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

Artiom Bondarenco, Gerhard Körtner, and Fritz Geiser
Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale NSW, Australia

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 rewarmed 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.

KEYWORDS
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, 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. 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. Moreover, in Australia, due to an absence of primary vertebrate tree excavators (e.g. woodpeckers, family Picidae), bats tend to roost in decaying trees, 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.

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. Even during summer, T_a can fall as low as 12°C at night in arid areas limiting foraging opportunities. 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.

Besides energetic benefits, 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. In addition, torpid animals do not require to dissipate metabolic heat, which in turn helps to reduce rates of evaporative water loss. 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.

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,2,6 or exposing themselves to the sun during an arousal process (i.e. basking).12 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.7 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 Ta, 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.4 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.1 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 ± 1.7 m; F1,12 = 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±46.1 cm and did not differ between species (t28 = 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 ± 1.2 days, whereas S. balstoni stayed in the same roost longer (2.9 ± 1.7 days; t48 = 2.27, p = 0.028). The maximum distance an individual bat was roosting from its capture site was longer for S. balstoni (1.36 ± 0.30 km) than for S. greyii (0.44 ± 0.33 km; t13 = 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 ± 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 ± 3.0 h (n = 7, N = 32). The overall time S. greyii spent torpid/day was 6.5 ± 6.0 h. On average S. greyii entered torpor at 04:33 ± 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 ± 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. TBD of this single bout ranged from 1.7 to 22.7 h and lasted on average 8.3 ± 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
TBD of 4.5 ± 5.5 h. The overall time bats spent torpid/day was 9.1 ± 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 ± 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 (log10) 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°C for S. greyii and 15.1°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 ± 2.8°C for S. greyii and 19.2 ± 3.6°C for S. balstoni. The minimum T_{skin} during torpor decreased rapidly with increasing TBD, but T_{skin} variability increased significantly after ~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.
Arousals 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* = 8, *N* = 26) 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*<sub>a</sub> started increasing. In contrast, most of active arousals occurred in the evening and during the night when *T*<sub>a</sub> was below the torpor threshold of 28°C (contingency table, *X*<sup>2</sup> (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*<sub>1,11</sub> = 0.77, *p* = 0.397; *n* = 13, *N* = 60) and it was 0.47 ± 0.26°C min<sup>−1</sup>. Mean maximum rate of passive rewarming over 10 min was slower, but also similar in both species (0.12 ± 0.07°C min<sup>−1</sup>; *F*<sub>1,13</sub> = 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*<sub>skin</sub> during torpor of individual torpid bats was usually ~20°C. Such long periods of torpor expression can contribute to extensive energy savings for these desert bats.22,23 Trees provide less thermal insulation form ambient conditions and generally constitute a drier environment than for example burrows or caves.2,24 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.18 For example, evaporative water loss during torpor in an arid zone dasyurid, the little red kaluta, *Dasykaluta rosamondae*, at *T*<sub>a</sub> 21°C was only...
26% of that in normothermic individuals. In torpid C. gouldii, found across all Australian climatic zones including arid habitats, evaporative water loss was only ~13% of that in normothermic bats over Ta 5–25°C. 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 and tend to forage in cluttered habitats under the tree canopy, 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 ± 0.15°C min⁻¹; F₂,₂₁ = 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. 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. 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. 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 Ta, and therefore Tskin 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 Tskin in torpor is to a large extent a function of Ta, and the metabolic rate of small heterotherms decreases exponentially with a fall in body temperature, a fast reduction in Tskin inside fast cooling roosts will result in a more pronounced reduction of energy and water expenditure. Moreover, such perforated roosts can actually facilitate convective heat loss in normothermic bats during the day as generally heat exchange in mammals increases with wind speed. However, this effect constitutes an energetic benefit only at Ta's below body temperature and can become detrimental at very high Ta's.

Consequently, and in contrast to bats from mesic areas, both species of bats were able to take advantage of the daily Ta 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, 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°28’S, 142°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-July 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*<sub>a</sub> in January (midsummer) ranging from 22.1°C to 36.2°C (Tibooburra Post Office NSW, Bureau of Meteorology, Australia). The area includes grasslands and open giber (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 ± 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 ± 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. For each bat, a receiver/data logger was placed near the roost tree to remotely record *T*<sub>skin</sub> data every 10 min 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*<sub>a</sub> was measured at 10-min intervals with temperature (resolution 0.5°C, iButton, DS1921G-F5) and temperature/humidity data loggers (resolution 0.0625°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. Ta recorded at the research site ranged from 12.7 to 48.1°C over the study periods.

Bats were considered to be torpid when *T*<sub>skin</sub> fell below 28°C for more than 30 min, which effectively distinguished between torpid and normothermic bats taking into account the typical 2.0°C maximal differential between body temperature and *T*<sub>skin</sub> in small torpid animals. Passive arousals are characterized by *T*<sub>skin</sub> closely following the increase in *T*<sub>a</sub>, whereas during active arousals *T*<sub>skin</sub> rapidly deviates from *T*<sub>a</sub> to above the torpor threshold (*T*<sub>skin</sub> > 28°C) while *T*<sub>a</sub> is either still below 28°C or sometimes even decreasing.

