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SHORT COMMUNICATION

Hot bats: extreme thermal tolerance in a desert heat wave

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Abstract Climate change is predicted to increase temperature extremes and thus thermal stress on organisms. Animals living in hot deserts are already exposed to high ambient temperatures (T_a) making them especially vulnerable to further warming. However, little is known about the effect of extreme heat events on small desert mammals, especially tree-roosting microbats that are not strongly protected from environmental temperature fluctuations. During a heat wave with record T_as at Sturt National Park, we quantified the thermal physiology and behaviour of a single free-ranging little broad-nosed (*Scotorepens greyii*, henceforth *Scotorepens*) and two inland freetail bats (*Mormopterus* species 3, henceforth *Mormopterus*) using temperature telemetry over 3 days. On 11 and 13 January, maximum T_a was ~45.0 °C, and all monitored bats were thermoconforming. On 12 January 2013, when T_a exceeded 48.0 °C, *Scotorepens* abandoned its poorly insulated roost during the daytime, whereas both *Mormopterus* remained in their better insulated roosts and were mostly thermoconforming. Maximum skin temperatures (T_{skin}) ranged from 44.0 to 44.3 °C in *Scotorepens* and from 40.0 to 45.8 °C in *Mormopterus*, and these are the highest T_{skin} values reported for any free-ranging bat. Our study provides the first evidence of extensive heat tolerance in free-ranging desert microbats. It shows that these bats can tolerate the most extreme T_{skin} range known for mammals (3.3 to 45.8 °C) and delay regulation of T_{skin} by thermoconforming over a wide temperature range and thus decrease the risks of dehydration and consequently death.

Keywords Arid · Bats · Desert · Extreme heat · *Scotorepens* · *Mormopterus*

Abbreviations

T_a	Ambient temperature
T_{skin}	Skin temperature
T_b	Body temperature
Scotorepens	*Scotorepens greyii* (little broad-nosed bat)
Mormopterus	*Mormopterus* species 3 (inland freetail bat)

Introduction

Due to recent increases in global temperature and a predicted rate of further warming at 0.10–0.23 °C per decade (Sánchez-Lugo et al. 2012; IPCC 2013), it is inevitable that more organisms around the world will be exposed to unprecedented high temperature extremes. This is especially challenging for desert organisms which already endure high ambient temperatures (T_a). Animals can use several key mechanisms to cope with the increasing global temperature including shifting their current distribution range (Parmesan and Yohe 2003; Pörtner and Farrell 2008), adjusting the timing of diel and/or seasonal activity (Thackeray et al. 2010), acclimating to new environmental conditions during postnatal development (Riek and Geiser 2012) or increasing tolerance to heat stress via natural selection (Feder and Hofmann 1999). However, these mechanisms require a gradual change in T_a to allow animals to adjust their thermal physiology and behaviour to new conditions and therefore do not safeguard against sudden changes in weather and abnormal temperature fluctuations such as cold snaps or heat waves. Such extreme weather anomalies are expected to intensify and become more frequent as a result of current climate change (IPCC 2013). In fact, exposure to

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short periods of extreme heat can be more dangerous for populations than slowly increasing global temperature (Parmesan et al. 2000) as they can result in mass die-offs and perhaps local extinctions of animals with limited ability to shelter from sudden extreme heat waves such as most birds and many bats (Welbergen et al. 2008; McKechnie and Wolf 2010; Sherwin et al. 2013).

Small, tree-roosting, insectivorous bats appear to be particularly vulnerable to high T_as due to their large surface area to volume ratio, reliance on evaporation for cooling body temperature (T_b) without access to drinking water and food during the daytime rest phase and little protection of their roost sites from external T_a and direct solar radiation. Unfortunately, data about physiological and behavioural responses of free-ranging bats to extreme heat (i.e. T_a >40 °C) are scarce and often limited to visual observations of bats exposed to high temperatures in their roosts without T_b measurements. These field studies have demonstrated that some species of bats, such as Yuma myotis (*Myotis yumanensis*), Mexican freetail bats (*Tadarida brasiliensis*), Angolan freetail bats (*Mops condylurus*) and eastern cave bats (*Vespadelus troughtoni*) can tolerate roost temperatures that at times exceed 40 °C (Licht and Leitner 1967a; Bronner et al. 1999; Law and Chidel 2007). On the other hand, T_as >42 °C appear to be lethal for flying foxes (*Pteropus* spp.) that regularly roost in the tree canopy directly exposed to temperature extremes and sun (Welbergen et al. 2008).

