J Comp Physiol B (2013) 183:1113–1122
DOI 10.1007/s00360-013-0779-7

ORIGINAL PAPER

Some like it cold: summer torpor by freetail bats in the Australian arid zone

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Received: 30 May 2013 / Revised: 7 August 2013 / Accepted: 16 August 2013 / Published online: 30 August 2013

Abstract Bats are among the most successful groups of Australian arid-zone mammals and, therefore, must cope with pronounced seasonal fluctuations in ambient temperature (T_a), food availability and unpredictable weather patterns. As knowledge about the energy conserving strategies in desert bats is scant, we used temperature-telemetry to quantify the thermal physiology of tree-roosting inland freetail bats (*Mormopterus* species 3, 8.5 g, $n = 8$) at Sturt National Park over two summers (2010–2012), when T_a was high and insects were relatively abundant. Torpor use and activity were affected by T_a. Bats remained normothermic on the warmest days; they employed one “morning” torpor bout on most days and typically exhibited two torpor bouts on the coolest days. Overall, animals employed torpor on 67.9 % of bat-days and torpor bout duration ranged from 0.5 to 39.3 h. At any given T_a, torpor bouts were longer in *Mormopterus* than in bats from temperate and subtropical habitats. Furthermore, unlike bats from other climatic regions that used only partial passive rewarming, *Mormopterus* aroused from torpor using either almost entirely passive (68.9 % of all arousals) or active rewarming (31.1 %). We provide the first quantitative data on torpor in a free-ranging arid-zone molossid during summer. They demonstrate that this desert bat uses torpor extensively in summer and often rewarms passively from torpor to maximise energy and water conservation.

Keywords Bat · Desert · *Mormopterus* · Torpor · Passive rewarming · Insect abundance

Communicated by I.D. Hume.

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Abbreviations

T_a	Ambient temperature
T_{skin}	Skin temperature
T_b	Body temperature
TBD	Torpor bout duration

Introduction

The large surface area to volume ratio of small endotherms requires relatively large amounts of energy to maintain a constant high body temperature (T_b), which can be particularly unfavourable for animals living in arid environments. In arid regions, animals have to cope with limited food and water supply and pronounced daily and seasonal fluctuations of ambient temperature (T_a) (Schmidt-Nielsen 1979). Perhaps, not surprisingly, a growing number of arid-zone mammals and birds have been shown to be heterothermic and use torpor for energy conservation (Serventy and Raymond 1973; Geiser 2004; Warnecke et al. 2008; Levy et al. 2011; Doucette et al. 2012). The reduction in metabolic rate and T_b during torpor reduces food and foraging requirements and also results in substantial water conservation apparently crucial for life under harsh desert conditions (Schmid and Speakman 2000; Cooper et al. 2005; Geiser and Brigham 2012; Ben-Hamo et al. 2013).

Bats are a large group of small mammals and are distributed over the entire Australian continent (Churchill 2008). Torpor is common in Australian temperate-zone bats including species with wide distribution ranges that extend into the arid zone (Geiser and Brigham 2000; Turbill et al. 2003a; Geiser 2004). However, most data on physiological ecology are restricted to the family

Vespertilionidae, whereas other bat families, like the freetail bats (Molossidae), have received little scientific attention, despite the fact that molossids are a widespread family found in many desert regions around the world (Hill and Smith 1988). Currently, there are no published data on thermal biology and torpor in free-ranging molossids from the arid zone.

Although mammalian torpor is most often used in winter, in bats, it is commonly expressed even in summer (Turbill et al. 2003a; Vivier and van der Merwe 2007; Stawski and Geiser 2010a). However, the bats observed to use summer torpor, at the time torpor was initiated, were exposed to T_as well below the thermo-neutral zone, the lower critical T_a of which is typically ~30 °C in small bats (Hock 1951; Geiser and Brigham 2000; Riek and Geiser 2013). In contrast, T_a can remain near or above the thermo-neutral zone for prolonged periods during summer in deserts and may limit torpor use. Prolonged exposure to T_as above the thermo-neutral zone will be challenging for small nocturnal mammals, especially those that dwell in poorly insulated tree roosts that are exposed to direct sunlight. Apart from limiting torpor use for energy conservation, this also will result in high rates of evaporative water loss during the daytime (Withers 1992). Nevertheless, insectivorous bats are one of the most successful groups of Australian arid-zone mammals with 22 species (~28.6 % of all Australian bat species) of five families living in arid or semi-arid habitats (Churchill 2008) and it has been proposed that the ability to employ torpor at high T_as may be crucial for their survival (Geiser 2004).

In this study, we aimed to provide the first quantitative data on thermal biology and torpor patterns in a desert molossid. The species was the endemic inland freetail bat (*Mormopterus* species 3 (Adams et al. 1988), henceforth *Mormopterus*), a small, tree-roosting insectivorous bat that is common in arid and semi-arid habitats (Churchill 2008). Considering the high T_as in the arid zone, we hypothesised that *Mormopterus* will have specific physiological adaptations to its habitat, and, therefore, tested whether *Mormopterus* use torpor often in the wild, how it is affected by thermal conditions and food availability, and whether and how their thermal biology differs from bats in mesic areas during summer.

