



# Temperature

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RESEARCH PAPER

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## How to keep cool in a hot desert: Torpor in two species of free-ranging bats in summer

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### ABSTRACT

Small insectivorous tree-roosting bats are among the most taxonomically diverse group of mammals in Australia's desert, yet little is known about their thermal physiology, torpor patterns and roosting ecology, especially during summer. We used temperature-telemetry to quantify and compare thermal biology and roost selection by broad-nosed bats *Scotorepens greyii* (6.3 g; n = 11) and *Scotorepens balstoni* (9.9 g; n = 5) in Sturt National Park (NSW Australia) over 3 summers (2010–13). Both vespertilionids used torpor often and the total time bats spent torpid was ~7 h per day. Bats rewarming using entirely passive rewarming on 44.8% (*S. greyii*) and 29.4% (*S. balstoni*) of all torpor arousals. Both bat species roosted in hollow, cracked dead trees relatively close to the ground (~3 m) in dense tree stands. Our study shows that torpor and passive rewarming are 2 common and likely crucial survival traits of *S. greyii* and *S. balstoni*.

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bats; desert; torpor; passive rewarming; *scotorepens greyii* and *scotorepens balstoni*

## Introduction

For small mammals, the maintenance of normothermy can be costly, especially in a resource-poor environment with extreme temperatures and unpredictable rainfall regimes such as deserts. Small, tree-roosting, insectivorous bats are particularly vulnerable to arid conditions due to their large surface area to volume ratio, high energetic costs of locomotion and little protection of their roost sites from pronounced ambient temperature ( $T_a$ ) fluctuations. Nevertheless, bats are one of the most diverse orders of mammals in Australia's desert, with 16 tree-roosting species (21% of all Australian bat species) of 3 families found in arid or semi-arid habitats,<sup>1</sup> but not all species are desert endemics and even some habitat generalists can be found. To avoid extreme desert conditions, many small-medium sized arid-adapted terrestrial species are burrow-dwelling.<sup>2</sup> Tree-roosting bats, on the other hand, have limited opportunities, because they cannot alter or create their roosts and require trees in specific stages of decay that contain cavities or have exfoliating bark.<sup>3</sup> Moreover, in Australia, due to an absence of primary vertebrate tree excavators (e.g. woodpeckers, family Picidae), bats tend to roost in decaying trees,<sup>3</sup> which are often dead and without canopy. Such roost trees provide less protection from solar radiation, and therefore bats

that occupy such roosts in a desert environment must be exposed to extreme heat at least occasionally.<sup>4</sup>

In addition to heat, insectivorous bats have to cope with fluctuating food availability that usually declines with a decrease in  $T_a$  and perhaps also extreme heat.<sup>5–7</sup> Even during summer,  $T_a$  can fall as low as 12°C at night in arid areas limiting foraging opportunities.<sup>7</sup> Therefore, the maintenance of constant high body temperature would be energetically counter-productive. Presumably for these reasons, many small insectivorous arid-zone mammals are heterothermic and employ torpor.<sup>7–14</sup>

Besides energetic benefits,<sup>15</sup> water conservation is a crucial aspect of torpor expression by small desert bats especially during summer. In torpid animals, overall water balance is achieved via improved levels of water retention that occur during processes such as respiration, defecation and urine formation.<sup>16,17</sup> In addition, torpid animals do not require to dissipate metabolic heat, which in turn helps to reduce rates of evaporative water loss.<sup>18,19</sup> This saved water could later be used for evaporative cooling during the hottest part of the day when  $T_a$  is often above the thermo-neutral zone.<sup>20</sup>

Although torpor saves energy and water, arousals at the end of a torpor bout can be energetically costly. To

minimise energetic costs of arousals, some small mammals, including bats, rewarm passively, which can be achieved by occupying poorly insulated roosts exposed to solar radiation,<sup>6,21</sup> or exposing themselves to the sun during an arousal process (i.e. basking).<sup>12</sup> Moreover, a recent study on inland freetail bats, (*Mormopterus petersi*, ~9 g; previously known as *Mormopterus* species 3), showed that this desert specialist can arouse from torpor using entirely passive rewarming without an obvious active component.<sup>7</sup> However, published data on how desert bats deal with energetic challenges and minimise costs of rewarming from torpor are limited to this one bat species, and it is unknown whether it is a common pattern employed by other Australian desert bats especially those that are not desert specialists, but occur over a wider range of habitats.