Here, we report the effect of extreme high T_a on thermal physiology and behaviour of one adult free-ranging little broad-nosed bat (*Scotorepens greyii*, Vespertilionidae, henceforth *Scotorepens*) and two adult inland freetail bats (*Mormopterus* species 3 (Adams et al. 1988), Molossidae, henceforth *Mormopterus*) during the most extreme hot weather in the past four decades in the Australian arid zone (Bureau of Meteorology 2013). These bats had been tagged during the heat wave and therefore provided a unique opportunity to examine their thermal biology and behaviour. While *Scotorepens* is found throughout arid and semi-arid regions and also subtropics and tropics of northern Australia, the distribution of *Mormopterus* is restricted to desert habitats (Churchill 2008).

Methods

Measurements were made at Sturt National Park near Mt Wood Homestead (29° 28′ S, 142° 14′ E; ~22 km east from Tibooburra; elevation ~183 m) located in the north-western corner of New South Wales (NSW), Australia, during 11–13 January 2013 (austral summer). The study area contains sparse, open woodlands along creek beds dominated by river red gum (*Eucalyptus camaldulensis*), coolabah (*Eucalyptus coolabah*) and gidgee (*Acacia cambagei*). During the tracking period, drinking water was available from two dams that capture flood water from a creek.

The climate of Sturt National Park is arid, and the long-term average daily T_a (93–103 years) during the hottest month (January) ranges from 22.1 to 36.2 °C. Temperatures in the shade above 45 °C are rare at the research site and have only been recorded on 66 days (~0.17 %) over 104 years (Tibooburra Post Office, Bureau of Meteorology, Australia). The Australian summer 2012–2013 (December–February) was the hottest on record since 1972–1973 with a prolonged hot spell observed in the country from 25 December to 18 January (Bureau of Meteorology 2013). Furthermore, January 2013 was the ninth warmest January since 1880 in the world (NOAA 2013).

Bats (one female *Scotorepens*, capture body mass=7.2 g; one male and one female *Mormopterus*, body mass=7.8±0.5 g) were captured between 9–11 January 2013, without knowledge of the imminent extreme heat, and fitted with external temperature-sensitive radio transmitters (0.43 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) following Bondarenco et al. (2013). Before attachment, transmitters were calibrated in a water bath against a precision mercury thermometer (±0.1 °C) traceable to a national standard over a temperature range of 10–42 °C. Skin temperature (T_{skin}) was then calculated using third-order polynomial regressions (all R^2=0.99) with all measured values falling within 0.5 °C of the calibration curve. For small animals, such as bats, resting T_{skin} measured with external transmitters is usually within 2–3 °C of core T_b, with T_{skin}–T_b differential decreasing with an increase in T_a (Audet and Thomas 1996; Barclay et al. 1996). To establish whether this is also correct at T_as>40 °C, we also measured T_{skin}–T_b differential of six *Scotorepens* and nine *Mormopterus* under laboratory conditions at T_as 40–42 °C using calibrated external radio transmitters (LB-2NT) attached as described above and a calibrated thermocouple thermometer (HH-71T, Omega Engineering, Stamford CT, USA) used to measure core T_b rectally to the nearest 0.1 °C. We found that T_{skin}–T_b differential was similar for both species, and it was only 0.4±0.7 °C at T_a 41.4±0.8 °C (T_{skin} 41.3±1.2 °C). The T_{skin}–T_b differential did not differ between the two species (intercept p<0.985) and increased steadily with the rise in T_a with the maximum error of only 1.4 °C at T_a 42.1 °C (Fig. 1). Therefore, we are confident that T_{skin} measured in the field with external transmitters provides a good representation of T_b. It should, however, be acknowledged that potentially T_{skin}–T_b differential could be higher at T_as >42 °C due to ambient heat affecting externally attached transmitters.