Methods

Study area and ambient conditions

Our study was conducted in summer 2010–2011 (December–January) and 2011–2012 (January–February) in Sturt National Park, New South Wales (NSW), Australia. The park is located in the north-western corner of the state and protects arid and semi-arid habitats. The work was conducted near the Mount Wood Historic Homestead (29°28′S, 142°14′E) located ~22 km east from Tibooburra NSW. The area is situated ~183 m above sea level and includes sparse, open woodlands growing along ephemeral creek lines, grasslands and open gibber and clay pans. Woodlands mainly comprise river red gum (*Eucalyptus camaldulensis*), coolibah (*Eucalyptus coolabah*) and gidgee (*Acacia cambagei*). The area contains two dams used to provide fresh water to the Mount Wood complex. Sturt National Park receives 230.3 mm of annual rainfall (mean over 127 years). The long-term average rainfall over 127 years for the December–February is 26.6 mm. The long-term average daily T_a (93–103 years) in January ranges from 22.1 to 36.2 °C (Tibooburra Post Office NSW, Bureau of Meteorology, Australia).

During the period of our study, T_a was measured with temperature/humidity dataloggers (resolution = 0.0625 °C, iButton hygrochron, Maxim Integrated Products Inc., Sunnyvale, California, USA) placed near two known bat roosts in the shade 2 m above the ground. The internal temperature of three occupied tree roosts was measured with iButtons (resolution = 0.5 °C) placed 10–20 cm inside the main entrance. The roost and skin temperature (T_{skin}) comparisons were only made, if roost temperature was available for occupied roosts. Prior to use, iButtons were calibrated against a precision mercury thermometer (±0.1 °C) traceable to a national standard in a water bath at temperatures between 5 and 45 °C. The rainfall data were obtained from the Australian Bureau of Meteorology measured at the Tibooburra Post Office NSW weather station.

Radiotracking

Mormopterus were captured with up to seven monofilament mist nets ranging in length from 6 to 12 m (mesh 14 mm) set up in the open area and in the tree canopy along the creek lines. Mist nets were opened approximately 10–15 min after sunset for 3–4 h on 25 evenings. On some occasions, we used a 6 m mist net set up in front of a known roost to catch bats emerging at dusk.

We radiotracked eight *Mormopterus* (two adult males and six adult females, body mass 8.5 ± 0.6 g). Data on a total of 34 bat-days were obtained from four individuals (1 ♂/3 ♀) in 2010–2011, and on 22 bat-days from four individuals (1 ♂/3 ♀) in 2011–2012.

Temperature-sensitive external radio transmitters (~0.5 g, LB-2XT and LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) were used to monitor T_{skin} and to locate roosts of tagged bats. Prior to attachment, transmitters were calibrated in a water bath against a precision mercury thermometer (±0.1 °C) over a temperature range of 10–40 °C. After a small patch of fur was clipped, radio tags were attached to the skin between the shoulder blades using a latex-based adhesive (SkinBond, Smith and Nephew United, Mount Waverley, VIC, Australia) in 2010–2011, and a silicon-based adhesive (MA200, Barnes Products Pty Ltd, Bankstown, NSW, Australia) in 2011–2012.

Tagged bats were released at the netting site within 2 h after their capture. In the morning, each marked bat was tracked to its roost. A receiver/data logger was then placed near the roost to record T_{skin} data every 10 min (Körtner and Geiser 1998). Tagged bats were tracked every day until the transmitter had failed or was shed, which varied from 3 to 18 days. If bats moved to another roost, loggers were moved to within the reception range. Several manual readings using a stop watch were also taken each evening with a receiver (Icom, IC-R10, Osaka, Japan) and Yagi antenna (Sirtrack, Havelock North, New Zealand) when active bats were out of the range of a datalogger to ensure that transmitter was still functioning and attached to a bat. We were unable to follow bats throughout the night. However, frequent returns to day roosts during the night suggest that *Mormopterus* regularly visited the same roosts for night and day resting.

Torpor and rewarming definitions

Torpor is often defined as a drop in T_{b} below 30 °C (Barclay et al. 2001). Because the difference between T_{b} and T_{skin} in torpid bats is $< \sim 2.0$ °C, even at low temperatures (Barclay et al. 1996), we considered bats to be in torpor whenever their T_{skin} fell below 28 °C for more than 30 min. On four occasions, torpid bats actively increased T_{skin} to approximately 26–27 °C for 10–20 min in the middle of a torpor bout and then cooled to near T_{a}. These occasions were considered as partial arousals and, thus, were included as a part of the bout.

Traces of T_{skin} of each arousal were visually compared to T_{a} for evidence of active or passive rewarming. Passive rewarming was characterised by T_{skin} tracking T_{a}. Arousals were considered to be active if T_{skin} rose well above T_{a} and with a final T_{skin}–T_{a} differential exceeding 8.0 °C. These active arousals took place at night or early in the morning when tree roosts occupied by bats were not exposed to solar radiation. On one occasion, T_{skin} of a bat increased from 23.2 °C (10:10 h) to 32.7 °C (10:30 h) over 20 min. We considered this arousal as active because the bat was roosting in a well-insulated tree roost, whose thick sides (~3–4 cm) prevented rapid passive increase of T_{skin} inside the roost.

Insects sampling

Insects were sampled with a light trap over three nights at the capture site during the first summer. In the second year, we intensified the insect sampling to investigate the effect of T_{a} on abundance of insects. We used two identical light traps placed ~200 m apart at the capture site to sample insects over 5 days. All traps were equipped with a 12 V ultraviolet light and a collecting container with a piece of paper towel sprayed with insecticide. The lights were turned on after sunset for 4 h on all of the sampling nights. This time was chosen because insect abundance generally peaks immediately after dusk, which coincides with high foraging activity of bats (Taylor and O'Neill 1988; Milne et al. 2005). Captured insects were desiccated in a drying oven over ~6 days at 70 °C and dry weight of insect samples was used for analysis.

