1   **Cool echidnas survive the fire**

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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

Introduction

The evolution of mammals has been hypothesised to be linked to the meteoroid impact at the Cretaceous-Palaeogene (K-Pg) boundary, about 65.5 million years ago, 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 their 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].

Divergence of monotreme and therian mammals is estimated to have occurred at least 170 million years ago [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 amongst the largest known deep hibernators [17] and can hibernate from a few days in warmer habitats to up to several months in colder habitats, with torpor bouts of 1-3 weeks interrupted by short bouts of normothermia [16, 18]. The wide geographical distribution and the 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: 21st 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 (±0.5°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 (0.2mg 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 (±0.5°C, iButton thermochron DS1921G, logging interval: 10 min) to record

103 external temperature. All animals weighed between 2600g and 3950g (mean mass: 3355±375g) 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 (±0.5°C, iButton thermochron DS1921G). Precipitation data were

110 obtained from the Bureau of Meteorology for the nearest (~7km) weather station (Caernarvon Park;

111 32.74°S 116.84°E). The T_as 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(control)= T_a(fire)*1.26 + 0.896). Daily T_a ranged from

113 a minimum of -0.5°C to a maximum of 34.5°C (Tab. 1). During the study period at 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°C [19] and therefore echidnas were

117 deemed 'normothermic' when T_b increased >27°C. Torpor bout durations of >24 hours ($T_b ≤ 27$ °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 ±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 $T_b \leq 25.6$°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 ± 125min;

164   range from 0 to 283min; n=4) in comparison to the control group (mean activity 474 ± 38min; 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_bs >27°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 ~ 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°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_bs 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≥5.31, p<0.001), mean T_bs 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≥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 ± 182min, N=128) than for the fire group (mean: 359 ± 164min, 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≥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 ± 5.3ha, N=14 vs. 16.9 ± 9.6ha, N=5 and 7.4 ± 6.0ha, N=19 vs. 10.0 vs.

195   10.2ha, 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=0.9980). Interestingly, whereas the daily foraging areas of the control group decreased over the time of the study from 11.0 ± 2.9ha (N=71) to 8.7 ± 1.1ha (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 ± 2.1ha, N=71 vs 8.9 ± 4.9ha, N=36; z=0.44, p= 0.9716).

Habitat use of the post-fire individuals was not notably affected by the fire (fire animals: 55.2 ± 6.7ha, N=75, n=4 vs. 51.0 ± 10.6ha, N=47, n=4; control animals: 61.2 ± 28.9ha N=71, n=5 vs. 39.9 ± 17.6ha N=60, n=5; ANOVA: $F_{3,6}$=2.81, p=0.1305) and no individual left its territory (Fig.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 due 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).

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 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 (7-months hibernation with bouts of ≤3 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 likely 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 due to reduced reaction times and locomotory performance at low T_b [28]. One echidna, known to be torpid at 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 due to a low T_b of 23.1°C, since echidnas were observed to move with similar low T_bs of around 23°C in this and other studies [29 and pers. observation JN], 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 to logs, seeking refuge in deep underground burrows at the time of a fire would likely 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 hours [31].

Echidnas not only reduced activity immediately after the burn, 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 likely an important aspect of the species' ability to persist in varied and changing landscapes.

The small marsupial antechinus, *Antechinus stuartii* (~20g), uses shallow daily torpor and reduces activity after fires to compensate for reduced food availability and to cope with increased exposure to predators due to reduction in ground cover [7]. For the rather large (~4kg) 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 hypothesise 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

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.

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).

Data accessibility

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

Competing interests

292 We have no competing interests.

Funding Statement

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.

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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_bs 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

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
Burn area		
#1	0	220.5
#2	43.5	422
#3	0	217.5
#4	0	288.5
#5	-	43.5
	10.9 ± 21.7[a]	**238.4 ± 136.9[b]**
Control area		
#1	0	64
#2	129	138
#3	60	142.5
#4	0	68
#5	0	0
	37.8 ± 57.2[a]	**82.5 ± 59.2[a]**