Individual bats were radiotracked daily to their roosts shortly after sunrise. After locating the roost tree, we used a coaxial cable attached to a 4-m long fishing rod connected to a receiver (Icom, IC-R10, Osaka, Japan) to find the exact bat location. For each animal, a receiver/data logger was placed near the roost tree to remotely record T_{skin} data every 10 min

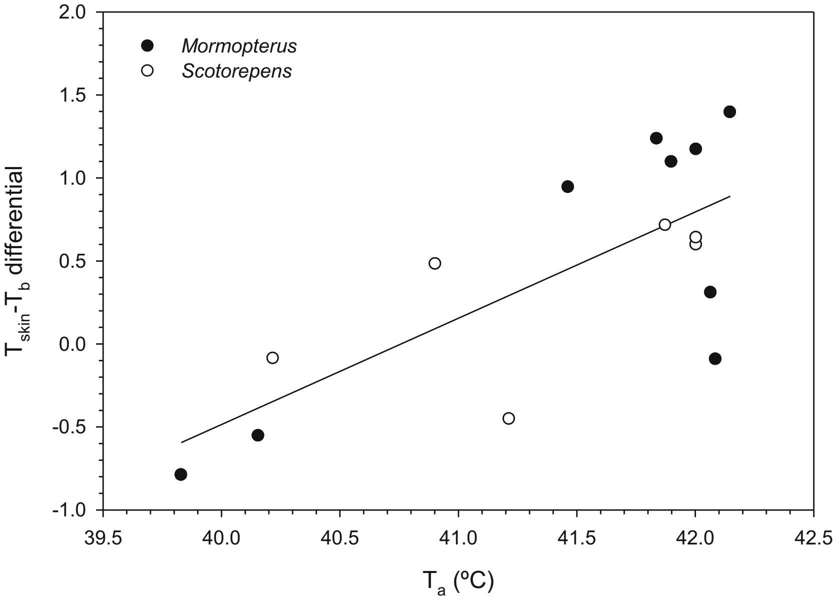


Fig. 1 The T_{skin}–T_b differential measured under laboratory conditions for nine *Mormopterus* and six *Scotorepens* plotted against T_a (linear mixed effects model—t_{11}=3.14, p=0.009, R^2= 0.99; n=15, N=15). The intercept was indistinguishable for both species (p<0.985)

(Körtner and Geiser 1998). During and after the heat wave, we also searched for dead bats at the Mt Wood Homestead complex and Tibooburra with the help of NPWS staff.

T_a was measured at 10-min intervals with temperature/humidity data loggers (resolution 0.0625 °C; iButton Hygrochron, DS1923, Maxim Integrated Products Inc., Sunnyvale, California, USA) placed at two locations in the shade 2 m above the ground. Both data loggers provided similar T_as, and only T_a from a data logger located within 300 m of occupied roosts was used in this study. Prior to use, iButtons were calibrated following Bondarenco et al. (2013).

The linear mixed effects model with *Mormopterus* as a reference group and species as a factor was computed to analyse differences in the T_{skin}–T_b differential between two species with individual bats entered as a random effect to account for repeated measurements (Fig. 1). General linear modelling was used to compare a heating rate among bats with T_{skin} as a dependent variable, time as an independent variable and individuals as a factor. All models were computed in R (R development Core Team 2012; package "nlme"), and the residuals of the models were checked for homoscedasticity and normality by analysing residual plots. We report numerical values as means ± SD, "*n*" for the number of individuals and "*N*" for the number of measurements.

Results

On the hottest day, 12 January, maximum T_a reached 48.1 °C, and mean daily T_a was 37.7 °C. Temperature conditions on 11 and 13 January were similar and only marginally cooler; maximum T_a was 45.6 and 45.9 °C, and mean daily T_a was 33.4 and 34.9 °C, respectively.