The aim of our study was therefore to collect and compare data on thermal biology, torpor patterns and roost selection of 2 desert bat species that are habitat generalists during the austral summer. The study species were the little broad-nosed bat (*Scotorepens greyii*, family Vespertilionidae) and the inland broad-nosed bat (*Scotorepens balstoni*, family Vespertilionidae). Because of pronounced daily fluctuations of  $T_a$ , food availability and exposure to extreme heat in summer, we hypothesized that thermal biology, torpor and roosting behavior of *S. greyii* and *S. balstoni* will show specific traits reflecting their arid habitat, perhaps moderated by their less developed tolerance to temperature extremes.<sup>4</sup> We specifically predicted that: a) desert *S. greyii* and *S. balstoni* will employ torpor readily in summer and torpor patterns will be similar between these 2 species; b) to escape temperature extremes, bats will select roosts in larger trees with a developed canopy; c) because of access to solar radiation and absence of closed tree canopy, *S. greyii* and *S. balstoni* will rewarm from torpor using mostly passive rewarming. These bat species are insectivorous, often roost in tree cavities and are common in Australia's arid, but also semi-arid and tropical habitats.<sup>1</sup> To our knowledge, no studies on thermal physiology and roost selection have been previously conducted on free-ranging *S. greyii* and *S. balstoni*.

## Results

### *Roosting behavior*

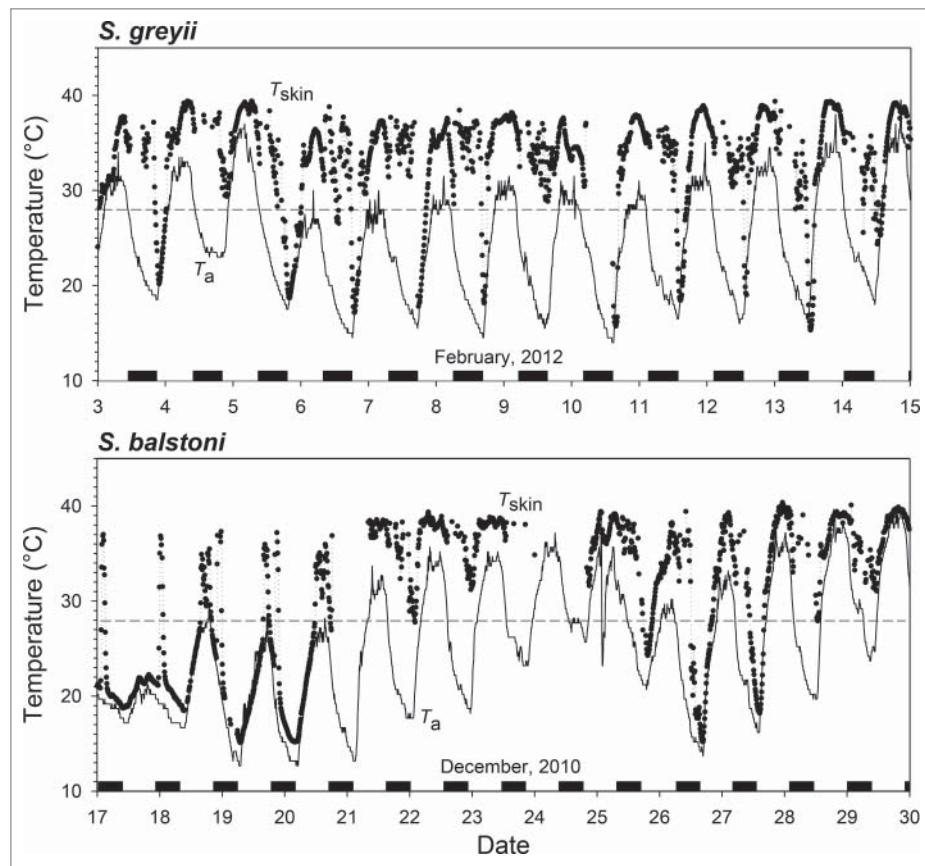
During summer *S. greyii* were tracked to 26 roosts (19 coolabahs, *Eucalyptus coolabah*, 4 river red gums,

