.4 <sup>c</sup> , n=5 |

Table 2: Total duration of multiday torpor (hours) 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 (hours) |                                  |
|---------------------|---|----------------------------------|
|                     | Pre-fire                                  | Post-fire                        |
| <b>Burn area</b>    |   |                                  |
| #1                  | 0   | 220.5                            |
| #2                  | 43.5                                      | 422                              |
| #3                  | 0   | 217.5                            |
| #4                  | 0   | 288.5                            |
| #5                  | -   | 43.5                             |
|                     | <b>10.9 ± 21.7<sup>a</sup></b>            | <b>238.4 ± 136.9<sup>b</sup></b> |
| <b>Control area</b> |   |                                  |
| #1                  | 0   | 64                               |
| #2                  | 129                                       | 138                              |
| #3                  | 60  | 142.5                            |
| #4                  | 0   | 68                               |
| #5                  | 0   | 0                                |
|                     | <b>37.8 ± 57.2<sup>a</sup></b>            | <b>82.5 ± 59.2<sup>a</sup></b>   |

## Figure legends

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

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

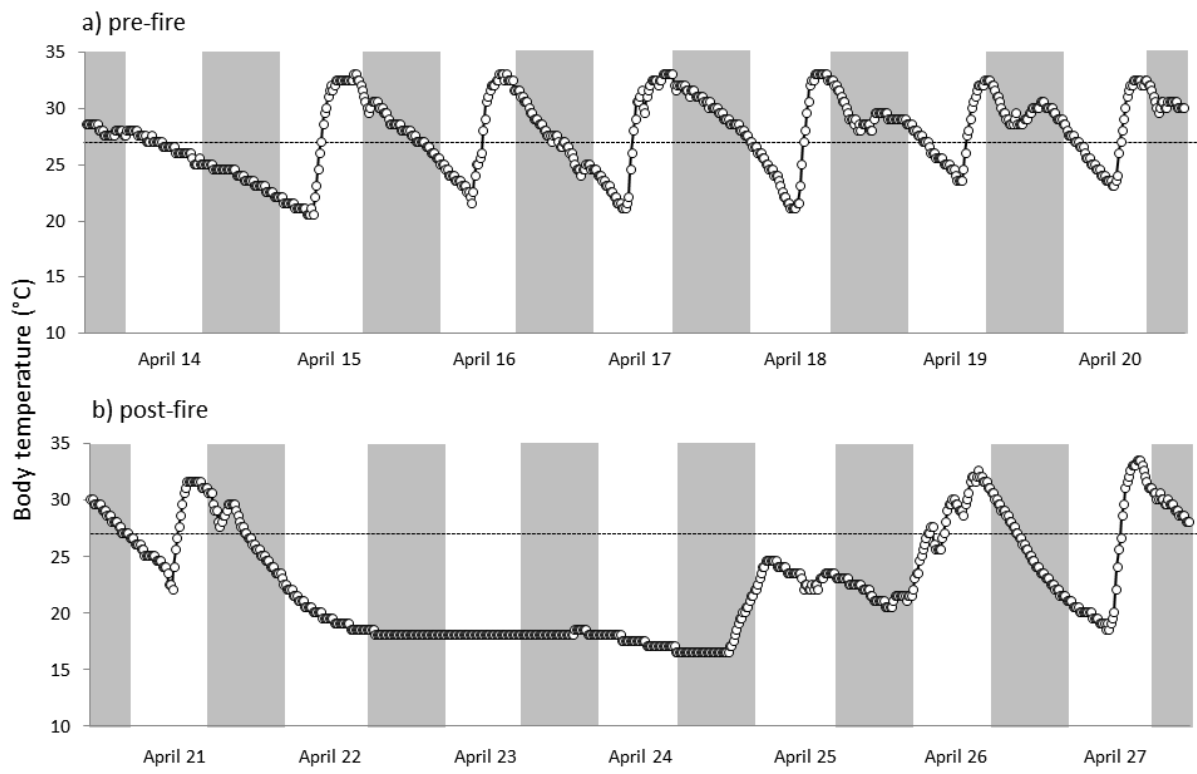
Figure 3: Mean body temperatures ( $T_b$ ) before and after the burn for a) the control echidnas ( $n=5$ ) and b) fire animals ( $n=5$ ; individual that died in the fire not shown) in relation to c) ambient conditions (maximum ambient temperature:  $T_{amax}$ ; minimum ambient temperature:  $T_{amin}$ ; 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.