**Statistics**

Statistical analyses were performed in SPSS (IBM SPSS Statistics for Windows, IBM Corp., version 20.0, Armonk, NY) and R. Interspecific comparison of slopes and intercepts of regression lines for relationships between the total time spent torpid vs. average daily *T*<sub>a</sub>, *T*<sub>skin</sub>–*T*<sub>a</sub> 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.40 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 Tskin during torpor, minimum daily Ta between days when Tskin 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 ± SD, “n” for the number of individuals and “N” for the number of measurements.

**Abbreviations**

T<sub>a</sub> ambient temperature  
TBD torpor bout duration  
T<sub>skin</sub> skin temperature

**Disclosure of potential conflicts of interest**

No potential conflicts of interest were disclosed.

**Acknowledgments**

The authors thank the NSW National Parks and Wildlife Service (NPWS) staff especially Ingrid Witte, Barb Hawerkamp and Dan Hough for their assistance with organizing the field work. Accommodation and transport at Sturt National Park were kindly provided by the NPWS.

**Funding**

Financial support was received from the University of New England to AB and the Australian Research Council to FG.

**References**

[1] Churchill, S. Australian bats. Crows Nest: Allen & Unwin, 2008.

[2] Degen, A.A. Ecophysiology of small desert mammals. Berlin: Springer-Verlag, 1997.

[3] Kunz, TH, Lumsden, LF. Ecology of cavity and foliage roosting bats. In: Kunz, T, Fenton, B, eds. Bat ecology. Chicago: University of Chicago Press, 2003:3-89.

[4] Bondarenco, A, Körtner, G, Geiser, F. Hot bats: extreme thermal tolerance in a desert heat wave. Naturwissenschaften 2014; 101:679-85; PMID:25005222; http://dx.doi.org/10.1007/s00114-014-1202-2

[5] Taylor, LR. Analysis of the effect of temperature on insects in flight. J Anim Ecol 1963; 32:99-117; http://dx.doi.org/10.2307/2520

[6] Turbill, C, Körtner, G, Geiser, F. Natural use of heterothermy by a small, tree-roosting bat during summer. Physiol Biochem Zool 2003; 76:868-76; PMID:14988802; http://dx.doi.org/10.1086/378915

[7] Bondarenco, A, Körtner, G, Geiser, F. Some like it cold: summer torpor by freetail bats in the Australian arid zone. J Comp Physiol B 2013; 183:1113-22; http://dx.doi.org/10.1007/s00360-013-0779-7

[8] Serventy, V, Raymond, R. Torpidity in desert animals. Australia’s Wildlife Heritage 1973; 14:2233-40.

[9] Geiser, F. The role of torpor in the life of Australian arid zone mammals. Aust Mammal 2004; 26:125-35.

[10] Geiser, F, Pavey, CR. Basking and torpor in a rock-dwelling desert marsupial: survival strategies in a resource-poor environment. J Comp Physiol B 2007; 177:885-92; http://dx.doi.org/10.1007/s00360-007-0186-z

[11] Rambaldini, DA, Brigham, RM. Torpor use by free-ranging pallid bats (Antrozous pallidus) at the northern extent of their range. J Mammal 2008; 89.933-41; http://dx.doi.org/10.1644/08-MAMM-A-029.1

[12] Warnecke, L, Turner, JM, Geiser, F. Torpor and basking in a small arid zone marsupial. Naturwissenschaften 2008; 95:73-8; PMID:17684718; http://dx.doi.org/10.1007/s00114-007-0492-7

[13] Körtner, G, Geiser, F. The key to winter survival: daily torpor in a small arid-zone marsupial. Naturwissenschaften 2009; 96:525-30; PMID:19082573; http://dx.doi.org/10.1007/s00114-008-0492-7

[14] Munn, AJ, Kern, P, McAllan, BM. Coping with chaos: unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (Sminthopsis crassicaudata). Naturwissenschaften 2010; 97:601-5; PMID:20442980; http://dx.doi.org/10.1007/s00114-010-0670-2

[15] Speakman, JR, Thomas, DW. Physiological ecology and energetics of bats. In: Kunz, TH, Fenton, MB, eds. Bat ecology. Chicago: University of Chicago Press, 2003:430-90.

[16] Schmidt-Nielsen, K. Desert animals: physiological problems of heat and water. New York: Dover Publications, 1979.