Statistics

Statistical analyses were conducted in SPSS (IBM SPSS Statistics for Windows, IBM Corp., version 20.0, Armonk, NY) and R (R Development Core Team 2012). The differences in T_{a} between days with different patterns of heterothermy, the timing of foraging activity, duration of activity and resting periods between different days were compared using one-way ANOVA followed by a post hoc Tukey test. Independent samples *t* tests (correcting for unequal variances if necessary) were used to compare ambient conditions between years, total time bats were torpid between "one torpor bout" and "two torpor bouts" days, duration and rates of rewarming from torpor and dry weight of insects between the two summers. The timing of torpor bout entry and arousal from torpor were examined for non-random distribution using a Rayleigh's test for which we reported mean angle (mean time), *z* (Rayleigh's *Z* statistic for test of uniform circular distribution) and *r* (mean vector length which is a measure of dispersion from the mean) values. Then, a Watson–Williams test was computed to compare mean times of torpor entry and arousal (Zar 1996).

Relationships between torpor bout duration (TBD) and T_{skin}, the overall time bats spent torpid per day and T_{a}, T_{skin} and T_{a} were examined by fitting linear mixed-effects model, where each individual was entered as a random effect to account for repeated measurements. General linear modelling was used to analyse the effect of T_{a} on insect abundance with the trap as a factor. To compare TBD of bats between desert and temperate climates, we computed least-squares means of TBD and 95.0 % confidence intervals (CI) adjusted for the minimum T_{skin} for *Mormopterus* and long-eared bats *(Nyctophilus geoffroyi*, 8 g, Vespertilionidae) from a temperate region. Data on *Nyctophilus geoffroyi* were kindly provided by Chris Turbill and are based on the Fig. 5 published in Turbill et al. (2003a). We used the allometric equation of Riek and Geiser (2013) to compute the lower critical T_{skin} (the temperature at the lower border of the thermo-neutral zone below which thermoregulation commences to compensate for heat loss) of *Mormopterus* based on the mean T_{skin} measured during daytime resting phase on “no torpor” days. We report numerical values as mean ± SD, “*n*” for the number of individuals and “*N*” for the number of measurements.

Results

Weather conditions

The average daily T_a over the two tracking periods was 27.1 ± 4.3 °C in 2010–2011, and 26.1 ± 2.2 °C in 2011–2012. The minimum daily T_a was 19.5 ± 4.0 °C in 2010–2011, and 18.6 ± 2.3 °C in 2011–2012. The maximum daily T_a was 34.8 ± 5.3 °C in 2010–2011, and 34.5 ± 4.4 °C in 2011–2012. The average daily T_a ($t_{42.7} = 1.14$, $p = 0.262$), minimum daily T_a ($t_{43.5} = 0.97$, $p = 0.338$) and maximum daily T_a ($t_{44} = 0.17$, $p = 0.865$) did not differ significantly between two study periods. The lowest/highest T_a measured in 2010–2011 was 12.7/42.6 and 14.0/40.5 °C in 2011–2012. The research site received 152.4 mm of rain in December–January 2010–2011 and 82.8 mm in January–February 2012, well above the long-term average.

Torpor patterns

In total, we recorded 46 torpor bouts in *Mormopterus* during the two summers. Animals used three general patterns of heterothermy and entered torpor on 67.9 % ($n = 38$) of bat-days ($n = 56$).

On 32.1 % of bat-days, *Mormopterus* remained normothermic throughout the day (“no torpor” days; Fig. 1a). The mean T_{skin} measured for each individual during the daytime resting phase was 35.6 ± 1.5 °C (mean $T_a = 30.0 \pm 2.0$ °C; $n = 5$, $N = 18$), the mean minimum T_{skin} was 31.5 ± 2.4 °C (mean $T_a = 26.4 \pm 2.7$ °C; $n = 5$, $N = 18$) and mean maximum T_{skin} was 38.6 ± 1.3 °C (mean $T_a = 35.3 \pm 2.7$ °C; $n = 5$, $N = 18$). The highest single T_{skin} recorded during daytime resting was 40.5 °C ($T_a = 39.2$ °C; time: 14:47) and the lowest single T_{skin} was 27.8 °C ($T_a = 23.7$ °C; roost temperature = 22.0 °C; time 06:51).

On 50.0 % of bat-days, animals employed one torpor bout per day usually early in the morning and maintained normothermy throughout the rest of day (“one torpor bout” days). TBD varied from 0.6 to 9.2 h and was on average 3.7 ± 2.0 h ($n = 6$, $N = 26$; Fig. 1b). The mean minimum T_{skin} during torpor was 21.3 ± 3.8 °C (mean $T_a = 20.4 \pm 4.1$ °C; $n = 6$, $N = 28$). The lowest single T_{skin} recorded was 12.3 °C ($T_a = 14.7$ °C; roost temperature = 13.0 °C; time 06:15). *Mormopterus* entered torpor between 23:56 and 07:49 h and aroused between 04:47 and 12:54 h. Timing of both torpor entry (mean angle = 05:30 ± 01:50 h, $z = 20.60$, $r = 0.90$, $p < 0.001$; $n = 6$, $N = 26$) and arousal from torpor (mean angle = 09:04 ± 01:48 h, $z = 22.41$, $r = 0.90$, $p < 0.001$; $n = 6$, $N = 28$) was non-random (Fig. 2a).

