Will Temperature Effects or Phenotypic Plasticity Determine the Thermal Response of a Heterothermic Tropical Bat to Climate Change?

Clare Stawski*¤, Fritz Geiser

Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, New South Wales, Australia

Abstract

The proportion of organisms exposed to warm conditions is predicted to increase during global warming. To better understand how bats might respond to climate change, we aimed to obtain the first data on how use of torpor, a crucial survival strategy of small bats, is affected by temperature in the tropics. Over two mild winters, tropical free-ranging bats (Nyctophilus bifax, 10 g, n = 13) used torpor on 95% of study days and were torpid for 33.5±18.8% of 113 days measured. Torpor duration was temperature-dependent and an increase in ambient temperature by the predicted 2 °C for the 21st century would decrease the time in torpor to 21.8%. However, comparisons among Nyctophilus populations show that regional phenotypic plasticity attenuates temperature effects on torpor patterns. Our data suggest that heterothermy is important for energy budgeting of bats even under warm conditions and that flexible torpor use will enhance bats’ chance of survival during climate change.

Introduction

It is predicted that global warming will expose organisms to new thermal challenges and will result in poleward or altitudinal shifts of animals [1]. While a change in distribution to deal with climate change may be an option for some species, the response of animals is often too slow and not all can move, resulting in mismatching phenologies with potentially detrimental effects [2–3]. However, predictions on how animals might respond to climate change often rely on geographic ranges of species and the climate within these [4] and generally assume that species are static and have limited functional flexibility. Contrary to this, endothermic mammals, which have received little attention with regard to climate change [5], may adjust form and function to better suit the thermal conditions they were exposed to during their development [6–7]. This is especially true for heterothermic mammals capable of expressing torpor, which are known to be highly flexible in adjusting their energy requirements seasonally and regionally [8–13]. Importantly, the phenotypic plasticity of energy expenditure afforded by the opportunistic use of torpor appears to be a key factor in reducing the risk of extinction in mammals [14–15] and may be crucial in dealing with climate change and other anthropogenic disturbances.

Heterothermic endotherms use reductions in metabolic rate (MR) and body temperature (Tb) during periods of torpor for energy conservation [16]. Torpor is used by diverse birds and mammals, often when food is limited, but also without apparent energetic stress to enhance fat stores for future energy demanding events, or to avoid predators [17–20]. Heterothermy is used by members of more than half of all mammalian orders [14] and is expressed especially in small species because their thermoregulatory energy expenditure can become costly during exposure to low ambient temperatures (Ta).

Torpor use appears paramount in small temperate bats and it is well established that they often express a sequence of multiday torpor bouts (i.e. hibernation) during winter and short bouts of torpor lasting for part of the day in summer [21–23]. In contrast, it was believed in the past that bats inhabiting tropical regions do not use torpor at all because of mild environmental conditions [24]. This view is no longer supported because short bouts of torpor have been observed in captive tropical bats [25–27], and because subtropical bats express multiday torpor in the wild [28–30]. However, in the tropics essentially all information on the use of mammalian torpor in nature is currently limited to dwarf lemur species [31–34], despite the enormous diversity of tropical bats. Although bats comprise >20% of all mammals and the vast majority of these live in the tropics [27], only two individuals of a single species have been examined with regard to torpor in the wild [11].

Global warming is predicted to increase the numbers of bats exposed to tropical or at least warm conditions. Because this will affect energy use and foraging requirements, understanding the thermal biology of tropical bats in the wild will provide potential insights into how bats from other climates might respond to...
climate change. Although an increased $T_a$ will reduce energy expenditure for normothermic thermoregulation at high $T_h$, if bats do not use torpor at all their energy requirements will be substantially increased even under warm conditions [35]. The purpose of our study was twofold. We (i) aimed to provide the first long-term quantitative data on torpor use and activity patterns in relation to ambient conditions by tropical free-ranging northern long-eared bats, Nycotophilus bifax, that are entirely restricted to subtropical/tropical regions. We (ii) used these data and data from the literature to make predictions about how thermal energetics and torpor patterns of bats from tropical and other climate zones may be affected by climate change.