*Eucalyptus camaldulensis*, 2 old fence posts and one gidgee, *Acacia cambagei*) and *S. balstoni* to 8 roosts (5 coolabahs, 2 gidgees and one river red gum). Most roosts of *S. greyii* were congregated near dams, whereas roosts of *S. balstoni* were located along dry creek beds. Both species roosted in crevices and hollow trunks of dead trees relatively close to the ground ( $3.3 \pm 1.7$  m;  $F_{1,12} = 0.29$ ,  $p = 0.598$ ;  $N = 33$ ). In addition, *S. balstoni* was also found roosting under exfoliating bark, and *S. greyii* roosted under flaking timber of a dead tree trunk and in a trunk of a fallen tree. The mean circumference of standing trees used for roosting was  $106.3 \pm 46.1$  cm and did not differ between species ( $t_{28} = 0.305$ ,  $p = 0.763$ ). Individual *S. greyii* occupied 1–4 separate roosts and *S. balstoni* 1–6. *S. greyii* switched roosts every  $1.9 \pm 1.2$  days, whereas *S. balstoni* stayed in the same roost longer ( $2.9 \pm 1.7$  days;  $t_{48} = 2.27$ ,  $p = 0.028$ ). The maximum distance an individual bat was roosting from its capture site was longer for *S. balstoni* ( $1.36 \pm 0.30$  km) than for *S. greyii* ( $0.44 \pm 0.33$  km;  $t_{13} = 4.80$ ,  $p < 0.001$ ).

### *Torpor patterns*

*S. greyii* was torpid on 83.3% ( $n = 10$ ,  $N = 50$ ) of all bat-days and showed 3 distinct thermoregulatory patterns (Fig. 1). Bats did not enter torpor on only 16.7% of bat-days ( $n = 7$ ;  $N = 10$ ). On 60.0% of bat-days animals employed a single torpor bout usually in the morning ranging from 0.5 to 27.1 h and lasting on average  $5.7 \pm 6.4$  h ( $n = 10$ ,  $N = 29$ ). On 23.3% of bat-days bats employed 2 to 4 torpor bouts throughout the day ranging from 0.7 to 11.5 h and averaging  $3.3 \pm 3.0$  h ( $n = 7$ ,  $N = 32$ ). The overall time *S. greyii* spent torpid/day was  $6.5 \pm 6.0$  h. On average *S. greyii* entered torpor at  $04:33 \pm 05:00$  h in the morning ( $z = 11.05$ ,  $r = 0.42$ ,  $p < 0.001$ ;  $n = 10$ ,  $N = 62$ ) and arousals occurred mid-morning at  $09:56 \pm 04:56$  h ( $z = 12.80$ ,  $r = 0.43$ ,  $p < 0.001$ ;  $n = 10$ ,  $N = 68$ ).

Torpor patterns in *S. balstoni* were similar to *S. greyii* (Fig. 1). Overall, *S. balstoni* entered torpor on 70.6% ( $n = 5$ ,  $N = 24$ ) of all bat-days and during these a single torpor bout pattern, usually in the morning, was employed on 44.1% of bat-days. TDB of this single bout ranged from 1.7 to 22.7 h and lasted on average  $8.3 \pm 7.6$  h ( $n = 4$ ,  $N = 14$ ). On 26.5% of bat-days animals exhibited 2 to 3 torpor bouts throughout the day each ranging from 0.5 to 17.4 h with average



**Figure 1.** Skin temperature fluctuations (upper trace, dotted line) of *S. greyii* and *S. balstoni* in summer with ambient temperature (lower trace, solid line) and torpor threshold (dashed line).

TBD of  $4.5 \pm 5.5$  h. The overall time bats spent torpid/day was  $9.1 \pm 7.3$  h. *S. balstoni* did not enter torpor on 29.4% of bat-days ( $n = 3$ ;  $N = 10$ ). On average, *S. balstoni* became torpid at  $03:14 \pm 05:02$  h ( $z = 5.80$ ,  $r = 0.42$ ,  $p = 0.003$ ;  $n = 5$ ,  $N = 33$ ), whereas arousal times showed a random distribution ( $z = 0.98$ ,  $r = 0.16$ ,  $p = 0.378$ ;  $n = 5$ ,  $N = 36$ ).