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 21th 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.
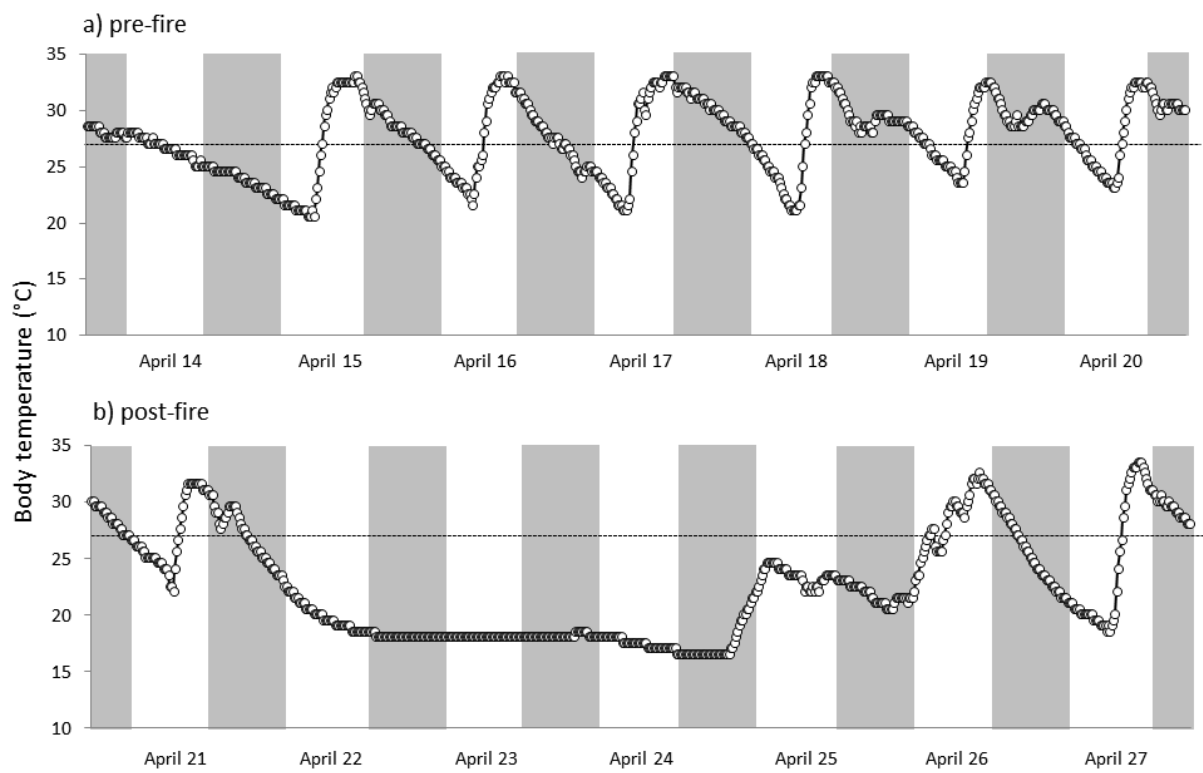