Materials and Methods

Permits to undertake the research were provided by the UNE Animal Ethics Committee (AEC08/046, AEC09/058) and Queensland Parks and Wildlife Service (WITK04955708). A small subset of the data were published previously [36], however, a substantial amount of new data were added and all were re-analysed.

The field study was undertaken over two consecutive austral winters in June 2008 and July/August 2009 at Djiru National Park (17°50’S, 146°03’E), located in the tropical north of the Australian east coast and within the northern parts of the distribution range of N. bifax [37]. During both years, $T_h$ was measured with temperature data loggers (±0.5°C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., USA) in the shade 2 m above the ground. Thermal conditions during the two winters were similar: the overall mean $T_a$ was 18.8 ± 0.2 m above the ground. Thermal conditions during the two winters in June 2008 and July/August 2009 were obtained for a total of 35 bat days ($n$ = 7 individuals, 4 females, 3 males; body mass: 10.4 ± 0.7 g.) in June 2008. During July/August 2009 data were obtained for a total of 78 bat days (n = 6 individuals, 4 females, 2 males; body mass: 9.9 ± 0.7 g.).

As the $T_p$-$T_{skin}$ differential during torpor is generally <2°C, we defined torpor bouts as the time when $T_{skin}$ was <28°C. Data analyses were performed using StatistiXL (V 1.8, 2007); data are reported as means ± SD ($n$ = number of individuals, $N$ = number of observations). Means of each individual were used to calculate means for repeated measures. Results were considered significant when alpha was <0.05. To determine whether timing of arousals and torpor entries differed significantly from random, a Rayleigh test was used. T-tests were used to compare independent means; data of the sexes were pooled because they were statistically indistinguishable. Linear regressions were fitted by the least squares method and ANCOVAs were used to compare linear regressions. If no difference in slope between individuals or study periods was observed, data were pooled and regressed together.

Results

Torpor Patterns

A total of 210 torpor bouts were recorded over both winters. Torpor was used on 83% (June 2008) and 100% (July/August 2009; both years combined 95%) of days on which data were collected. In both years, bats expressed different patterns of thermoregulation, entering 0 to 4 torpor bouts/day; some bats remained torpid for an entire day (5.7% of torpor days; Fig. 1).

The two most common temporal patterns were one torporbout/day (31.1%) and two torpor bouts/day (33.0%), typically with one bout in the morning and the other in the afternoon. Four bouts/day were rare (6.6%), but three bouts/day were relatively common (23.6%; Fig. 1), with the third bout occurring during the night before a possible early morning foraging period.

Mean torpor bout duration for both winters was 4.5 ± 3.1 h ($n$ = 13, $N$= 210; years did not differ: $P$ = 0.7, $T_{11}$ = 0.4). The longest torpor bout recorded was 33.3 h and a total of 31 torpor bouts (out of 210) were >10 h. Torpor bouts were negatively correlated with minimum $T_h$ ($R^2$ = 0.2, $P$< 0.001; Fig. 2). The two

![Figure 1](image.png)
longest torpor bouts recorded for each individual were strongly affected by minimum $T_a$ ($R^2 = 0.8$, $P < 0.001$; Fig. 2) and the thermal response for this relationship was pronounced ($Q_{10} = 10$). Skin Temperature

Mean daily minimum $T_{skin}$ in torpid *N. bifax* during both winters was $20.1 \pm 3.1^\circ C$ ($n = 13$, $N = 102$; years did not differ: $P = 0.1$, $T_{11} = 1.8$). The lowest individual $T_{skin}$ value recorded was $11.3^\circ C$ ($T_a = 10.6^\circ C$). The daily minimum torpid $T_{skin}$ was correlated with $T_a$ ($R^2 = 0.5$, $P < 0.001$; Fig. 3). The mean differential between daily minimum $T_{skin}$ during torpor and the corresponding $T_a$ was $2.1 \pm 1.7^\circ C$ ($n = 13$, $N = 101$; years did not differ: $P = 0.7$, $T_{0.4} = 0.4$).