On 17.9 % of bat-days, *Mormopterus* displayed two torpor bouts per day (“two torpor bouts” days). Bats employed at least one long torpor bout ranging from 4.4 to 16.9 h, with one exception of 39.3 h, and lasting on average for 13.3 ± 10.6 h ($n = 3$, $N = 9$). These torpor bouts were

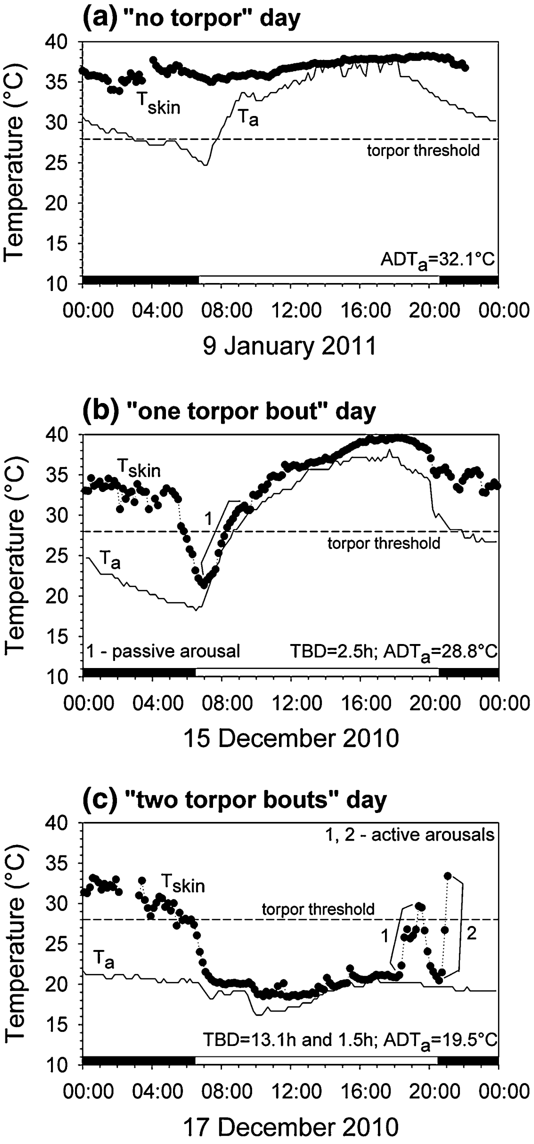

Fig. 1 T_{skin} of free-ranging *Mormopterus* (*dotted line*), T_a (*solid line*) and torpor threshold (*dashed line*) on “no torpor” (**a**), “one torpor bout” (**b**) and “two torpor bouts” (**c**) days with an example of long (06:15–19:24 h) and short (19:34–21:04 h) torpor bouts observed on a “two torpor bouts” day and passive (**b** *1*) and active (**c** *1*, *2*) arousals. ADT$_a$ = average daily T_a

preceded or followed by one short bout ranging from 0.5 to 2.5 h (1.4 ± 0.7 h; $n = 3$, $N = 9$) usually observed in the evening before foraging activity or during the night (Fig. 1c). The mean minimum T_{skin} during long torpor bouts was 18.1 ± 2.9 °C (mean $T_{\mathrm{a}} = 17.3 \pm 3.4$ °C; $n = 3$, $N = 9$) and 24.0 ± 2.9 °C (mean $T_{\mathrm{a}} = 21.4 \pm 3.8$ °C; $n = 2$, $N = 9$) during additional short bouts. The lowest single T_{skin} recorded during a long bout was 14.0 °C ($T_{\mathrm{a}} = 13.2$ °C; roost temperature = 12.5 °C; time 05:05) and 19.2 °C during a short bout ($T_{\mathrm{a}} = 15.7$ °C; roost temperature = 17.0 °C; time 02:57). Time of torpor entry (mean angle = 03:17 ± 03:12 h, $z = 4.45$, $r = 0.70$, $p = 0.008$; $n = 3$, $N = 9$) and arousal (mean angle = 13:37 ± 03:05 h, $z = 4.69$, $r = 0.72$, $p = 0.006$; $n = 3$, $N = 9$) for long bouts, as well as time of torpor entry (mean angle = 22:15 ± 02:54 h, $z = 5.05$, $r = 0.75$, $p = 0.003$; $n = 3$, $N = 9$) and arousal (mean angle = 23:39 ± 02:40 h, $z = 5.52$, $r = 0.78$, $p = 0.002$; $n = 3$, $N = 9$) for short bouts were non-randomly distributed (Fig. 2b).

Time of torpor entry did not differ between “one torpor bout” and “two torpor bouts” days ($F_{1,42} = 0.02, p = 0.880$, Watson–Williams test) but bats aroused later on days when two torpor bouts were exhibited ($F_{1,44} = 12.14$, $p = 0.001$, Watson–Williams test). Consequently, the overall time bats spent torpid per day (all torpor bouts combined) was longer when animals employed “two torpor bouts” pattern (14.7 ± 11.0 h) when compared to “one torpor bout” pattern (3.7 ± 2.0 h; $t_{8.2} = 2.98$, $p = 0.017$).

Overall TBD was negatively correlated with minimum T_{skin} (linear mixed-effects model: $t_{37} = 8.45$, $p < 0.001$, $R^2 = 0.50$; $n = 6, N = 44$; Fig. 3) and the overall time bats spent torpid per day was negatively correlated with average daily T_{a} (linear mixed-effects model: $t_{28} = 6.82, p < 0.001$, $R^2 = 0.64$; $n = 6$, $N = 35$; Fig. 4). The minimum daily T_{skin} for all bats was positively correlated with minimum daily T_{a} (linear mixed-effects model: $t_{55} = 10.57$, $p < 0.001$, $R^2 = 0.76$; $n = 8$, $N = 64$; Fig. 5).