On 12 January, *Scotorepens* roosted inside a slender branch (circumference ~30 cm), ~2 m above the ground, which was exposed to direct sunlight. On this day (Fig. 2a, b), T_{skin} passively followed T_a with a ~2-h delay from T_{skin} 31.8 °C in the morning until T_{skin} reached the maximum 44.0 °C (T_a 46.1 °C). We define this lack of regulatory response to the increasing T_a as thermoconforming behaviour as opposite to a regulated T_{skin} (see below; Fig. 2b). After T_{skin} of *Scotorepens* reached its maximum, even though T_a continued to increase, T_{skin} began to decrease and to fluctuate (i.e. T_{skin} was regulated), presumably, indicating active thermoregulation leading to elevated heat dissipation (Fig. 2b). During this time, *Scotorepens* cooled its T_{skin} from 44.0 °C (T_a 46.1 °C) to 41.2 °C (T_a 47.0 °C), and at the maximum T_a 48.0 °C, T_{skin} was 42.5 °C (5.5 °C below T_a). Nevertheless, *Scotorepens* abandoned its roost 3.2 h after the start of active thermoregulation, at 14:46 (T_{skin} 43.0 °C; T_a 47.3 °C). The transmitter was later found on the ground ~100 m from the original roost under an alive tree with exfoliating bark and a well-developed tree canopy providing shade where, presumably, this bat was sheltering.

On the same day (12 January), the male *Mormopterus* was roosting in the partly alive main trunk of a river red gum (circumference ~190 cm), and the female was found in a smaller dead branch (circumference ~110 cm) adjacent to the main trunk of the same tree. Both roosts were ~6 m above the ground and shaded by branches and leaves. On this day, T_{skin} patterns of both individuals were similar, but the amplitude of T_{skin} fluctuations differed between the two individuals (Fig. 2c–f). T_{skin} of the female roosting in the branch increased from a minimum of 33.2 °C in the morning to a maximum of 45.8 °C (T_a 47.9 °C); T_{skin} of the male found in the tree trunk increased from a minimum of 36.1 °C to a maximum of 45.4 °C (T_a 47.6 °C).