Timing of Torpor and Activity

Entries into torpor in 2008 (Fig. 4) displayed a peak at a mean time (angle) of $8:14 \pm 5:10$ h ($n = 7$, $N = 43$); in 2009 the mean time was $2:50 \pm 5:15$ h ($n = 6$, $N = 167$; 2009), but timing of torpor entries did not differ significantly from random (2008: Rayleigh $Z = 0.3$, $P = 0.2$; 2009: $Z = 0.5$, $P = 0.2$). Arousals were non-randomly distributed in 2008 ($Z = 6.0$, $P = 0.002$) with a mean time of $16:20 \pm 4:17$ h ($n = 7$, $N = 43$), but not in 2009 (mean: $15:02 \pm 5:04$ h, $n = 6$, $N = 167$, $Z = 2.5$, $P = 0.1$). Evening arousals likely for foraging occurred at sunset $\pm 0:06$ h ($n = 7$, $N = 22$; 2008) and slightly before sunset $00:06 \pm 0:04$ h ($n = 6$, $N = 60$; 2009). The proportion of a night *N. bifax* remained normothermic.
during both winters was positively correlated with mean nightly $T_a$ ($R^2 = 0.4$, $P < 0.001$; Fig. 5).

**Discussion**

Our study provides the first long-term quantitative data of torpor use and patterns in a tropical bat in its natural environment. It also is the first to show that tropical bats can remain torpid for $>1$ day. While this was a rare occurrence, torpor was frequently used (95% of all study days) even though weather conditions were mild. Our extensive field study of *N. bifax* and a recent brief field study on two individual *N. geoffroyi* during winter in a tropical habitat [11] confirm earlier findings from laboratory work [25–26] that torpor is indeed widely used by tropical bats for energy conservation in the wild. Further, data on tropical bats and on other mammals such as lemurs and tenrecs from Madagascar [31–33] show that, contrary to the widely held view, torpor use is prevalent in tropical regions. Frequent use of torpor by bats during winter in tropical regions, as reported here for *N. bifax*, highlights the importance of energy conservation for small microbats even under relatively mild conditions.

Several different patterns of torpor were expressed by *N. bifax* during both winters, with a peak in arousals from torpor bouts just before sunset. The variation in use of torpor by *N. bifax* is likely in response to variations in weather conditions and food abundance and *N. bifax* were normothermic/active longer on warmer nights like other bat species [23,30]. For insectivorous bats specifically it makes sense to use more torpor at low $T_a$ to save energy when feeding is difficult. In the current study torpor bout duration at minimum $T_a$ varied widely above and below the regression line, whereas at minimum $T_a <14 ^\circ C$ all torpor bouts fell above the regression line (Fig. 2). This effect of $T_a$ may reflect insect availability, which decreased significantly at $T_a <16 ^\circ C$ in the study region [41]. It is also important to note in this context that the thermal response of torpor bout duration of *N. bifax* was pronounced ($Q_{10} = 10$), which is about 3-fold of that usually observed in temperate bats ($Q_{10} = 2.6$ to 3.9, [42]). This high thermal sensitivity will permit tropical *N. bifax* to use relatively long torpor bouts in response to a small reduction of $T_a$ and, on the other hand, be active for much of the night when $T_a$ increases.

