Chapter 9
Comparison of Variables of Torpor Between Populations of a Hibernating Subtropical/Tropical Bat at Different Latitudes

Clare Stawski

Abstract Torpor use differs among heterothermic species and data comparing populations of a single hibernating species at different latitudes could reveal how animals adapt to different climates. I investigated variables of torpor in free-ranging *Nyctophilus bifax*, a hibernating subtropical/tropical insectivorous microbat, during winter from a subtropical region and a tropical region. Mean torpor bout duration was significantly shorter and mean minimum skin temperature of torpid bats was significantly higher in the tropical population in comparison to the subtropical population. In both populations torpor bout duration was negatively correlated with ambient temperature and the slope of this relationship differed significantly ($P = 0.02$) between the populations when examined under the same thermal conditions. The differences found in these variables of torpor were most likely due to regional differences in weather and insect abundance and suggest that populations of heterothermic mammals can adapt or acclimatize to the local climate of the habitat that they occupy, even when thermal conditions are mild.

C. Stawski
Centre for Behavioural and Physiological Ecology, Zoology,
University of New England, Armidale, NSW 2351, Australia

Present Address
C. Stawski (✉)
Institute of Environmental Sciences, Jagiellonian University,
ul. Gronostajowa 7, 30-387 Kraków, Poland
e-mail: clare.stawski@gmail.com

9.1 Introduction

In most regions of the world, weather and temperature change daily and seasonally and generally influence food supply. During winter in temperate regions when ambient temperatures (T_a) are reduced or during the dry season in tropical regions, many plants cease to grow and insects reduce or halt activities. Decreases in food availability in turn will affect the energy balance of many animals. Endotherms are especially affected as they need large amounts of energy to maintain high, normothermic body temperatures (T_b), particularly at low T_a (Bartholomew 1982). However, many animals use a variety of energy saving mechanisms to overcome such periods and the most effective of these is torpor, which is characterized by controlled reductions in T_b, metabolic rate (MR) and water loss (Geiser 2004). Torpor is employed by a wide variety of animals and is especially prolific among small mammals (Geiser and Körtner 2010) due to their large surface area to volume ratio, which increases heat loss during cold exposure. Torpor use has been well documented in temperate species (e.g. Hall 1832; Hock 1951; Speakman and Thomas 2003; Geiser 2006; Turbill and Geiser 2008), but until recently relatively few quantitative data on torpor use in subtropical and tropical species were available (for review see Geiser and Stawski 2011).

Even fewer studies have compared variables of torpor between populations of a single species inhabiting different climates. Climate and weather patterns vary between regions and it is possible that the use of torpor may vary among populations of a species whose range encompasses various habitats. Generally, latitude and elevation do affect the variables and energetics of torpor (Geiser and Ferguson 2001; Fenn et al. 2009). For example, woodchucks (*Marmota monax*) increase the length of torpor bouts in the more northern latitudes of their range, i.e. where winters are colder (Zervanos et al. 2010). Different populations of big brown bats (*Eptesicus fuscus*) and eastern red bats (*Lasiurus borealis*) are also known to differ in the thermal physiology of torpor bouts (Dunbar and Brigham 2010). Therefore, populations of the same species appear to be able to adapt variables of torpor and thermal physiology to the local climate conditions of the habitat they occupy.

The thermal physiology of *Nyctophilus bifax*, a hibernating Australian microbat endemic to subtropical/tropical regions, differed between a subtropical and a tropical population primarily in regard to the T_a at which torpid bats defended their T_b (Stawski and Geiser 2011). This was suggested to be an adaptation to the climate of the region where each population resided. In the current analysis I compared the differences in variables of torpor specifically during winter between a tropical and a subtropical population of *N. bifax*. I predicted that torpor bout durations would be shorter and shallower during winter in the tropical region in comparison to the subtropical region. Further, I hypothesized that local weather conditions would affect variables of torpor of both subtropical and tropical *N. bifax*, but that these relationships would differ between the regions.

9.2 Materials and Methods

Field studies were undertaken during the Austral winter to obtain data on the differences in variables and patterns of torpor. This research was conducted at two sites (i) the subtropical Iluka Nature Reserve (29°24′S, 153°22′E) during July/August 2007 and (ii) ∼2,000 km north at the tropical Djiru National Park (17°50′S, 146°03′E) during June 2008 and July/August 2009. Some of the data collected from these studies have been published previously (Stawski et al. 2009; Stawski and Geiser 2010), however, new data have been added and all data have been re-analyzed for this comparison. Throughout the study periods T_a was measured ∼2 m off the ground in the shade with data loggers (±0.5°C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, California, USA).