When the relationship between patterns of heterothermy and T_{a} was analysed, average daily T_{a} differed significantly between each of the three patterns ($F_{2,44} = 31.14$, $p < 0.001$; Tukey tests, $p < 0.001$). *Mormopterus* were normothermic throughout days with the highest average daily T_{a} (30.1 ± 2.1 °C), one torpor bout per day occurred on days with a mild average daily T_{a} (26.3 ± 2.2 °C) and two torpor bouts were employed on days with the lowest average daily T_{a} (22.4 ± 2.8 °C). In addition, the minimum daily T_{a} ($F_{2,44} = 28.66$, $p < 0.001$) differed significantly between “no torpor” (22.7 ± 2.1 °C) and “one torpor bout” days (17.8 ± 2.3 °C; Tukey test, $p < 0.001$), “no torpor” and “two torpor bouts” days (16.0 ± 3.0 °C; Tukey test, $p < 0.001$), but did not differ between “one torpor bout” and “two torpor bouts” days (Tukey test, $p = 0.178$). The maximum daily T_{a} differed significantly ($F_{2,44} = 13.02$, $p < 0.001$) between “two torpor bouts” (29.5 ± 4.6 °C) and “one torpor bout” days (35.2 ± 3.8 °C; Tukey test, $p < 0.001$), “two torpor bouts” and

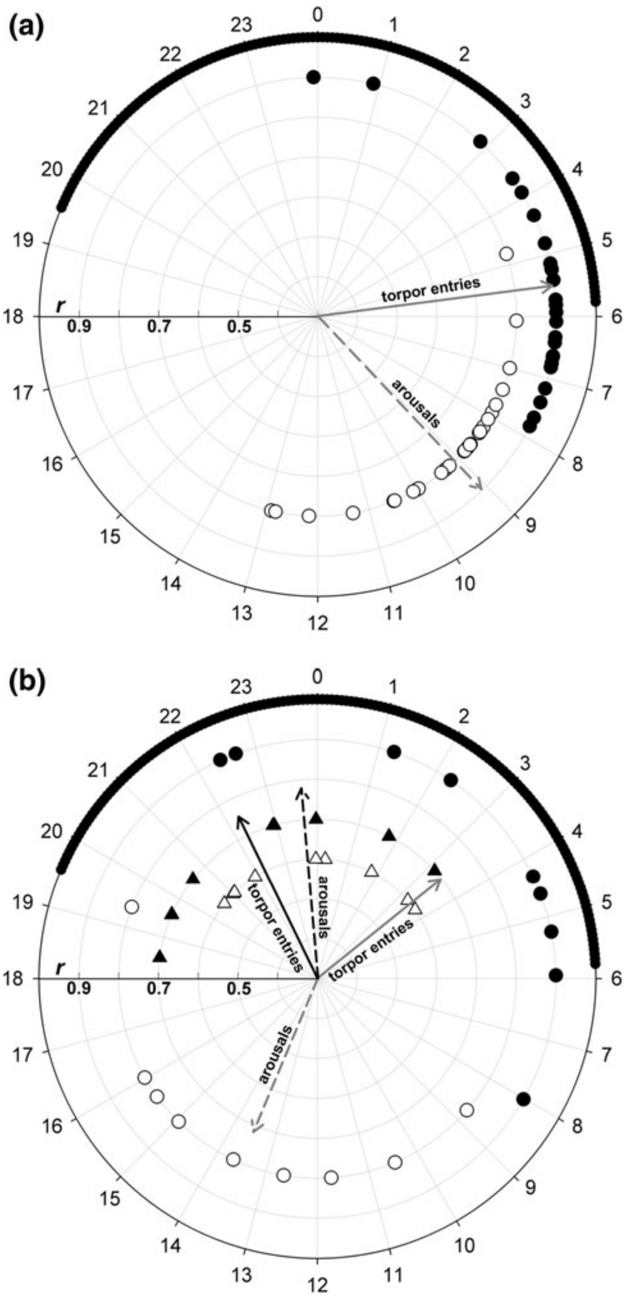

Fig. 2 Circular distribution of the time of day (24 h clock) for occurrence of torpor during “one torpor bout” (**a**) and “two torpor bouts” (**b**) days. *Black symbols*-torpor entries, *white symbols*-arousals. “two torpor bouts” days: *circles*-long torpor bouts; *triangles*-short torpor bouts. Position of *symbols* on different radial axes is for illustration only. The radial axis represents *r* (mean vector length, 0–1) which is a measure of dispersion from the mean, derived from the Rayleigh’s test. The position of vectors indicates mean times. *Solid vectors*-torpor entries, *dashed vectors*-arousals; *grey vectors*-torpor bouts on “one torpor bout” days and long torpor bouts on “two torpor bouts” days; *black vectors*-short torpor bouts on “two torpor bouts” days. The *black half-sphere* indicates the dark phase