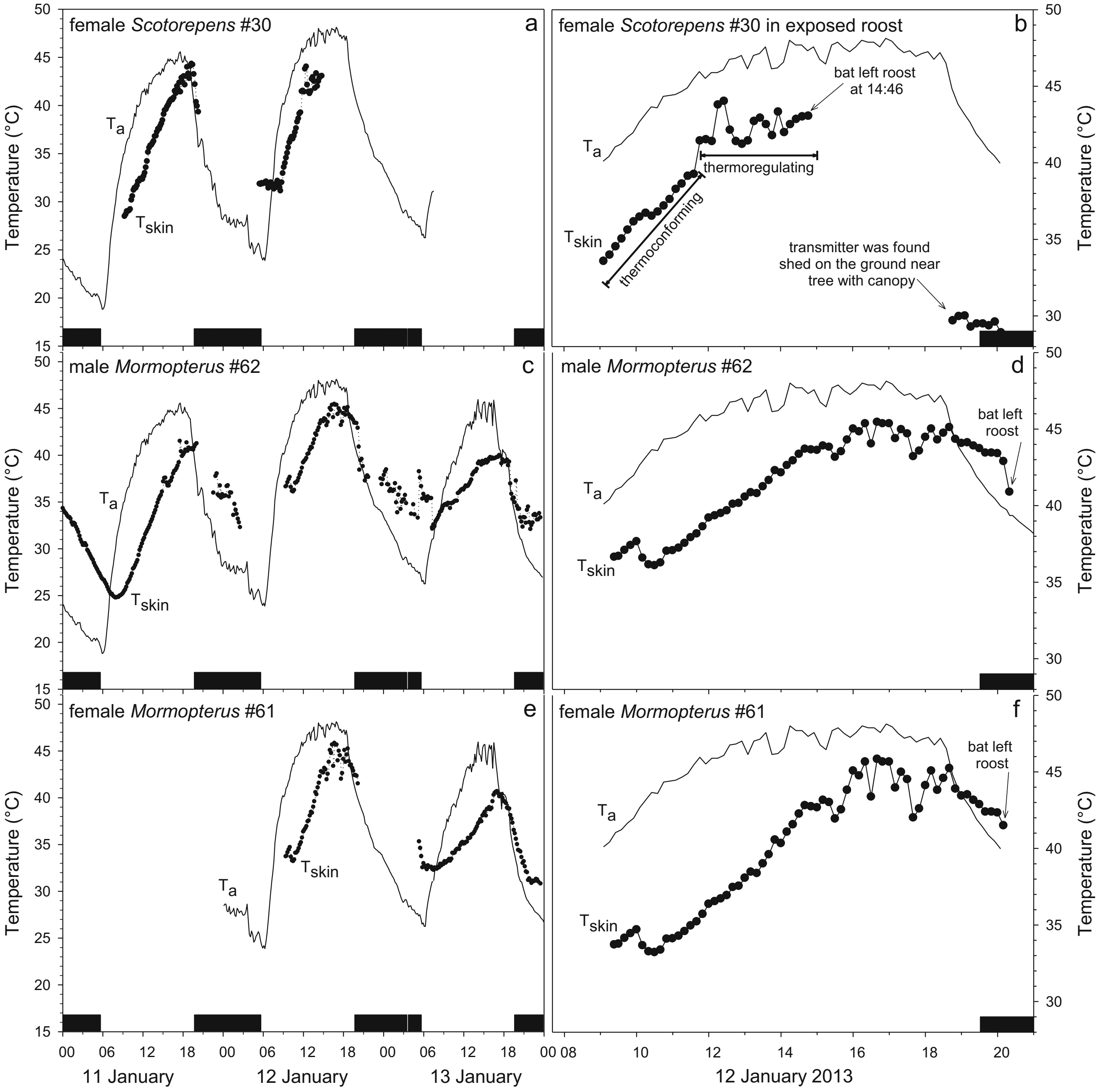
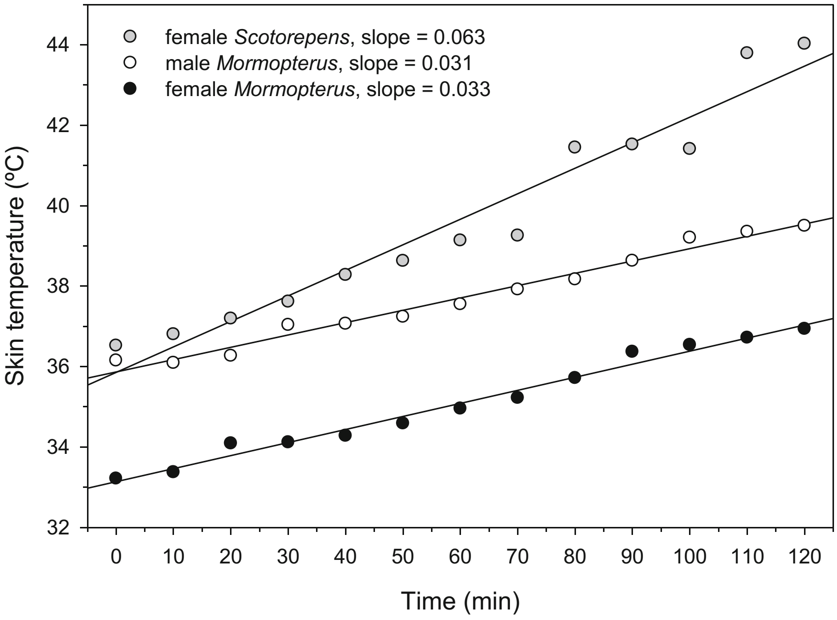


Fig. 2 Fluctuations in T_{skin} (*lower trace*, *dotted line*) and T_{a} (*upper trace*, *solid line*) of the female *Scotorepens* (**a**), male (**c**) and female (**e**) *Mormopterus* during the heat wave on 11–13 January 2013; detailed $T_{\mathrm{skin}}/T_{\mathrm{a}}$ recordings for the female *Scotorepens* (**b**), male (**d**) and female (**f**) *Mormopterus* during the extreme hot weather on 12 January 2013. *Black bars* represent night

Interestingly, T_{skin} of both *Mormopterus* reached its maximum 4.2 h later (16:40) than in *Scotorepens* (12:26). Hence, T_{skin} was tracking T_{a} with a ~5-h delay (Fig. 2d, f). Furthermore, the mean rate of T_{skin} increase (heating rate) in *Scotorepens* was about double (0.063 °C min^{-1}; $p<0.001$) and significantly higher (general linear model—$F_{5.33}=331.2$, $p<0.001$, $R^2=0.98$; $n=3$, $N=39$) than in the male (0.031 °C min^{-1}; $p<0.001$) and female (0.033 °C min^{-1}; $p<0.001$) *Mormopterus* (Fig. 3).