The $T_{\text{skin}}$ of torpid *N. bifax* approached $T_a$ with a minimum $T_a - T_{\text{skin}}$ differential of $\sim 2 ^\circ C$. Even on particularly cold days when

![Figure 5. The proportion of a night that *N. bifax* spent normothermic as a function of mean nightly $T_a$. This relationship is represented by the following equation: proportion night normothermic $= -0.9+0.09(T_a - C)$; $R^2 = 0.4$, $P < 0.001$, $F_{1,95} = 51.1$. doi:10.1371/journal.pone.0040278.g005](image)

![Figure 6. Measured and predicted changes in torpor bout duration in relation to predicted increases in $T_a$. Measured (black bars) and predicted (white and grey bars) torpor bout duration in tropical and subtropical *N. bifax* (A), and in tropical and temperate *N. geoffroyi* (B). Measured values are those obtained at the tropical sites at the mean minimum $T_a$ ($T_a 16.4 ^\circ C$ and $T_a 16.4+2 ^\circ C$) *N. bifax*, $T_a 19.2 ^\circ C$ only for *N. geoffroyi* because no $T_a$-torpor bout duration regression is available. Predicted torpor bout durations were calculated from regressions in subtropical *N. bifax* [36] and from temperate *N. geoffroyi* in summer (white bars, [22]) and winter (grey bar, [23]). doi:10.1371/journal.pone.0040278.g006](image)
$T_{\text{skin}}$ was very low, bats apparently continued to thermo-conform because the $T_{\text{b}}-T_{\text{skin}}$ differential remained constant suggesting that torpid bats did not thermoregulate. The lowest $T_{\text{skin}}$ recorded was $11.3\, ^\circ\text{C}$, which is rather low for a tropical mammal and suggests that individuals of this population of $N$. bifax can approximate the low $T_{\text{b}}$ values characteristic of hibernation in cold climates [16,35]. This is supported by laboratory data showing that tropical $N$. bifax commenced thermoregulation during torpor only at $T_{\text{b}}$ of $6.7\, ^\circ\text{C}$ and the minimum $T_{\text{b}}$ was $7.3\, ^\circ\text{C}$ [43]. Therefore, the generally high $T_{\text{skin}}$ in the current study compared to cold-climate hibernators appears to be mainly a reflection of the high $T_{\text{b}}$ bats experienced. However, the minimum $T_{\text{b}}$ measured in the laboratory was also somewhat higher than in temperate hibernators and this trait appears to be selected by the $T_{\text{a}}$ animals are exposed to in the wild [8,36].

What are the implications of our data for the effect of climate change on bats? We used two approaches to assess this: (i) We assumed that the thermal physiology of bats is constant and estimated using data from the present study and published data how a predicted $T_{\text{b}}$ increase by $2\, ^\circ\text{C}$ will affect torpor patterns and consequently energy use, and (ii) used data on thermal biology from free-ranging subtropical and temperate $Nycotophilus$ populations to test these predictions.

If we (i) use data presented here and those on thermal energetics of tropical $N$. bifax [43], we can estimate energy expenditure during torpor from mean $T_{\text{skin}}$ and MR regressions because the animals were thermo-conforming and rewarmed largely passively, in comparison to normothermic thermoregulation over the same time period. At a mean $T_{\text{a}}$ of $18.8\, ^\circ\text{C}$, $N$. bifax remained torpid for $33.5\%$ of the time, or $8.02\, \text{h/day}$, with a mean $T_{\text{skin}}$ of $24.3\, ^\circ\text{C}$ [44]). Resting normothermic bats at $T_{\text{a}}$ of $18.8\, ^\circ\text{C}$ would have used $7,710\, \text{J}$, and the energy saved by using torpor would be $7,183\, \text{J}$ ($895.8\, \text{J/h}$) or $28\%$ of the daily energy expenditure of a temperate bat ($25.88\, \text{kJ/d}$, [45]). The thermal response of torpor bout duration (Fig. 2) predicts that a $2\, ^\circ\text{C}$ increase in $T_{\text{a}}$ will shorten the duration of torpor to $21.8\%$ of the time ($5.23\, \text{h/day}$), and energy expenditure during torpor will be $467\, \text{J}$. Resting normothermic bats at $T_{\text{b}}$ of $20.5\, ^\circ\text{C}$ would need less energy for thermoregulation ($4,131\, \text{J}$) and energy savings due to torpor would be $3,664\, \text{J}$ ($700\, \text{J/h}$) or $14\%$ of the predicted daily energy expenditure [45]. Thus, even at the higher $T_{\text{b}}$ energy savings by using torpor are substantial and biologically meaningful.