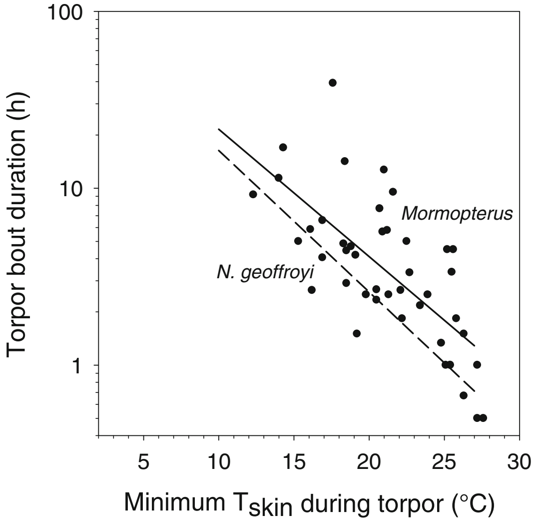

Fig. 3 Duration of torpor bouts as a function of minimum T_{skin} in *Mormopterus*, *solid line* [linear mixed-effects model: $t_{37} = 8.45$, $p < 0.001$, $R^2 = 0.50$; $\log_{10}$ TBD (h) = –0.072 × minimum T_{skin} (°C) + 2.054; $n = 6$, $N = 44$] and temperate *Nyctophilus geoffroyi*, *dashed line* only [linear mixed-effects model: $t_{54} = 10.19$, $p < 0.001$, $R^2 = 0.69$; $\log_{10}$ TBD (h) = –0.080 × minimum T_{skin} (°C) + 2.013; $n = 7$, $N = 62$] the equation was derived by reanalysing original data from Turbill et al. (2003a). Note, the *y* axis is log-transformed, therefore TBD in *Mormopterus* is about twofold that of *Nyctophilus*

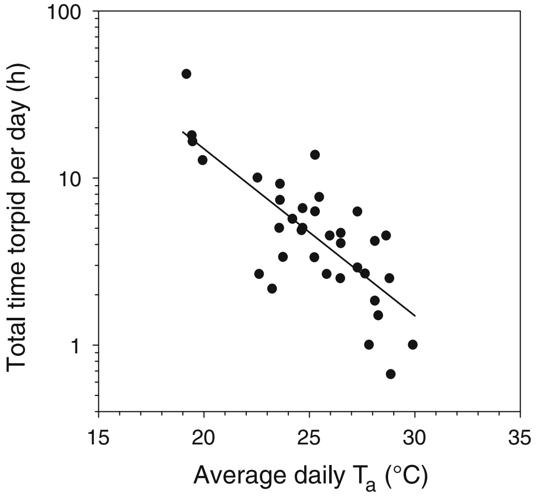

Fig. 4 Total time *Mormopterus* spent torpid per day (all torpor bouts combined) as a function of average daily T_a (linear mixed-effects model: $t_{28} = 6.82$, $p < 0.001$, $R^2 = 0.64$; $\log_{10}$ Total time torpid (h) = −0.100 × minimum T_{skin} (°C) + 3.175; $n = 6$, $N = 35$)

“no torpor” days (37.6 ± 2.6 °C; Tukey test, $p < 0.001$), but did not differ between “no torpor” and “one torpor bout” days (Tukey test, $p = 0.108$).

Rewarming patterns

Bats aroused from torpor using passive rewarming on 68.9 % ($n = 6$, $N = 31$; Fig. 1b: 1) and active rewarming on 31.1 % ($n = 4$, $N = 14$; Fig. 1c: 1, 2) of all measured arousals. Importantly, with one exception, active arousals were not preceded by passive rewarming. On this occasion, a bat rewarmed passively to $T_{\mathrm{skin}} = 22.7$ °C after which it used active heating. During “one torpor bout” days, bats employed active rewarming on 14.8 % ($n = 2$, $N = 4$) of arousals, and 55.5 % ($n = 3$, $N = 10$) of arousals during “two torpor bouts” days. In general, *Mormopterus* used passive rewarming during morning arousals and active rewarming was used usually in the evening or during the night and only occasionally in the morning.

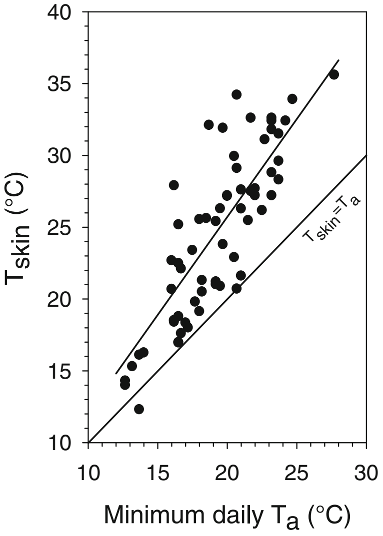

Fig. 5 Minimum daily T_{skin} of eight *Mormopterus* as a function of minimum daily T_a (linear mixed-effects model: $t_{55} = 10.57$, $p < 0.001$, $R^2 = 0.76$; minimum daily T_{skin} (°C) = 1.363 × minimum daily T_a (°C) − 1.541; $n = 8$, $N = 64$)

Times required for active arousals were on average shorter (30.6 ± 22.1 min) than passive arousals (171.2 ± 139.5 min; $t_{33.2} = 5.46$, $p < 0.001$) and mean maximum rate of active rewarming over 10 min was higher (0.3 ± 0.2 °C min^{-1}) than the passive rewarming (0.2 ± 0.1 °C min^{-1}; $t_{43} = 2.70$, $p = 0.010$). Nevertheless, maximum individual rates of rewarming over 10 min were 0.9 °C min^{-1} (passive) and 0.6 °C min^{-1} (active).

Activity patterns

Bats left their roosts 53.6 ± 37.5 min ($n = 8$, $N = 52$) after sunset irrespective of days with different patterns of heterothermy ($F_{2,49} = 3.0$, $p = 0.056$). In contrast, activity ended earlier ($F_{2,46} = 14.40$, $p < 0.001$) when “two torpor bouts” pattern (332.4 ± 188.6 min before sunrise; $n = 3$, $N = 9$) was displayed when compared to “one torpor bout” days (149.4 ± 115.2 min before sunrise; $n = 6$, $N = 24$) and “no torpor” days (76.1 ± 38.2 min before sunrise; Tukey tests, $p < 0.001$; $n = 5$, $N = 16$). The end of activity did not differ significantly between “one torpor bout” and “no torpor” days (Tukey test, $p = 0.131$).