On the previous day, 11 January, the female *Scotorepens* was roosting inside a sun-exposed old fence post (circumference ~100 cm), ~1 m above the ground. During much of this "cooler" day, T_{skin} was passively tracking T_{a} with a ~4-h delay (Fig. 2a). T_{skin} for this individual increased from a minimum of 28.5 °C in the morning to a maximum of 44.3 °C (T_{a} 42.5 °C). It should be noted, however, that although the maximum T_{skin} during this day was higher than on 12 January, it was observed in the evening when T_{a} started to cool off

Fig. 3 T_{skin} of the female *Scotorepens*, male and female *Mormopterus* over 120 min calculated from the time T_{skin} of all three individuals was steadily increasing (~10:30) until T_{skin} of *Scotorepens* reached its maximum and started to decrease (12:26) during the extremely hot 12 January 2013. Note the steeper slope of this relationship in *Scotorepens* than *Mormopterus* indicating poor insulation of *Scotorepens*' roost



whereas on the hottest day, T_a was still increasing when T_{skin} maximum was reached. During the same day, the male *Mormopterus* was roosting in a trunk of a dead coolabah (circumference ~130 cm), ~3 m above the ground. The bat was torpid with a minimum T_{skin} of 24.8 °C in the morning, and it was thermoconforming for most of the day with T_{skin} tracking T_a with a ~5.5-h delay (Fig. 2c); maximum T_{skin} was 41.5 °C (T_a 45.6 °C).

On 13 January, both *Mormopterus* occupied the same roosts as on 12 January. Bats were thermoconforming throughout this day, and the maximum T_{skin} was 40.7 °C (T_a 43.6 °C) in the female and 40.0 °C (T_a 40.7 °C) in the male *Mormopterus*. T_{skin} of the female *Mormopterus* was tracking T_a with a ~5.5-h delay, and T_{skin} of the male *Mormopterus* was lagging ~6.0 h behind T_a (Fig. 2c, e).

Although the tagged *Scotorepens* likely and *Mormopterus* definitely survived the extreme heat wave, one recently dead little pied bat (*Chalinolobus picatus*; body mass ~6 g; arid to subtropical distribution range) was found on the floor in a house in Tibooburra on 11 January. Another recently dead animal, Gould's wattled bat (*C. gouldii*; body mass ~10 g; distribution wide range), was found hanging on the mesh of a floor vent at Mt Wood Homestead a few days after the heat wave on 23 January. Several other non-identified dead microbats (likely *C. picatus* based on the description from NPWS staff) were also found during the heat wave inside buildings in Tibooburra.

Discussion

Our study provides the first insight into the physiological response of three individuals of small free-ranging arid zone bats to an extreme heat event. Our data show that appropriate roost selection can be a key factor for the survival of bats during severe heat. Nevertheless, both *Scotorepens* and *Mormopterus* had to endure a substantially elevated T_{skin} and T_b. The T_{skin} values observed in both species were the highest reported for any free-ranging bat and, considering the differential between T_{skin} and T_b of ~0.4 °C, were above the measured lethal T_b for most placental mammals (42–44 °C; Schmidt-Nielsen 1997). It is also astonishing that *Mormopterus* can tolerate enormous seasonal T_{skin} fluctuations ranging from a minimum of only 3.3 °C in winter (Bondarenco 2014) to a maximum of 45.8 °C reported here, giving it a total T_{skin} range of 42.5 °C. To our knowledge, this is the most extreme T_{skin} range observed in any mammal and, taking into account T_{skin}–T_b differential, appears to exceed even the widest known T_b fluctuations among endotherms reported for arctic ground squirrels (*Spermophilus parryii*, total T_b range ~41 °C; Barnes 1989).

While quantitative data on T_b of bats exposed to extreme heat measured under natural conditions are not available, visual observations suggest that heat tolerance does differ among species. For example, in a mixed species roost in a barn loft, pallid bats (*Antrozous pallidus*) moved away from the ceiling areas when T_a reached only 38 °C, whereas Yuma myotis (*Myotis yumanensis*) did not move until T_a at the ceiling beams exceeded 40 °C. Finally, Mexican freetail bats (*Tadarida brasiliensis*) only retreated to the cooler parts of the roost after T_a of beams reached 41–42 °C (Licht and Leitner 1967a).