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.



Figure 1ab





**Figure 2ab**

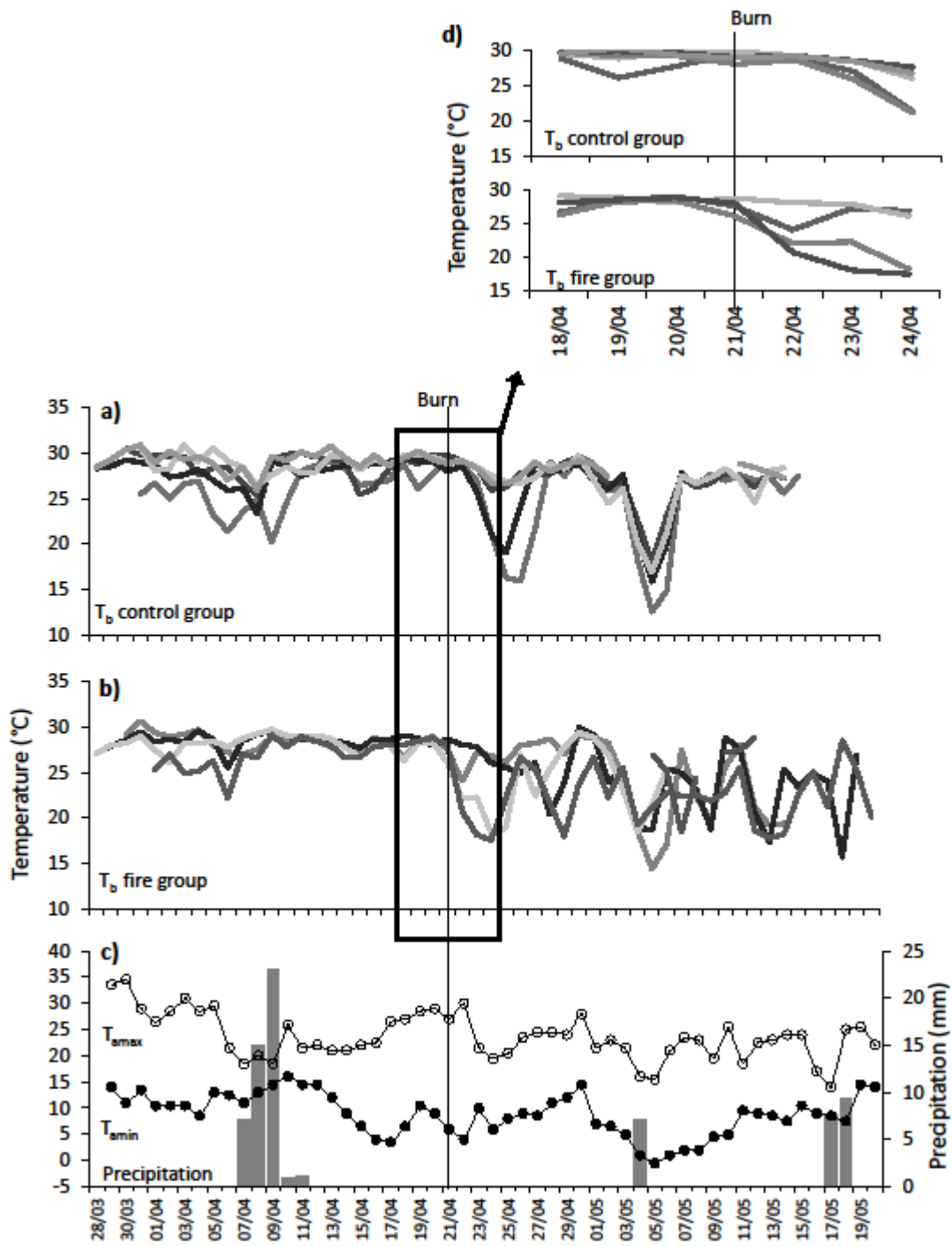


Figure 3abcd

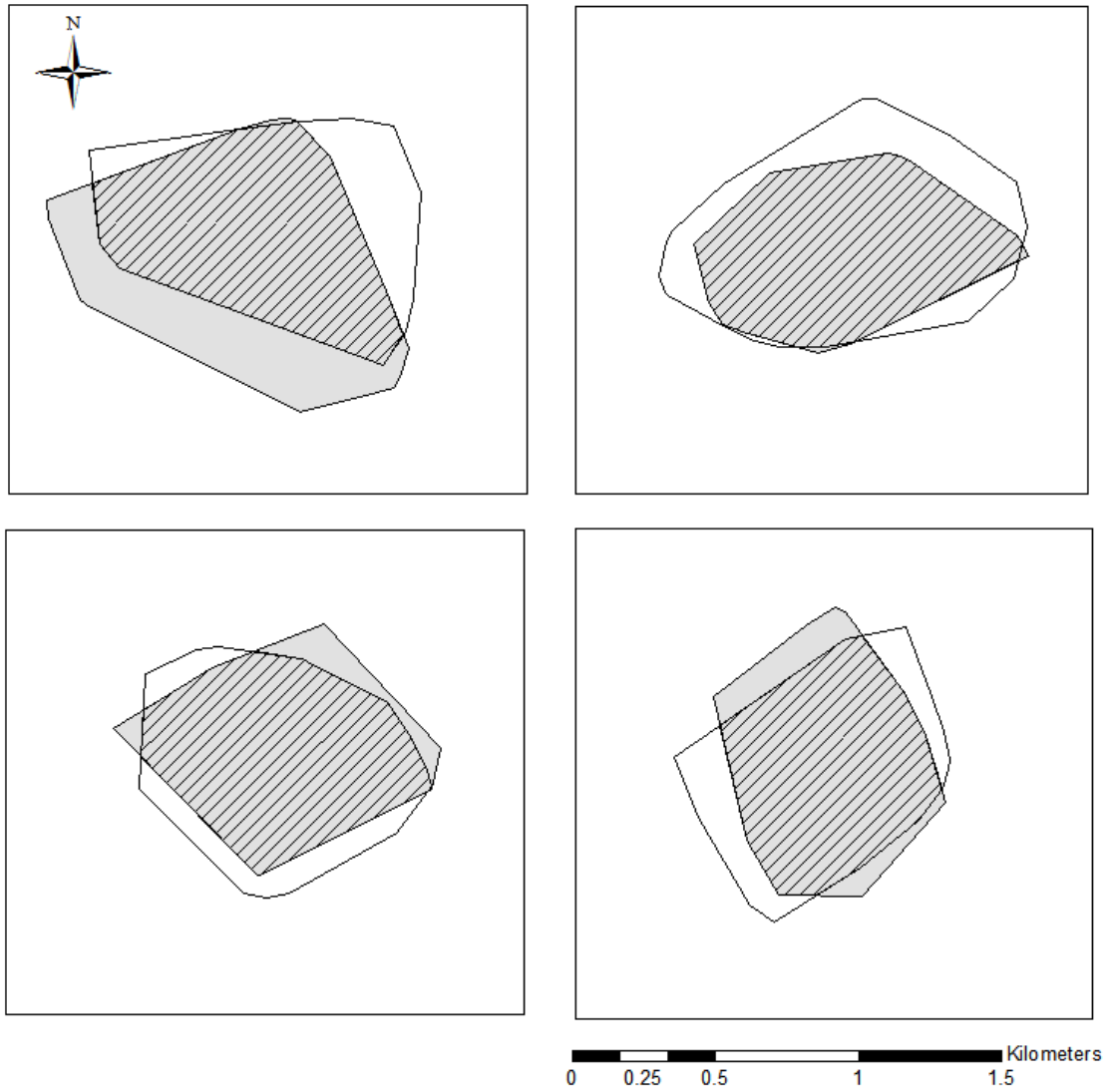


Figure 4