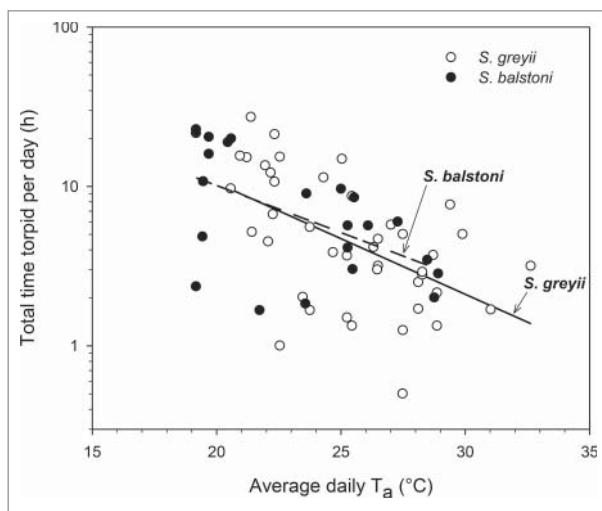
Total time bats spent torpid per day ( $\log_{10}$ ) increased with decreasing average daily  $T_a$  in a similar fashion in both species (Fig. 2). Both, the slopes of regressions (*S. greyii*:  $-0.08$ ; *S. balstoni*:  $-0.09$ ;  $p = 0.729$ ) as well as the intercepts did not differ between species (*S. greyii*: 2.74; *S. balstoni*: 2.90;  $p = 0.805$ ). Likewise, sex had no effect on this relationship (likelihood-ratio test, *S. greyii*:  $X^2 (1) = 0.005$ ,  $p = 0.943$ ;  $n = 10$ ,  $N = 42$ ; *S. balstoni*:  $X^2 (1) = 0.17$ ,  $p = 0.678$ ;  $n = 5$ ,  $N = 22$ ).

The lowest individual skin temperature ( $T_{skin}$ ) recorded for torpid bats was  $15.3^\circ\text{C}$  for *S. greyii* and  $15.1^\circ\text{C}$  for *S. balstoni*. The mean minimum torpor  $T_{skin}$  for each individual was similar for both species ( $t_{13} = 0.55$ ,  $p = 0.588$ ;  $N = 15$ ) and was  $20.1 \pm 2.8^\circ\text{C}$  for *S. greyii* and  $19.2 \pm 3.6^\circ\text{C}$  for *S. balstoni*. The minimum

$T_{skin}$  during torpor decreased rapidly with increasing TBD, but  $T_{skin}$  variability increased significantly after  $\sim 1$  h of torpor entry (Fig. 3a). Because after initial cooling  $T_{skin}$  during longer torpor becomes mainly a function of  $T_a$ , we used the differential between minimum  $T_{skin}$  during torpor and daily minimum  $T_a$  to further analyze  $T_{skin}$ -TBD relationship. This relationship was well described by an exponential function (Fig. 3b). The differential between minimum  $T_{skin}$  during torpor and minimum daily  $T_a$  reached a plateau during longer torpor bouts. While sex had no effect on this relationship for *S. greyii* (likelihood-ratio test,  $X^2 (1) = 0.09$ ,  $p = 0.759$ ;  $n = 10$ ,  $N = 62$ ), for *S. balstoni* it did ( $X^2 (1) = 8.43$ ,  $p = 0.003$ ;  $n = 5$ ,  $N = 33$ ). However, this effect was likely due to the significantly higher minimum daily  $T_a$  during the times when females were measured compared to the males ( $t_{32} = 6.68$ ,  $p < 0.001$ ;  $n = 5$ ,  $N = 34$ ).

#### Rewarming from torpor

*S. greyii* and *S. balstoni* used both active and passive rewarming from torpor or a combination of the two.