In comparison, although we could not observe bat activity inside roosts, T_{skin} data show that *Scotorepens* and *Mormopterus* were mostly thermoconforming during the hot days on 11 and 13 January. If thermoregulation, evaporative cooling or movement did occur during this time, T_{skin} patterns were not obviously affected. Another approach, employed by bats studied here, was using torpor (see also Bondarenco et al. 2013) or at least a substantial reduction in T_{b} in the early morning. Reduced T_{skin} during thermoconforming behaviour and torpor is usually associated with low metabolic heat production and water loss. This is especially crucial for the survival of small endotherms as less heat needs to be dissipated and, therefore, hyperthermia is delayed or prevented, which will save water that may be required for evaporative cooling during the hottest part of the day (Schmidt-Nielsen et al. 1957; Licht and Leitner 1967b; Bradley and Yousef 1972).

In contrast, when exposed to the extreme heat on 12 January, *Scotorepens* only initially thermoconformed, but when T_{skin} reached ~44.0 °C, the bat appeared to commence active thermoregulation, possibly in conjunction with a retreat to a cooler part of the roost. Such increased thermoregulatory effort has to involve active evaporative cooling such as panting, saliva spreading and/or wing flapping (Reeder and Cowles 1951; Licht and Leitner 1967b; Withers 1992; Schmidt-Nielsen 1997; Speakman and Thomas 2003). Heating for both *Mormopterus* commenced later and at the slower rate. Overall, it appears that both *Mormopterus* were mostly thermoconforming even during 12 January. Although eventually T_{skin} in *Mormopterus* also started to fluctuate, the fluctuation patterns were similar for bats and were probably caused by variations in T_{a}/sun exposure, due to changes in wind, cloud cover or by canopy shading rather than commencement of active T_{skin} regulation. Evidently, the large-diameter tree trunks and branches used by *Mormopterus* provide better insulation against extreme temperatures than slender ones, and alive trees provide more insulation and even cooling than dead cracked ones due to differences in water content/flow (Kunz and Lumsden 2003; Briscoe et al. 2014), thus resulting in delayed and slower heating. Moreover, the presence of a developed tree canopy and branches provide additional protection from direct sunlight. Therefore, T_{skin} of *Scotorepens*, roosting in a smaller dead coolabah without canopy, was increasing earlier and at a higher rate, forcing this bat to commence heat dissipation earlier and eventually to abandon its roost to avoid pathological hyperthermia when environmental conditions became extreme. For a bat, leaving a roost in daylight, especially during hot weather, is associated with extreme risks firstly by overheating during flight (Voigt and Lewanzik 2011) and secondly by predation from birds (Speakman et al. 1994). Obviously, such behaviour was the last option available to the *Scotorepens*. Moreover, dead bats found inside buildings suggest that even man-made structures do not always provide enough insulation from extreme heat.

While appropriate roost selection appears to be a key factor for bats' survival under severe heat stress conditions, for those roosting in trees and ceilings, hyperthermia cannot be avoided altogether. The ability of tree-roosting desert bats to tolerate moderate hyperthermia will delay or prevent the onset of evaporative cooling, which is important as these bats have no access to drinking water or food during the daytime and have to rely entirely on the body fluids for heat dissipation. Nevertheless, the provision of artificial watering points at our study site and throughout the Australian arid zone provides desert bats with an opportunity to restore water balance quickly at dusk. Similarly to other water-dependent species across arid and semi-arid Australia (James et al. 1999), this may be especially important for the survival of those bat species that are not desert specialists, such as *Scotorepens*, which is usually found near water (Churchill 2008).

In conclusion, our data show that in contrast to many fruit bats that often roost in the open, microbats can have a better chance of overcoming extreme heat events because of roost protection against radiation, the ability to tolerate high T_{b} and opportunistic use of torpor or at least a low T_{b} in the morning (Geiser et al. 2011; Bondarenco et al. 2013). However, despite these adaptations, even desert tree-roosting bats can only deal with a limited increase in T_{a} as demonstrated by the dead bats found. This shows that small, tree-roosting microbats are not immune from the negative effects of climate change and, because they already experience T_{b}s near their thermal limit, may be among the first mammalian species that will be adversely affected by extreme heat events in arid areas around the world.

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