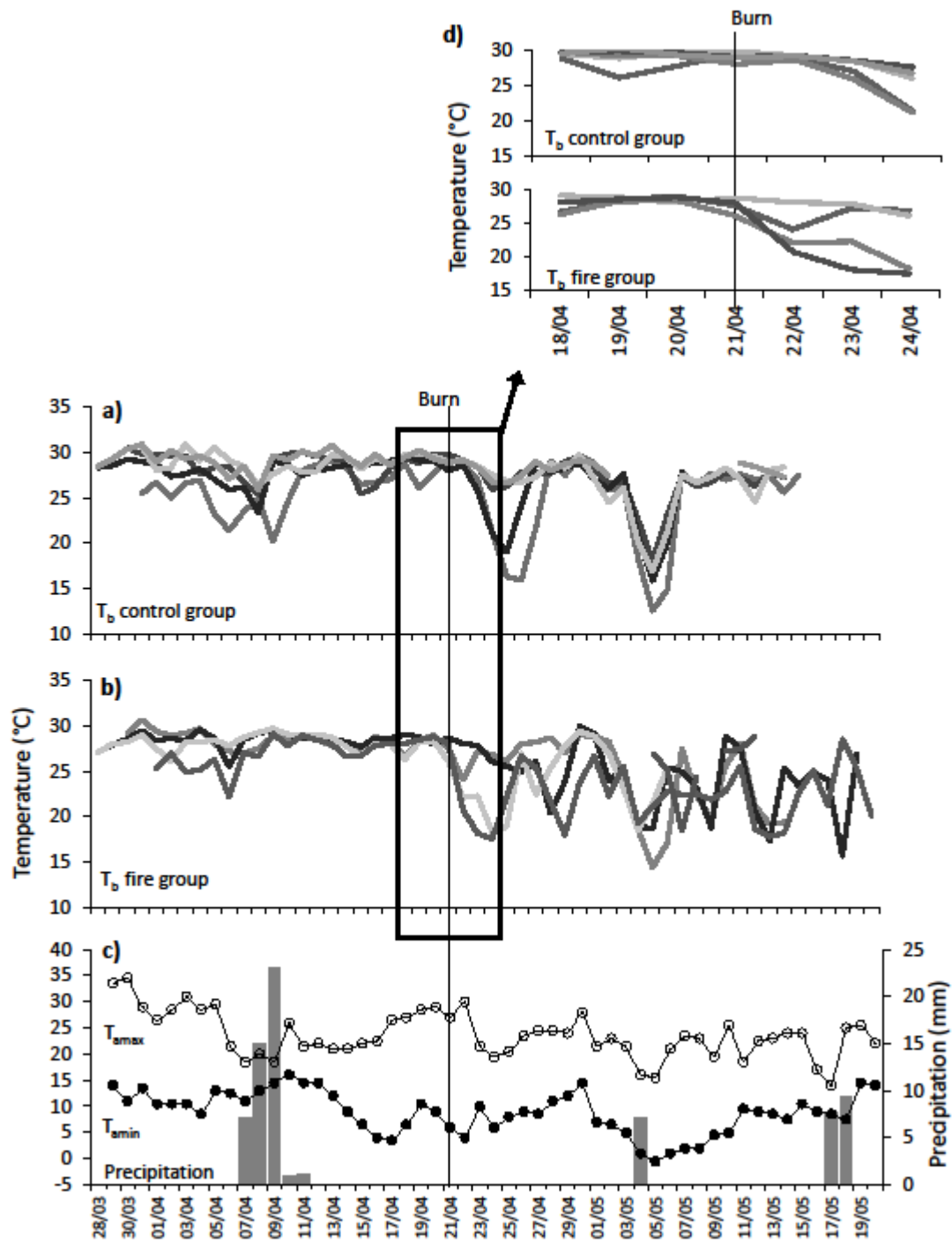
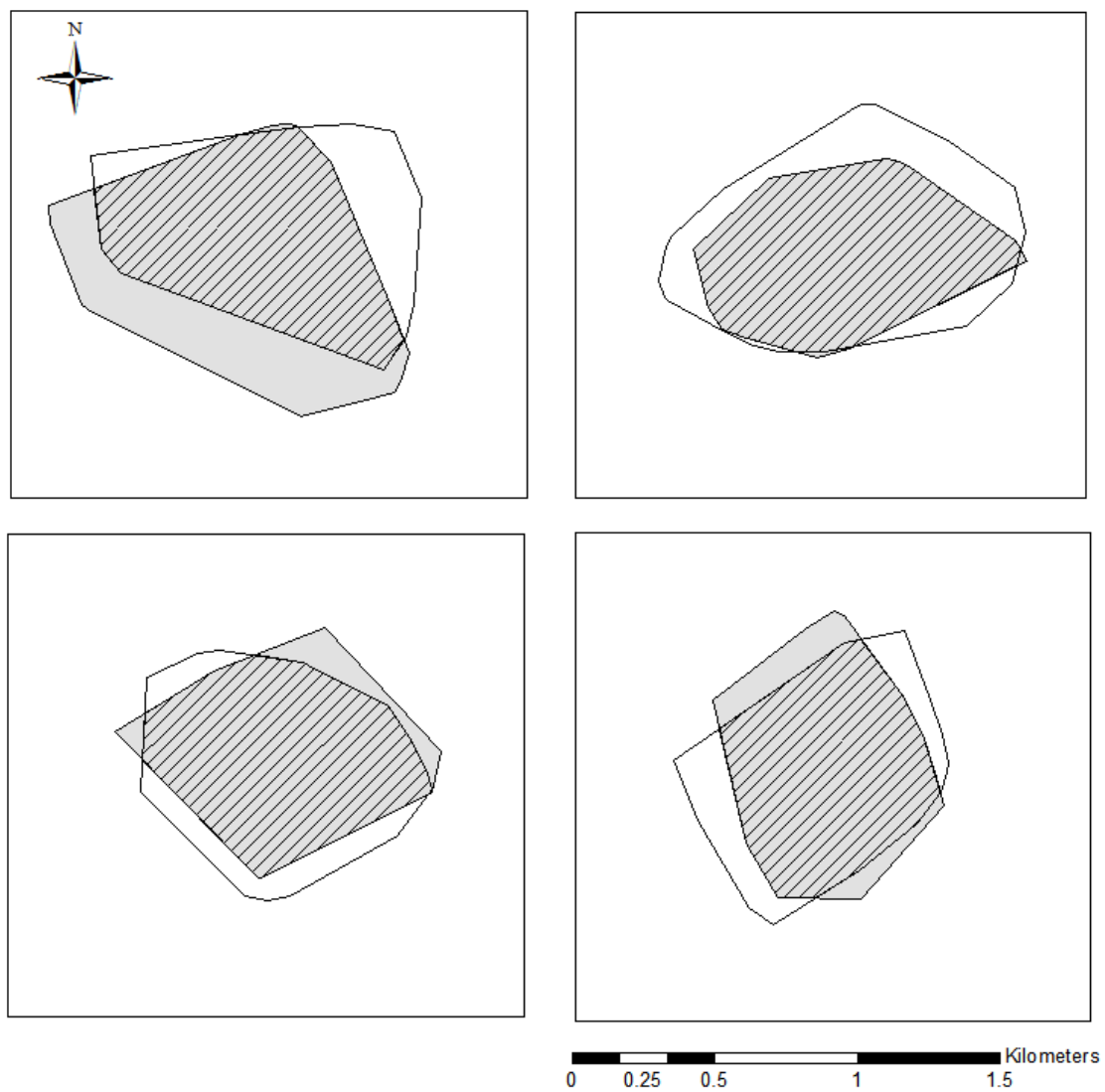**Figure 1ab**

Figure 2ab

Figure 3abcd

Figure 4