Pronounced discrepancies were observed when we (ii) examined whether and how the thermal biology of populations of bat species in the wild differs from that predicted from regressions. In $N$. bifax mean torpor bout duration of a subtropical population [36] is predicted to decrease from $3.0$ to $1.8\, \text{h}$ if $T_{\text{a}}$ increases by $2\, ^\circ\text{C}$ from the tropical mean minimum $T_{\text{b}}$ of $16.4\, ^\circ\text{C}$ to $18.4\, ^\circ\text{C}$ (Fig. 2, 6). However, measured torpor bout duration at the tropical site at $T_{\text{b}}$ of $16.4\, ^\circ\text{C}$ is in fact $3.0\, \text{h}$ (127% of predicted) and $2.4\, \text{h}$ at $T_{\text{b}}$ of $10.4\, ^\circ\text{C}$ (136% of predicted). This shows that temperature effects on torpor bout duration vary among populations and suggests that either the tropical bats have acclimated or have been selected to maintain relatively long torpor bouts at warm $T_{\text{a}}$. Measured and predicted values differ even more in the congener $N$. geoffroyi (Fig. 6), distributed over almost the entire Australian continent. Data from $N$. geoffroyi from a temperate region in summer [22] predict that torpor bout duration at the mean minimum $T_{\text{b}}$ of $19.2\, ^\circ\text{C}$ in tropical Northern Territory is only $1.7\, \text{h}$ and will decline to $1.2\, \text{h}$ with a $2\, ^\circ\text{C}$ rise of $T_{\text{a}}$. Measured torpor bout duration in tropical $N$. geoffroyi at a mean minimum $T_{\text{b}}$ of $19.2\, ^\circ\text{C}$ is in fact $4.9\, \text{h}$ [11], $2.0\, \text{h}$-times that predicted from temperate bats. Winter data [23] predict that torpor bout duration of temperate $N$. geoffroyi at a minimum $T_{\text{b}}$ of $19.2\, ^\circ\text{C}$ and a mean $T_{\text{skin}}$ of $26.2\, ^\circ\text{C}$ is only $1.0\, \text{h}$, only $21\%$ of that measured in the tropics.

As torpor is usually associated with cold, whereas climate change with global warming, what do our projections actually tell us about bats in a warming climate? During periods of high temperatures, heat waves are known to induce hyperthermia and can kill large pteropod bats [46]. However, pteropodids comprise only a rather small number (~20%) of bat species and many large members of this family may roost at exposed sites often directly affected by $T_{\text{a}}$ extremes. In contrast, most ‘microbats’ roost in sheltered areas like caves, mines, houses, under bark or leaves that are buffered from thermal extremes, and, in addition to using torpor, can also be tolerant of extremely high $T_{\text{a}}$ exceeding $50\, ^\circ\text{C}$ [47]. Thus, our and previously available data suggest that using torpor opportunistically and by being able to tolerate high $T_{\text{a}}$, small bats may be better equipped to deal with climate change than is predicted from bio-climatic data, especially those species that can shift their distribution to cooler habitats [49].