Mist nets were used to capture a total of eight *N. bifax* from the subtropical region and a total of 13 *N. bifax* from the tropical region. Once captured, a small patch of fur was removed from between the shoulder blades of each individual and a temperature-sensitive radio-transmitter (∼0.5 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) was attached to the exposed skin using a latex-based adhesive (SkinBond, Smith and Nephew United, Mount Waverley, NSW, Australia). Before attachment to the bat each transmitter was calibrated to the nearest 0.1°C in a water bath between 5 and 40°C against a precision thermometer. Each individual was released at the site of capture following this procedure. On the subsequent morning each individual was located via radio-tracking and their roost locations were marked with flagging tape. An antenna and a remote receiver/logger (Körtner and Geiser 2000) were placed within range of the bats' transmitter signal. This receiver/logger recorded the pulse interval of the transmitter signal once every 10 min and data from the receiver/loggers were downloaded every 2–5 days to prevent loss of data. Data were converted into skin temperatures (T_{skin}) of the bat and torpor bouts included any period of time that T_{skin} was <28°C for periods >30 min. This definition of torpor was used as it has previously been suggested that a $T_b < 30$°C is appropriate to define torpor (Barclay et al. 2001) and because it has often been shown that the difference between T_{skin} and T_b of a small torpid animal is <2°C.

Statistical analyses were conducted using Stastitixl (V 1.8, 2007) and null hypotheses were rejected if alpha was <0.05. The means of each individual were used to calculate means involving repeated measures and data were reported as means ±SD (n = the number of individuals or days, N = the number of observations). t tests were used to compare the two regions and ANCOVAs were used when comparing linear regressions. Data from the two winters at Djiru National Park (June 2008 and July/August 2009) were combined as no differences were found.

Table 9.1 Mean ± SD for the given environmental variables during winter for the tropical site ($n = 50$ days) and subtropical site ($n = 29$ days)

Region	Mean min T_a (°C)	Mean max T_a (°C)	Mean daily T_a fluctuations (°C)	Mean daily T_a (°C)	Mean nightly T_a (°C)
Tropical	16.2 ± 2.4	21.9 ± 1.7	5.8 ± 2.4	18.8 ± 1.6	17.7 ± 2.1
Subtropical	8.2 ± 2.2	17.4 ± 2.3	9.2 ± 1.9	12.4 ± 2.2	10.9 ± 2.4
P-value	<0.001	<0.001	<0.001	<0.001	<0.001

Significance of difference from two sample t tests

Table 9.2 Mean ± SD for the given variables for all free-ranging *N. bifax* during winter from the tropical and subtropical sites

Region	Body mass (g)	Longest individual bouts (h)	Mean torpor bout duration (h)	Daily minimum T_{skin} (°C)
Tropical	10.2 ± 0.7 (13)	11.4 ± 8.6 (13)	4.5 ± 3.1 (13, 210)	20.1 ± 3.1 (13, 102)
Subtropical	10.1 ± 1.3 (8)	83.7 ± 27.6 (8)	26.8 ± 11.3 (8, 114)	14.7 ± 2.4 (8, 147)
P-value	0.9	<0.001	<0.001	<0.001

Significance of difference from two sample t tests from the means of individuals. Body mass at capture. The brackets show: the number of individuals, the number of observations

9.3 Results

During winter at the tropical site T_a ranged from a minimum of 10.6°C to a maximum of 25.3°C; at the subtropical site T_a ranged from a minimum of 4.0°C to a maximum of 25.0°C. Mean minimum T_a, mean maximum T_a, mean daily (24 h) T_a, and mean nightly (sunset–sunrise) T_a were all significantly lower at the subtropical site in comparison to the tropical site (Table 9.1). However, the mean daily (24 h) fluctuations of T_a were significantly higher at the subtropical site in comparison to the tropical site (Table 9.1). The timing of sunset differed between the two field sites ($P < 0.001$) and at the subtropical site sunset occurred at 17:11 ± 00:04 h ($n = 29$) and at the tropical site sunset occurred at 17:52 ± 00:07 h ($n = 50$).