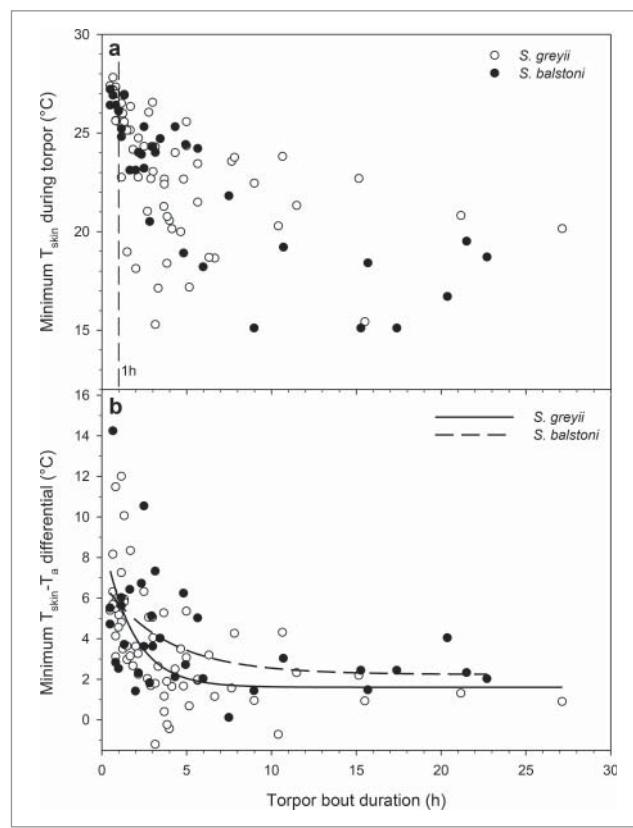


**Figure 2.** Total time bats spent torpid per day as a function of average daily  $T_a$  for *S. greyii* (linear mixed-effects model:  $t_{31} = 5.28$ ,  $p < 0.001$ ,  $R^2 = 0.71$ ;  $\log_{10}$  Total time torpid [h] =  $-0.080 \times$  average daily  $T_a$  [ $^{\circ}\text{C}$ ] + 2.690;  $n = 10$ ,  $N = 42$ ) and for *S. balstoni* (linear mixed-effects model:  $t_{16} = 7.46$ ,  $p < 0.001$ ,  $R^2 = 0.91$ ;  $\log_{10}$  Total time torpid [h] =  $-0.098 \times$  average daily  $T_a$  [ $^{\circ}\text{C}$ ] + 3.098;  $n = 5$ ,  $N = 22$ ).

Arousal from torpor using only passive rewarming occurred on 44.8% of all arousals for *S. greyii* ( $n = 10$ ,  $N = 30$ ) and 29.4% for *S. balstoni* ( $n = 4$ ,  $N = 10$ ). *S. greyii* used a combination of passive and active rewarming on 16.4% ( $n = 4$ ,  $N = 11$ ) and *S. balstoni* on 23.5% ( $n = 4$ ,  $N = 8$ ) of all arousals. *S. greyii* aroused via active heating on 38.8% of all arousals ( $n = 8$ ,  $N = 26$ ) and *S. balstoni* on 47.1% ( $n = 5$ ,  $N = 16$ ). In both species, majority of passive arousals occurred soon after sunrise between 06:00 and 08:00 when  $T_a$  started increasing. In contrast, most of active arousals occurred in the evening and during the night when  $T_a$  was below the torpor threshold of  $28^{\circ}\text{C}$  (contingency table,  $X^2(2) = 2.3$ ,  $p = 0.313$ , i.e. similar in both species) (Fig. 4). Mean maximum rate of active rewarming over 10 min was similar between species ( $F_{1,11} = 0.77$ ,  $p = 0.397$ ;  $n = 13$ ,  $N = 60$ ) and it was  $0.47 \pm 0.26^{\circ}\text{C min}^{-1}$ . Mean maximum rate of passive rewarming over 10 min was slower, but also similar in both species ( $0.12 \pm 0.07^{\circ}\text{C min}^{-1}$ ;  $F_{1,13} = 0.74$ ,  $p = 0.403$ ;  $n = 15$ ,  $N = 58$ ).