Bats conducted 1–3 foraging bouts/night on “two torpor bouts” days and 1–5 on “one torpor bout” and “no torpor” days. On one occasion, during a cool and rainy day, a bat (only one monitored at that time) did not leave the roost at all and remained torpid overnight (mean night $T_a = 18.5$ °C).

Individual foraging bouts were significantly longer ($F_{2,11} = 5.69$, $p = 0.004$) when “one torpor bout” pattern (122.1 ± 101.8 min; $n = 6$, $N = 54$) was displayed when compared to “no torpor” days (70.9 ± 51.1 min; Tukey test, $p = 0.004$; $n = 5$, $N = 45$) but it did not differ between “one torpor bout” and “two torpor bouts” days (81.2 ± 24.7 min; Tukey test, $p = 0.158$; $n = 3$, $N = 16$), “no torpor” and “two torpor bouts” days (Tukey test, $p = 0.891$). Consequently, the overall time bats spent active per night was significantly longer ($F_{2,47} = 7.95, p = 0.001$) during “one torpor bout” nights (263.7 ± 105.4 min; $n = 6$, $N = 25$) when compared to “two torpor bouts” nights (130.0 ± 85.5 min; Tukey test, $p < 0.001$; $n = 3$, $N = 10$) but it did not differ between “no torpor” (212.7 ± 59.6 min; $n = 5$, $N = 15$) and “one torpor bout” days (Tukey test, $p = 0.204$), “no torpor” and “two torpor bouts” (Tukey test, $p = 0.074$). Individual resting periods between foraging bouts were 129.2 ± 69.5 min ($n = 8$, $N = 67$) and did not differ between days with different patterns of heterothermy ($F_{2,64} = 0.14, p = 0.865$).

Insect abundance

The mean dry weight of insect samples did not differ significantly between the two summers ($t_{2.0} = 1.55$, $p = 0.258$) and was 101.3 ± 9.1 g ($n = 3$) in 2010–2011 and 194.2 ± 103.1 g ($n = 3$, days with the highest dry weight of insect samples) in 2011–2012. However, as the average daily T_a increased the dry weight of insect samples per trap also increased [general linear model: $F_{2,7} = 9.25$, $p = 0.010$, $R^2 = 0.72$; $\log_{10}$ insect dry weight (g) $= 0.070 \times$ average daily T_a (°C) $+ 0.167$; $n = 10$] and the extreme values were 62.1 g per trap at the average daily $T_a = 23.2$ °C and 311.7 g at the average daily $T_a = 31.0$ °C.

Discussion

Our study provides the first data on the thermal biology of a free-ranging arid-zone molossid in summer. *Mormopterus* used torpor on 67.9 % of bat-days, and torpor bouts were longer under the same thermal conditions when compared to bats from milder climates, suggesting that torpor is an important physiological trait of this species in Australia’s arid zone. Arousals from torpor often were passive without an obvious active component, likely facilitated by hot summer weather in the desert.

As the climatic conditions during our study were unusual with above average rainfall resulting in higher insect abundance, our results may underestimate the use of torpor in these bats when compared to dry years. Perhaps, these good conditions explain why the overall torpor occurrence in *Mormopterus* was lower than, for example, in two temperate-zone vespertilionids i.e. *Nyctophilus geoffroyi*, 8.0 g, which employed torpor on 100.0 % of bat-days (Turbill et al. 2003a), and *Chalinolobus morio*, 7.9 g, that used torpor on 88.0 % of bat-days (Turbill 2006). Even subtropical *Nyctophilus bifax*, 10.0 g, used torpor in summer on 85.0 % of bat-days (Stawski and Geiser 2010a). Nevertheless, our study demonstrates that bats do use torpor extensively even at high T_a and when food is abundant. Importantly at any given T_a, torpor bouts were longer in *Mormopterus* than in bats from temperate and subtropical habitats. For example, *Mormopterus* employed long torpor bouts lasting up to 39.3 h at a maximum daily $T_a = 29.5$ °C, whereas temperate *Nyctophilus geoffroyi* remained torpid up to 40.5 h at a maximum daily T_a that was about 11 °C lower (18.6 °C; Turbill et al. 2003a). Mean TBD in *Mormopterus* was 13.3 h at an average daily $T_a = 22.4$ °C, whereas subtropical *Nyctophilus bifax* employed torpor bouts that were 4-times shorter (3.2 h) at a similar average daily $T_a = 21.2$ °C (Stawski and Geiser 2010b). Moreover, at the mean minimum $T_{skin} = 19.7$ °C, TBD for *Mormopterus* was 4.4 h (95.0 % CI 3.4, 6.1 h; $t_{11} = 10.24$, $p < 0.001$), almost twofold and significantly longer than the predicted TBD of 2.7 h (95.0 % CI 2.6, 2.9 h; $t_{11} = 8.21$, $p < 0.001$) in temperate *Nyctophilus geoffroyi* (Fig. 3). These data suggest that although TBD of bats generally increases at lower T_a, the “critical T_a” at which bats enter torpor and remain torpid is significantly higher in arid zone *Mormopterus* than in species from other habitats. Such differences in torpor expression between different climate zones raise the question as to why *Mormopterus* should employ frequent and longer torpor bouts at high T_a and whether it is a physiological trait of this particular species only or an adaptation to an arid environment.