Body mass of individuals did not differ between the tropical and subtropical populations (Table 9.2). However, the length of the longest torpor bout recorded in a subtropical individual (128.5 h) was ∼fourfold longer than the longest torpor bout recorded in a tropical individual (33.3 h) and the mean of all the individuals' longest bouts was ∼sevenfold longer in the subtropical population compared to the tropical population (Table 9.2). Further, mean torpor bout duration was ∼sixfold longer in the subtropical population in comparison to the tropical population (Table 9.2). Even when compared under similar thermal conditions (minimum T_a during each torpor bout in the range of 10.5–19.5°C), mean torpor bout duration was also significantly longer (∼twofold) in the subtropical population (11.3 ± 8.0 h, $n = 8$, $N = 52$) in comparison to the tropical population (5.3 ± 4.8 h, $n = 13$, $N = 165$; $P < 0.001$). Mean daily minimum T_{skin} was 5.4°C lower in the subtropical population in comparison to the tropical population
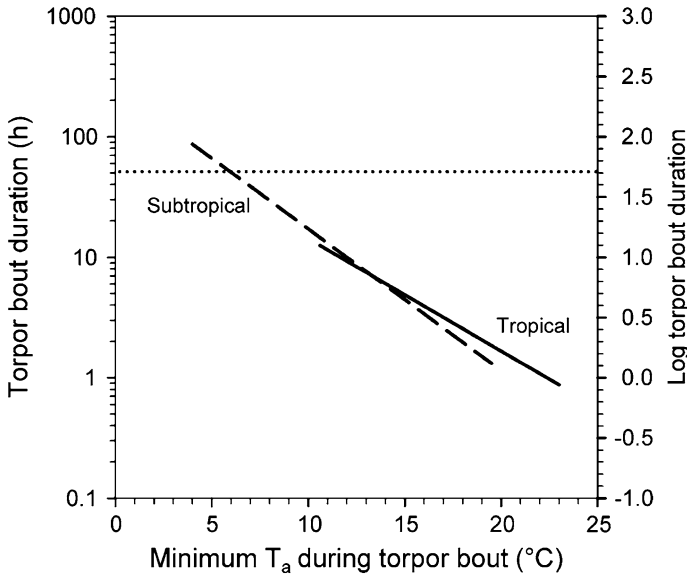
Fig. 9.1 The relationship between duration of torpor bouts ($\log_{10}$) and minimum T_a during winter at the tropical site (*solid line*; $\log_{10}$ TBD $= 2.1-0.09[T_a°C]$; $R^2 = 0.2$, $P < 0.001$, $F_{78,131} = 1.4$) and during winter at the subtropical site (*dashed line*; $\log_{10}$ TBD $= 2.4-0.12[T_a°C]$; $R^2 = 0.7$, $P < 0.001$, $F_{25,82} = 21.8$). The *dotted horizontal line* represents torpor bout durations of 48 h

(Table 9.2). However, when compared under similar thermal conditions (corresponding T_a in the range of 10.5–16.5°C), mean daily minimum T_{skin} did not differ between the subtropical population (16.9 ± 2.5°C, $n = 8$, $N = 45$) and the tropical population (16.7 ± 2.1°C, $n = 13$, $N = 46$; $P = 0.7$).

Torpor bout duration and the minimum T_a experienced during each torpor bout were negatively correlated in both the tropical population ($\log_{10}$ TBD $= 2.1-0.09[T_a°C]$, $R^2 = 0.2$, $P < 0.001$, $F_{78,131} = 1.4$; Fig. 9.1) and the subtropical population ($\log_{10}$ TBD $= 2.4-0.12[T_a°C]$, $R^2 = 0.7$, $P < 0.001$, $F_{25,82} = 21.8$; Fig. 9.1). For this relationship both slope ($P = 0.1$) and intercept ($P = 0.8$) did not differ between the populations. However, when this relationship was compared under similar thermal conditions (minimum T_a during each torpor bout in the range of 10.5–19.5°C) there was no common slope ($P = 0.02$) between the tropical and subtropical populations.