Obviously, there will be a limit to how far $T_{\text{a}}$ can rise before torpor will become ineffective and a tolerance of high $T_{\text{a}}$ will be exceeded. Moreover, some hibernating mammals are restricted to mountain tops that do not permit further altitudinal adjustments to climate change [2,49]. Consequently, those heterothermic mammals with a period of winter dormancy that is strongly dependent on historical phenological patterns, which are also often those restricted to limited mountain habitats, are likely to be adversely affected. Recent evidence also shows that hibernating bats are susceptible to new pathogens, such as white-nose syndrome, which kills bats by interfering with their seasonal hibernation [50]. In contrast, opportunistic heterothermic species and those able to use torpor efficiently even under varying thermal conditions, may be able to deal with climate change and other detrimental factors better than predictions from current models might suggest.

**Acknowledgments**

We thank Alexander Foster, Gerhard Körntner, Alexander Rick and Margaret Stawski for their help with field work.

**Author Contributions**

Conceived and designed the experiments: CS FG. Performed the experiments: CS FG. Analyzed the data: CS FG. Contributed reagents/materials/analysis tools: CS FG. Wrote the paper: CS FG.

**References**

1. Porter HO, Farrell AP (2008) Physiology and climate change. Science 322: 690-692
2. Inouye DW, Barr B, Armistage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. P Nad Acad Sci USA 97: 1630-1633
3. Visser ME (2012) Birds and butterflies in climate debt. Nature Clim Change 2: 77-78
4. Kearney M, Porter W (2009) Mechanistic modelling: combining physiological and spatial data to predict species’ range. Ecol Lett 12: 334-350
5. Boyles JG, Seebacher F, Smit B, McKechnie AE (2011) Adaptive thermoregulation in endotherms may alter responses to climate change. Integ Comp Biol 51: 676-690
6. Heath M, Ingram DL (1983) Thermoregulatory heat production in cold-reared and warm-reared pigs. Am J Physiol 244: R273-R278
7. Rick A, Geiser F (2012) Developmental phenotypic plasticity in a marsupial mammal. J Exp Biol 215: 1552-1558
8. Geiser F, Ferguson C (2001) Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feather-tailed gliders. J Comp Physiol B 171: 569-576
9. Dunbar MB, Brigham RM (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. J Comp Physiol B 180: 885–893.
10. Canale CI, Henry P-Y (2010) Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Climate Res 45: 133–147.
11. Geiser F, Stawski C, Bondarenko A, Pavy CR (2011) Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals? Naturwissenschaften 98: 447–452.
12. Zervanos SM, Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical bat. J Comp Physiol B 168: 233–239.
13. Turbill C, Geiser F (2009) Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften 96: 1235–1240.
14. Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC (2009) Lower extinction in sleep-or-hide mammals. Am Nat 173: 264–272.
15. Boyer BB, Barnes BM (1999) Molecular and metabolic aspects of mammalian hibernation. Bioscience 49: 713–724.
16. Carpenter FL, Huon MA (1988) A new function for torpor: fat conservation in a wild migrant hummingbird. Condor 90: 373–378.
17. Bieber C, Ruf T (2009) Summer dormancy in edible dormice (Glis glis) without energetic constraints. Naturwissenschaften 96: 165–176.
18. Stawski C, Geiser F (2010) Fat and fed: frequent use of summer torpor in a subtropical bat. Naturwissenschaften 97: 29–35.
19. Geiser F, Brigham RM (2012) The other functions of torpor. In: Ruf T, Bieber C, Arnold W, Millesi E, eds. Living in a seasonal world. Berlin Heidelberg: Springer-Verlag. 109–121.
20. Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Tenton MB, eds. Bat Ecology. Chicago: University of Chicago Press. 430–492.
21. Turbill C, Körtner G, Geiser F (2003) Natural use of torpor by a small, tree-roosting bat during summer. Physiol Biochem Zool 76: 868–876.
22. Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. J Comp Physiol B 178: 597–606.
23. Kendrew RE (1970) Thermoregulation in bats. In: Slaughter BH, Walton DW, eds. About bats. Dallas: Southern Methodist University Press. 188–232.
24. Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal, the northern blossom-bat Macroglossus minimus (Megachiroptera). J Comp Physiol B 168: 233–239.
25. Kelm DH, von Helversen O (2007) How to budget metabolic energy: torpor in a small Neotropical mammal. J Comp Physiol B 177: 667–677.
26. Geiser F, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. Integr Comp Biol 51: 317–348.
27. Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat (Nyctophilus bifax). J Comp Physiol B 179: 435–441.
28. Kelm DH, van Helversen O (2007) How to budget metabolic energy: torpor in a small Neotropical mammal. J Comp Physiol B 177: 667–677.
29. Geiser F, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. Integr Comp Biol 51: 317–348.
30. Liu J-N, Karasov WH (2011) Hibernation in warm hibernacula by free-ranging Formosan leaf-nosed bats, Hipposideros trivittatus, in subtropical Taiwan. J Comp Physiol B 181: 125–135.
31. Daunmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429: 825–826.
32. Lovegrove BG, Grinfin F (2008) Torpor and hibernation in a basal placental mammal the lesser hedgehog tenrec Echinops telfairi. J Comp Physiol B 178: 691–705.
33. McKechnie AE, Milski K (2011) Heterothermy in Afrotropical mammals and birds: a review. Integr Comp Biol 51: 349–363.
34. Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66: 239–274.
35. Geiser F (2009) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66: 239–274.
36. Stawski C (2012) Comparisons of variables of torpor between populations of a hibernating subtropical/tropical bat from different latitudes. In: Ruf T, Bieber C, Arnold W, Millesi E, eds. Living in a seasonal world. Berlin Heidelberg: Springer-Verlag. 99–108.
37. Churchill S (2008) Australian Bats, 2nd edn. Crows Nest: Allen and Unwin.
38. Barclay RMR, Kalcounis MC, Crampton LH, Stefan C, Vonhof MJ, et al. (1996) Can external radiotransmitters be used to assess body temperature and torpor in bats? J Mammal 77: 1102–1106.
39. Körtner G, Geiser F (2009) Torpor and activity patterns in free-ranging sugar gliders Petaurus breviceps (Marsupialia). Oecologia 123: 350–357.
40. Barclay RMR, Lausen CL, Hollis L (2001) What’s hot and what’s not: defining torpor in free-ranging birds and mammals. Can J Zool 79: 1885–1890.
41. Richards GC (1989) Nocturnal activity of insectivorous bats relative to temperature and prey availability in tropical Queensland. Aust Wildlife Res 16: 151–158.
42. Twee JW, Twee J, Brack V (1985) The duration of the period of hibernation of three species of vespertilionid bats. II Laboratory studies. Can J Zool 63: 2955–2961.
43. Stawski C, Geiser F (2011) Do season and distribution affect thermal energetics of a hibernating bat endemic to the tropics and subtropics? Am J Physiol 301: R342–R347.
44. Schmid J, Speakman JR (2009) Torpor and energetic consequences in free-ranging grey mouse lemurs Microcebus murinus: a comparison of dry and wet forests. Naturwissenschaften 96: 609–620.
45. Schmid J, Speakman JR (2009) Torpor and energetic consequences in free-ranging grey mouse lemurs Microcebus murinus: a comparison of dry and wet forests. Naturwissenschaften 96: 609–620.
46. Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying foxes. Proc R Soc B 275: 419–425.
47. Maloney SK, Bruneer GN, Bullenstein R (1999) Thermoregulation in the Angelina free-tailed bat Motu condylurus: A small mammal that uses hot roosts. Physiol Biochem Zool 72: 382–396.
48. Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418: 313–316.
49. Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. J Comp Physiol B 163: 153–157.
50. Warnecke L, Turner JM, Bollinger TK, Lorch JM, Misra V, et al. (2012) Inoculation of bats with European Geomyces destructans supports the novel pathogen hypothesis for the origin of white-nose syndrome. Proc Natl Acad Sci 109: 6999–7003.