One explanation could be the energetic benefits animals can gain from employing long torpor bouts at high T_a. Metabolic rates of small bats during torpor may be reduced by 90.0 % in comparison to normothermic values even at $T_a = 25.0$ °C, therefore, saving considerable amounts of energy (Geiser and Brigham 2000). Energetic savings can be enhanced by using longer and deeper torpor bouts during cool and wet weather. In our study, TBD increased with decreasing T_a (Fig. 4) and the longest torpor bout exceeded 24 h, suggesting that *Mormopterus* maximise torpor use during cool weather when heat loss will be increased. Appropriate use of heterothermy is particularly important for small mammals living in desert environments with unpredictable daily and seasonal fluctuations of T_a, food abundance and water availability (Lovegrove 2000; Munn et al. 2010).

High rates of evaporative water loss, during hot and dry weather (Withers 1992), could be another reason to remain torpid at high T_a. Torpor is commonly employed by many small arid-zone animals (Serventy and Raymond 1973; Cooper et al. 2005; Warnecke et al. 2008; Körtner and Geiser 2009; Doucette et al. 2012) perhaps because evaporative water loss can be dramatically reduced in torpid animals (Thomas and Geiser 1997; Maloney et al. 1999; Schmid and Speakman 2009). For example, evaporative water loss in torpid *Chalinolobus gouldii*, 17.5 g, can be reduced by 90.0 % (Hosken and Withers 1997). *Mormopterus* usually do not have access to water during daytime until nightfall and rely mainly on stored body fluids. Thus, remaining torpid longer at high T_a, rather than rewarming actively earlier in the day, should aid in saving water needed for evaporative cooling during the hot part of a day, as a low T_b will delay the time cooling required.

Bat activity is affected by activity and abundance of insects (Hickey and Fenton 1996; Meyer et al. 2004) and insect activity increases with increasing T_a (Taylor 1963; Turbill et al. 2003a). This general trend also occurred in nocturnal insect activity in our arid-zone site during summer. Therefore, high food availability on warm days could be a reason for *Mormopterus* to forage longer and limit torpor use, albeit the minimum nightly T_a (23.1 °C) measured during "no torpor" days was well below the thermoneutral zone of similar-sized *Nyctophilus geoffroyi* (29.1–33.2 °C; Geiser and Brigham 2000) and the predicted lower critical T_{skin} for *Mormopterus* (30.8 °C; Riek and Geiser 2013). On the contrary, low insect abundance during cooler days probably did not satisfy energetic needs without resorting to fat reserves and usually resulted in torpor use. In our study, *Mormopterus* reduced their overall activity times per night, returned to their roosts on average 5.5 h before sunrise on "two torpor bouts" days, and once a bat did not emerge at all during cool, wet weather and remained torpid overnight. However, whereas patterns of activity varied with T_a, surprisingly, the length of the intermittent resting periods remained constant. As one of the functions of resting is likely digestion (Kunz 1982), it appears likely that *Mormopterus* managed up to four "meals" on warm nights and a maximum of two on cool nights. Thus, low prey availability could be a strong stimulus for frequent torpor use in arid regions, particularly at low T_as.

Although torpor saves a lot of energy, active rewarming at the end of a torpor bout is costly. Therefore, rewarming passively from torpor with the increase in T_a, reduces the high energetic costs of active arousals (Lovegrove et al. 1999; Geiser and Drury 2003) and can be another reason why desert *Mormopterus* use torpor so often, and also contributed to the rather long TBD under warm conditions. Generally, active rewarming rates of *Mormopterus* were similar to those measured in temperate bats in summer and usually, active rewarming was faster than passive rewarming (Turbill et al. 2003a; Turbill 2006). However, on some occasions, passive arousals in *Mormopterus* were $\sim 1/3$ faster than active arousals due to rapid changes in T_a.

In many free-ranging bats, a combination of passive and active rewarming appears to be common, probably due to an exposure to cooler T_as in the studied environments (Chruszcz and Barclay 2002; Turbill et al. 2003a; Turbill et al. 2003b; Turbill 2006; Turbill and Geiser 2008; Stawski et al. 2009). In contrast, *Mormopterus*, except on one occasion, used entirely passive rewarming (68.9 %, mainly during the day time) throughout the arousal process. Factors like absence of a closed tree canopy, access to solar radiation, and pronounced daily T_a fluctuations can facilitate extensive use of passive rewarming in arid habitats. During our work, most of arousals occurred before noon when T_a usually reached thermoneutral levels, presumably permitting *Mormopterus* to use radiant heat and/or exposure to elevated T_a to rewarm passively without employing an active heating component. To our knowledge, this is the first observation of almost entirely passive rewarming in bats. However, this also has been observed in e.g. the tropical fat-tailed dwarf lemur, *Cheirogaleus medius* (Dausmann et al. 2005).

Our study is the first to show extensive torpor use by a desert bat in summer. It demonstrates that *Mormopterus* use more frequent and longer torpor bouts at relatively high T_a when compared to species from other regions which likely to minimise energy expenditure and water loss. Contributing further to energy conservation, *Mormopterus* often rewarm passively from torpor, which is possible because of pronounced daily T_a fluctuations and access to solar radiation in the desert.

Acknowledgments Special thanks go to Ingrid Witte and the New South Wales National Parks and Wildlife Service for providing accommodation, a quad bike and help with organising the field work. Ulrike Klöcker, Barb Hawerkamp and Dan Hough helped during the field work. We are grateful to Chris Turbill for permission to use his data on *Nyctophilus geoffroyi*. Stuart Cairns and Thomas Ruf helped and advised with statistical procedures. Daniella Rojas and Shannon Currie helped with different aspects of this project. The research was conducted under permits from the New South Wales National Parks and Wildlife Service and the UNE Animal Ethics Committee. Financial support was received from the University of New England to AB and the Australian Research Council to FG.

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