Daily minimum T_{skin} and the corresponding T_a during winter were positively correlated for both the tropical population (minimum $T_{skin}[°C] = 2.4 + 1.0[T_a°C]$; $R^2 = 0.5$, $P < 0.001$, $F_{61,39} = 3.0$; Fig. 9.2) and the subtropical population (minimum $T_{skin}[°C] = 9.1 + 0.6[T_a°C]$; $R^2 = 0.3$, $P < 0.001$, $F_{24,119} = 4.9$; Fig. 9.2). The slope differed significantly ($P < 0.001$) between the populations for this relationship. In contrast, there was a common slope ($P = 0.6$) and intercept ($P = 0.4$) between the populations when this relationship was compared under similar thermal conditions (corresponding T_a in the range of 10.5–16.5°C).

Fig. 9.2 The relationship between daily minimum T_{skin} and the corresponding T_a during winter at the tropical site (*solid line*; minimum T_{skin} [°C] = 2.4 + 1.0[T_a°C]; R^2 = 0.5, P < 0.001, $F_{61,39}$ = 3.0) and during winter at the subtropical site (*dashed line*; minimum T_{skin} [°C] = 9.1 + 0.6[T_a°C]; R^2 = 0.3, P < 0.001, $F_{24,119}$ = 4.9). The *dotted regression line* represents $T_b = T_a$
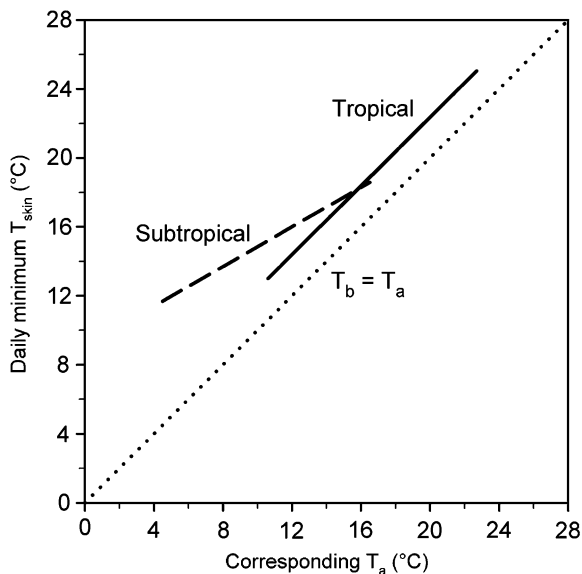

9.4 Discussion

The weather conditions recorded during winter differed significantly between the regions such that, as expected, in the northern tropical part of their range *N. bifax* were experiencing much milder winters in comparison to the southern subtropical part of their range. Further, during winter the number of insects captured during a night at the tropical site was significantly greater (~fourfold) than that captured at the subtropical site (Stawski 2010). These differences in weather patterns and food availability between the tropics and subtropics likely were responsible, as predicted, for differences in the variables of torpor between the subtropical and tropical populations of *N. bifax*. For example, mean torpor bout durations and the longest torpor bouts recorded during winter were significantly shorter in tropical *N. bifax* in comparison to subtropical *N. bifax*, likely a result of the more favorable foraging conditions in the tropical habitat. Nevertheless, as both tropical and subtropical *N. bifax* have to deal with a reduction in food availability during winter (Stawski 2010) and T_as that are frequently well below the TNZ in both regions, both populations show frequent use of torpor to conserve energy.

Similarly to temperate hibernating bats (Ransome 1971; Park et al. 2000; Rambaldini and Brigham 2008; Turbill and Geiser 2008), the amount of time an individual spent torpid was negatively affected by the minimum T_a experienced during each torpor bout in both the tropical and subtropical populations. The slope and intercept of this relationship did not differ between the populations, however, when this relationship was compared between the populations under similar thermal conditions the slopes did differ resulting in longer torpor bouts in subtropical individuals. While previous studies have shown that MR and temperature