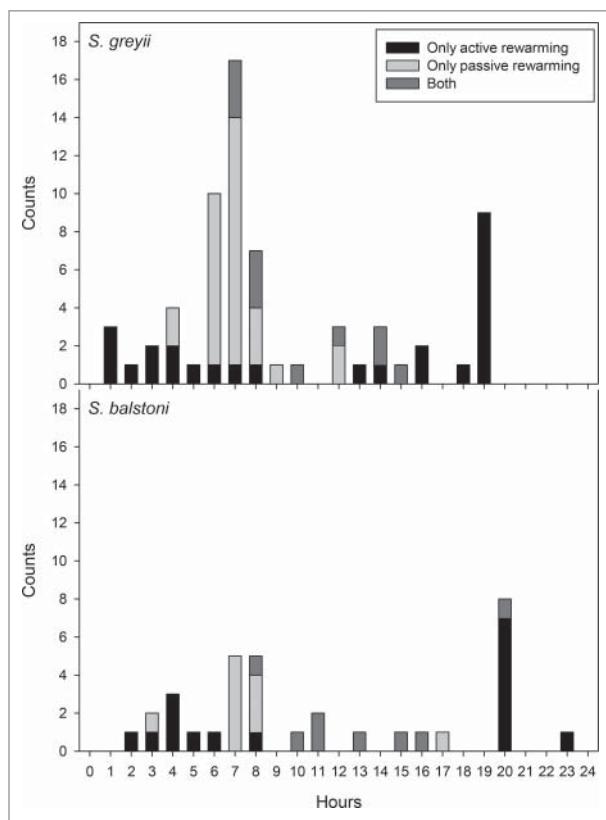
## Discussion

As predicted, our research showed that torpor was regularly employed in the wild by *S. greyii* and *S. balstoni* during summer. On average, these bats were torpid for 7 h per day and the mean minimum  $T_{\text{skin}}$



**Figure 3.** Minimum  $T_{\text{skin}}$  during torpor as a function of TBD (a) and the differential between minimum  $T_{\text{skin}}$  during torpor and minimum daily  $T_a$  as a function of TBD (b) described by an exponential function (*S. greyii*:  $y = 1.603 + 7.620 \times e^{(-0.570 \times x)}$ ,  $F_{2,59} = 22.25$ ,  $R^2 = 0.43$ ,  $p < 0.001$ ; *S. balstoni*:  $y = 2.237 + 4.594 \times e^{(-0.271 \times x)}$ ,  $F_{2,30} = 4.33$ ,  $R^2 = 0.22$ ,  $p = 0.022$ ). Note the increase in  $T_{\text{skin}}$  variability after 1 h into torpor (a, dashed line).

during torpor of individual torpid bats was usually  $\sim 20^{\circ}\text{C}$ . Such long periods of torpor expression can contribute to extensive energy savings for these desert bats.<sup>22,23</sup> Trees provide less thermal insulation from ambient conditions and generally constitute a drier environment than for example burrows or caves.<sup>2,24</sup> Therefore, tree-roosting bats will experience temperature extremes and desiccating conditions and those that can reduce energy expenditure and water loss when required, will have better prospects of surviving in hot desert climates. In summer, bats usually do not have access to drinking water for more than 14 h per day. During this period torpor can be advantageous because endogenous heat production and consequently body temperature are low in torpid animals thus, reducing water loss by evaporation and convection.<sup>18</sup> For example, evaporative water loss during torpor in an arid zone dasyurid, the little red kaluta, *Dasykaluta rosamondae*, at  $T_a$   $21^{\circ}\text{C}$  was only



**Figure 4.** Distribution of start times of reawakening from torpor over 24 h for *S. greyii* and *S. balstoni*. Most often, passive only arousals occurred between 06:00 and 08:00 in both species.

26% of that in normothermic individuals.<sup>25</sup> In torpid *C. gouldii*, found across all Australian climatic zones including arid habitats,<sup>1</sup> evaporative water loss was only ~13% of that in normothermic bats over  $T_a$  5–25°C.<sup>26</sup> These data suggest that torpor is an essential mean for maintaining water balance, especially in the arid zone.

The location of roost sites could be another factor that facilitates torpor use in small desert bats. *S. greyii* and *S. balstoni* preferred roosting sites in dense tree stands along creek lines or near dams and roosts were usually close to the ground (~3 m above ground). This preference might be explained by *S. greyii* and *S. balstoni* flight patterns. Both species are agile, slow fliers<sup>27</sup> and tend to forage in cluttered habitats under the tree canopy,<sup>1</sup> which presumably partially reflects their roost selection. However, the location of roosts can also affect the thermoregulatory behavior of bats. In the morning, roosts located in shaded habitats and close to the ground would be protected from the rising sun hence usually warm up slower (in the absence of wind) than roosts located in open areas and/or high above the ground. Indeed, it appears that the mean

maximum rate of passive rewarming of *S. greyii* and *S. balstoni* was significantly lower than in another desert species, *M. petersi* ( $0.20 \pm 0.15^\circ\text{C min}^{-1}$ ;  $F_{2,21} = 4.58$ ,  $p = 0.022$ ;  $n = 24$ ,  $N = 97$ ; Tukey,  $p = 0.018$ –0.047). This species, at the same study location, roosts in open areas, high above the ground (~5.5 m) and exposed to the sun.<sup>7</sup>