[17] Levin, E, Plotnik, B, Amichai, E, Braulke, L, Landau, S, Yom-Tov, Y, Kronfeld-Schor, N. Subtropical mouse-tailed bats use geothermally heated caves for winter hibernation. Proc R Soc B-Biol Sci 2015; 282:2014-781; http://dx.doi.org/10.1098/rspb.2014.2781

[18] Bradley, WG, Yousef, MK. Small mammals in the desert. In: Yousef, MK, Horvath, SM, Bullard, RW, eds. Physiological adaptations: desert and mountain. New York: Academic Press, 1972:127-42.

[19] Geiser, F. Aestivation in mammals and birds. In: Navas, CA, Carvalho, JE, eds. Aestivation Molecular and physiological aspects. Heidelberg: Springer-Verlag, 2010:95-111.
[20] Cory Toussaint, D, McKechnie, AE. Interspecific variation in thermoregulation among three sympatric bats inhabiting a hot, semi-arid environment. J Comp Physiol B 2012; 182:1129-40; http://dx.doi.org/10.1007/s00360-012-0683-6

[21] Turbill, C, Geiser, F. Hibernation by tree-roosting bats. J Comp Physiol B 2008; 178:597-605; http://dx.doi.org/10.1007/s00360-007-0249-1

[22] Geiser, F, Brigham, RM. Torpor, thermal biology, and energetics in Australian long-eared bats (Nyctophilus). J Comp Physiol B 2000; 170:153-62; http://dx.doi.org/10.1007/s003600050270

[23] Geiser, F. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 2004; 62:239-74; PMID:14977403; http://dx.doi.org/10.1146/annurev.physiol.66.032102.115105

[24] Kunz, T, Fenton, B. Bat ecology. Chicago: University of Chicago Press, 2003.

[25] Withers, PC, Cooper, CE. Thermal, metabolic, and hydric physiology of the little red kaluta, Dasykaluta rosamondae (Dasyuromorphia: Dasyuridae). J Mammal 2009; 90:752-60; http://dx.doi.org/10.1644/08-MAMM-A-286R.1

[26] Hosken, DJ, Withers, PC. Temperature regulation and metabolism of an Australian bat, Chalinolobus gouldii (Chiroptera: Vespertilionidae) when euthermic and torpid. J Comp Physiol B 1997; 167:71-80; http://dx.doi.org/10.1007/s003600050049

[27] Bullen, R, McKenzie, NL. Bat airframe design: Flight performance, stability and control in relation to foraging ecology. Aust J Zool 2001; 49:235-61; http://dx.doi.org/10.1071/ZO00037

[28] Lyman, CP, Willis, JS, Malan, A, Wang, LC. Hibernation and torpor in mammals and birds. New York: Academic Press, 1982.

[29] Song, X, Körtner, G, Geiser, F. Thermal relations of metabolic rate reduction in a hibernating marsupial. Am J Physiol-Regulatory Integrative Comparative Physiol 1997; 273:R2097-R104.

[30] Willis, CK, Turbill, C, Geiser, F. Torpor and thermal energetics in a tiny Australian vespertilionid, the little forest bat (Vespadelus vulturinus). J Comp Physiol B 2005; 175:479-86; http://dx.doi.org/10.1007/s00360-005-0008-0

[31] Tregear, RT. Hair density, wind speed, and heat loss in mammals. J Applied Physiol 1965; 20:796-801; PMID:5838737

[32] Bakken, GS, Kunz, TH. Microclimate methods. In: Kunz TH, ed. Ecological and behavioral methods for the study of bats. Washington: Smithsonian Institute, 1988:303-32.

[33] Chruszcz, Bj, Barclay, RM. Thermoregulatory ecology of a solitary bat, Myotis evotis, roosting in rock crevices. Funct Ecol 2002; 16:18-26; http://dx.doi.org/10.1046/j.0269-8463.2001.00602.x

[34] Turbill, C, Law, BS, Geiser, F. Summer torpor in a free-ranging bat from subtropical Australia. J Therm Biol 2003; 28:223-6; http://dx.doi.org/10.1016/S0306-4565(02)00067-0

[35] Geiser, F, Stawski, C. Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. Integr Comp Biol 2011; 51:337-48; PMID:21700575; http://dx.doi.org/10.1093/icb/icr042

[36] Körtner, G, Geiser, F. Ecology of natural hibernation in the marsupial mountain pygmy-possum (Burramys parvus). Oecologia 1998; 113:170-8; http://dx.doi.org/10.1007/s004420050365

[37] Barclay, RM, Kalcounis, MC, Crampton, LH, Stefan, C, Vonhof, MJ, Wilkinson, L, Brigham, RM. Can external radiotransmitters be used to assess body temperature and torpor in bats? J Mammal 1996; 77:1102-6; http://dx.doi.org/10.2307/1382791

[38] Willis, CK, Brigham, RM. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. J Comp Physiol B 2003; 173:379-89; http://dx.doi.org/10.1007/s00360-003-0343-y

[39] R development Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, 2012.

[40] Zar, JH. Biostatistical analysis. Englewood Cliffs: Prentice Hall, 1996.