Fig. 9.3 Population-specific threshold T_a as a function of the mean of the lowest 10% of minimum T_a among temperate (*N. geoffroyi*, taken from Geiser and Brigham 2000), subtropical (*N. bifax*, taken from Stawski and Geiser 2011) and tropical (*N. bifax*, taken from Stawski and Geiser 2011) regions. This linear relationship is described by the following equation: population-specific threshold T_a (°C) = $-2.91 + 1.24 T_a$ (°C), $r^2 = 0.9$ (Stawski and Geiser 2011)
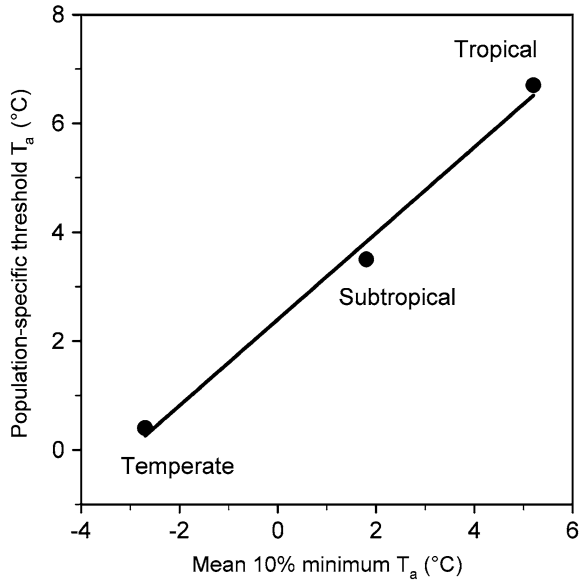
influence torpor bout durations (French 1985; Geiser and Kenagy 1988), the data presented here suggest that there are also other factors that influence the length of torpor bouts. Some of these factors are ecological, for example, at a similar T_a there were twice as many insects captured during winter at the tropical site in comparison to the subtropical site (Stawski 2010), suggesting that tropical *N. bifax* would have more success foraging for food and therefore able to avoid prolonged torpor bouts at the same T_a when subtropical *N. bifax* cannot. Therefore, additionally to temperature and MR, the amount of food an individual obtains before becoming torpid or able to obtain after arousal may influence the length of a torpor bout (Geiser and Mzilikazi 2011).

Even though torpor bout duration varied between the populations, the lack of difference in MRs (Stawski and Geiser 2011) strongly suggests that like *N. bifax* from the subtropical population (Stawski et al. 2009), *N. bifax* from the tropical population are also able to enter prolonged bouts of torpor when conditions are unfavorable. Nevertheless, along with different torpor bout durations, the population-specific threshold T_a at which torpid individuals thermoregulate also varied between the populations, similarly to big brown bats (Dunbar and Brigham 2010). There was a positive relationship found between the population-specific threshold T_a of *Nyctophilus* species and the ambient conditions of the specific habitat they occupy (Fig. 9.3; Stawski and Geiser 2011), which also reveals that there are some long-term adaptations to the climate in which a population resides.

The higher daily minimum torpid T_{skin} in tropical *N. bifax* in comparison to subtropical *N. bifax* is likely due to the higher T_as experienced during the tropical winter in comparison to the subtropical winter, as under the same thermal

conditions daily minimum torpid T_{skin} was similar between the populations. Further, under the same thermal conditions the slope of the positive relationship between daily minimum torpid T_{skin} and the corresponding T_a did not differ between the populations, but the slope did differ when all of the data was examined together. The slope of this relationship for the tropical population was similar to $T_b = T_a$, however, the regression line for the tropical population was $\sim 2°C$ above $T_b = T_a$, which is the typical difference between T_{skin} and T_b. On the contrary, the slope of this relationship for the subtropical population was much shallower in comparison to both the tropical population and $T_b = T_a$. During the studies at both the subtropical and tropical field sites T_a was only measured in one location and not at each individual roost. Therefore, the shallower regression line for the subtropical population may be explained by the use of thermally buffered roosts, such as tree hollows, by the bats and that consequently they were experiencing much smaller daily T_a fluctuations within the roosts in comparison to the ambient conditions outside of the roost (Stawski et al. 2008). Conversely, it appears that individuals in the tropical population were most likely roosting in more open locations, such as under leaves, as their T_{skin} largely approximated the measured T_a (Stawski et al. 2008). Roost choice is important to hibernators because, while thermally buffered roosts will promote larger energy savings during prolonged torpor bouts as experienced by subtropical *N. bifax*, the large daily passive fluctuations of thermally unstable roosts can eradicate the large energetic costs of the arousal process for tropical *N. bifax* that arouse daily by passively re-warming (Chruszcz and Barclay 2002; Brack 2007; Turbill and Geiser 2008; Boyles and McKechnie 2010; Cory Toussaint et al. 2010).