The effect of roost selection on thermal biology has been reported in other bats. For example, in summer and winter in a cool-temperate area, lesser long-eared bats, *Nyctophilus geoffroyi*, prefer roosting on the northern, sun-exposed side of a tree trunk likely to increase the extent of passive heating.<sup>6,21</sup> In winter, such selective roosting behavior allows this bat to rewarm passively up to 20°C from torpor, and thus reducing energetic costs of arousals.<sup>21</sup> Importantly, over-heating is an unlikely risk factor in mesic climates, whereas during a desert summer it is, and *S. greyii* and *S. balstoni* apparently prefer shaded roosts which can prolong torpor duration in the morning, and therefore enhance energy and water conservation.

Contrary to our prediction, most of the identified roost trees did not have canopy themselves, but were dead and hollow trunks with multiple holes and cracks situated among other trees. Due to this lack of insulation, roost temperature closely followed  $T_a$ , and therefore  $T_{\text{skin}}$  of *S. greyii* and *S. balstoni* decreased quickly and substantially after bats entered torpor, and it reached its minimum within ~1 hour after torpor entry (Fig. 3). Because  $T_{\text{skin}}$  in torpor is to a large extent a function of  $T_a$ ,<sup>28</sup> and the metabolic rate of small heterotherms decreases exponentially with a fall in body temperature,<sup>22,29,30</sup> a fast reduction in  $T_{\text{skin}}$  inside fast cooling roosts will result in a more pronounced reduction of energy and water expenditure. Moreover, such perforated roosts can actually facilitate convectional heat loss in normothermic bats during the day as generally heat exchange in mammals increases with wind speed.<sup>31,32</sup> However, this effect constitutes an energetic benefit only at  $T_{\text{as}}$  below body temperature and can become detrimental at very high  $T_{\text{as}}$ .

Consequently, and in contrast to bats from mesic areas,<sup>6,21,33–35</sup> both species of bats were able to take advantage of the daily  $T_a$  cycle and the intense solar radiation to often arouse from torpor using entirely passive rewarming (29 to 45% of all arousals). The selection of dead and hollow roost trees with the absence of a closed tree canopy probably facilitated this feat. Such entirely passive arousals in bats have

only been previously observed in *M. petersi* studied at the same location,<sup>7</sup> suggesting that entirely passive rewarming from torpor is an important and general strategy of desert bats to minimise energy expenditure and water loss. However, roost selection in this two habitat generalists suggested also the avoidance of temperature extremes with roosts generally being low to the ground and situated in stands of trees along creek lines and water bodies. It therefore appears that unlike *M. petersi*, the two *Scotorepens* species are spatially more constrained to wooded habitat and, in the case of *S. greyii*, perhaps to the proximity of water bodies that constitute only a small part of Australia's arid zone.

## Materials and methods

The study was conducted at Sturt National Park near the Mt Wood Homestead complex ~22 km east from Tibooburra ( $29^{\circ}28'S$ ,  $142^{\circ}14'E$ ) located in the north-western corner of New South Wales, Australia. Our study was undertaken during the austral summer 2010–11 (December–January), summer 2011–12 (January–7th March) and summer 2012–13 (January–February).

Sturt National Park is situated ~183 m above sea level and has an arid climate with 229.4 mm of annual rainfall and mean minimum and maximum  $T_a$  in January (midsummer) ranging from  $22.1^{\circ}\text{C}$  to  $36.2^{\circ}\text{C}$  (Tibooburra Post Office NSW, Bureau of Meteorology, Australia). The area includes grasslands and open gibber (ironstone pebbles) and clay pans as well as sparse, open woodlands along several creek lines dominated by river red gum (*Eucalyptus camaldulensis*), coolabah (*Eucalyptus coolabah*) and gidgee (*Acacia cambagei*).