My study has shown that even though the thermal physiology of *N. bifax* is largely similar throughout their range, there is some plasticity in torpor use that allows local populations to match the climatic and ecological conditions of the habitat they occupy. These variations most likely represent a response to the local energetic challenges faced by a population. The data presented here add to the limited knowledge that populations of the same species inhabiting different latitudes may vary in regard to torpor use and thermal physiology (Geiser and Ferguson 2001; Fenn et al. 2009; Dunbar and Brigham 2010; Zervanos et al. 2010). They demonstrate that research on a single population may lead to incorrect assumptions about the thermal biology and habitat usage of the species as a whole. Further, such data is particularly important for species with wide distribution ranges (Boyles et al. 2011) and may provide information on how animals respond to changes in the climate and ecology of their habitats.

References

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

Bartholomew GA (1982) Body temperature and energy metabolism. In: Gordon MS (ed) Animal physiology: principles and adaptations. MacMillian Publishing Co. Inc., New York, pp 333–406

Boyles JG, McKechnie AE (2010) Energy conservation in hibernating endotherms: Why "suboptimal" temperatures are optimal. Ecol Model 221:1644–1647

Boyles JG, Seebacher F, Smit B, McKechnie AE (2011) Adaptive thermoregulation in endotherms may alter responses to climate change. Integr Comp Biol 51:676–690

Brack V Jr (2007) Temperatures and locations used by hibernating bats, including *Myotis sodalis* (Indiana bat), in a limestone mine: implications for conservation and management. Environ Manage 40:739–746

Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. Funct Ecol 16:18–26

Cory Toussaint D, McKechnie AE, van der Merwe M (2010) Heterothermy in free-ranging male Egyptian free-tailed bats (*Tadarida aegyptiaca*) in a subtropical climate. Mamm Biol 75:466–470

Dunbar MB, Brigham RM (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. J Comp Physiol B 180:885–893

Fenn AM, Zervanos SM, Florant GL (2009) Energetic relationships between field and laboratory woodchucks (*Marmota monax*) along a latitudinal gradient. Ethol Ecol Evol 21:299–315

French AR (1985) Allometries of the durations of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. J Comp Physiol B 156:13–19

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Geiser F (2006) Energetics, thermal biology, and torpor in Australian Bats. In: Zubaid A, McCracken GF, Kunz TH (eds) Functional and evolutionary ecology of bats. Oxford University Press, New York, pp 5–22

Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). J Comp Physiol B 170:153–163

Geiser F, Ferguson C (2001) Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feathertail gliders. J Comp Physiol B 171:569–576

Geiser F, Kenagy GJ (1988) Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. Physiol Zool 61:442–449

Geiser F, Körtner G (2010) Hibernation and daily torpor in Australian mammals. Aust Zool 35:204–215

Geiser F, Mzilikazi N (2011) Does torpor of elephant shrews differ from that of other heterothermic mammals? J Mammal 92:452–459

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 51:337–348

Hall M (1832) On hybernation. Philos T Roy Soc Lond 122:335–360

Hock RJ (1951) The metabolic rates and body temperatures of bats. Biol Bull 101:289–299

Körtner G, Geiser F (2000) Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). Oecologia 123:350–357

Park KJ, Jones G, Ransome RD (2000) Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). Funct Ecol 14:580–588

Rambaldini DA, Brigham RM (2008) Torpor use by free-ranging pallid bats (*Antrozous pallidus*) at the northern extent of their range. J Mammal 89:933–941

Ransome RD (1971) The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. J Zool 164:353–371

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat Ecology. University of Chicago Press, Chicago, pp 430–492

Stawski C (2010) Ecology and thermal physiology of an insectivorous bat restricted to subtropical and tropical Australia. Dissertation, University of New England

Stawski C, Geiser F (2010) Seasonality of torpor patterns and physiological variables of a free-ranging subtropical bat. J Exp Biol 213:393–399

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:R542–R547

Stawski C, Turbill C, Geiser F (2008) Prolonged torpor use during winter by a free-ranging bat in subtropical Australia. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: hibernation, torpor and cryobiology. University of KwaZulu-Natal, Pietermaritzburg, pp 353–360

Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). J Comp Physiol B 179:433–441

Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. J Comp Physiol B 178:597–605

Zervanos SM, Maher CR, Waldvogel JA, Florant GL (2010) Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). Physiol Biochem Zool 83:135–141