Bats were captured using monofilament mist nets (Ecotone, Poland; mesh 14 mm) along dry creek beds, near 2 dams that provide fresh water to the Mt Wood complex and close to known roosts. We report data for a total of 11 *S. greyii* (6 males/5 females, BM  $6.3 \pm 0.7$  g) obtained over 60 bat-days during the summers 2011–12 (8 individuals) and 2012–13 (3 individuals) and 5 *S. balstoni* (3 males/2 females, BM  $9.9 \pm 0.9$  g) obtained over 34 bat-days during the summer 2010–11. Only adult non-reproductive and/or post-lactating individuals were used for this study. Captured bats were fitted with calibrated temperature-sensitive external radio transmitters (0.3–0.5 g LB-2XT/LB-

2NT, Holohil Systems Inc., Carp, Ontario, Canada) and radio-tracked daily to their roosts at sunrise following Bondarenco et al.<sup>7,4</sup> For each bat, a receiver/data logger was placed near the roost tree to remotely record  $T_{\text{skin}}$  data every 10 min<sup>36</sup> that were then downloaded to a portable computer. After locating the roost tree, a coaxial cable attached to a 4-m long fishing rod connected to a receiver (Icom, IC-R10) was used to determine the exact bat location. Each roost found was described by defining the tree species, circumference at breast height, living state, type of a roost and height determined with a clinometer or measuring tape.

$T_a$  was measured at 10-min intervals with temperature (resolution  $0.5^{\circ}\text{C}$ , iButton, DS1921G-F5) and temperature/humidity data loggers (resolution  $0.0625^{\circ}\text{C}$ , iButton Hygrochron, DS1923, Maxim Integrated Products Inc., Sunnyvale, California, USA) placed at 2 locations in the shade 2 m above the ground. Prior to use, iButtons were calibrated following Bondarenco et al.<sup>7</sup>  $T_a$  recorded at the research site ranged from  $12.7$  to  $48.1^{\circ}\text{C}$  over the study periods.

Bats were considered to be torpid when  $T_{\text{skin}}$  fell below  $28^{\circ}\text{C}$  for more than 30 min, which effectively distinguished between torpid and normothermic bats taking into account the typical  $2.0^{\circ}\text{C}$  maximal differential between body temperature and  $T_{\text{skin}}$  in small torpid animals.<sup>4,7,23,37,38</sup> Passive arousals are characterized by  $T_{\text{skin}}$  closely following the increase in  $T_a$ , whereas during active arousals  $T_{\text{skin}}$  rapidly deviates from  $T_a$  to above the torpor threshold ( $T_{\text{skin}} > 28^{\circ}\text{C}$ ) while  $T_a$  is either still below  $28^{\circ}\text{C}$  or sometimes even decreasing.<sup>21,7</sup>

## Statistics

Statistical analyses were performed in SPSS (IBM SPSS Statistics for Windows, IBM Corp., version 20.0, Armonk, NY) and R.<sup>39</sup> Interspecific comparison of slopes and intercepts of regression lines for relationships between the total time spent torpid vs. average daily  $T_a$ ,  $T_{\text{skin}} - T_a$  differential vs. torpor bout duration (TBD), rewarming rates and roost height were carried out using linear mixed-effects modeling (package "nlme" in R) with species set as a factor and individual bats as a random effect. A one-way ANOVA using linear mixed-effects models followed by a post-hoc Tukey test was used to compare the mean maximum rate of passive rewarming of *S. greyii*/*S. balstoni* to *M.*

*petersi*. The significance of sex was tested with likelihood-ratio tests by comparing two linear mixed models (package “lme4” in R), with and without the factor (sex). All model residuals were checked for homoscedasticity and normality by analyzing residual plots. A Rayleigh’s test was used to examine whether the timing of torpor bout entry and arousal from torpor differed significantly from a random circular distribution.<sup>40</sup> A contingency table analysis was carried out in SPSS to compare frequencies of different rewarming patterns between species. Independent samples t-tests (correcting for unequal variances if necessary) were used to compare the mean minimum individual  $T_{\text{skin}}$  during torpor, minimum daily  $T_a$  between days when  $T_{\text{skin}}$  of males and females of *S. balstoni* was measured, circumference of occupied tree roosts, number of days roosts were occupied by bats and distance from a capture site. We report numerical values as means  $\pm$  SD, “n” for the number of individuals and “N” for the number of measurements.

## Abbreviations

$T_a$	ambient temperature
TBD	torpor bout duration
$T_{\text{skin}}$	skin temperature

## Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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