



## SYMPOSIUM

# Hibernation and Torpor in Tropical and Subtropical Bats in Relation to Energetics, Extinctions, and the Evolution of Endothermy

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**Synopsis** Torpor, the most effective means of energy conservation available to endotherms, is still widely viewed as a specific adaptation in a few high-latitude, cold-climate endotherms with no adaptive function in warm regions. Nevertheless, a growing number of diverse terrestrial mammals and birds from low latitudes (0–30°), including species from tropical and subtropical regions, are heterothermic and employ torpor. Use of torpor is especially important for bats because they are small, expend large amounts of energy when active, rely on a fluctuating food supply, and have only a limited capacity for storage of fat. Patterns of torpor in tropical/subtropical bats are highly variable, but short bouts of torpor with relatively high body temperatures ( $T_b$ ) are most common. Hibernation (a sequence of multiday bouts of torpor) has been reported for free-ranging subtropical tree-dwelling vespertilionids, cave-dwelling hipposiderids, and house-dwelling molossidids. The observed range of minimum  $T_b$  is ~6–30°C, and the reduction of energy expenditure through the use of torpor, in comparison to normothermic values, ranges from 50 to 99%. Overall, torpor in the tropics/subtropics has been reported for 10 out of the currently recognized 18 bat families, which contain 1079 species, or 96.7% of all bats. Although it is unlikely that all of these are heterothermic, the large majority probably will be. Frequent use of torpor, including hibernation in diverse groups of tropical/subtropical bats, suggests that heterothermy is an ancestral chiropteran trait. Although data especially from the field are still scarce, it is likely that torpor, highly effective in reducing requirements for energy and water even under warm conditions, plays a crucial role in the long-term survival of the majority of small tropical and subtropical bats. Discovering how bats achieve this provides numerous opportunities for exciting new research.

## Introduction

Why, one might ask, should bats in the tropics and subtropics employ torpor? Torpor is usually defined as a controlled and pronounced reduction in body temperature ( $T_b$ ) and metabolic rate (MR) (Lyman et al. 1982; Geiser and Ruf 1995; Speakman and Thomas 2003) and traditionally it is viewed as an adaptation exclusively used at low ambient temperatures ( $T_a$ ) or when food is severely limited. Exposure to cold requires a large increase in endogenous heat production to maintain a constant, high  $T_b$  and therefore necessitates access to energy in the form of food (Lyman et al. 1982; Withers 1992; Geiser and Ruf 1995; Speakman and Thomas 2003). The tropics and subtropics are relatively warm and

at least do not expose bats to thermal challenges near or below  $T_a$  0°C that are often associated with torpor. While torpor is viewed as most effective for energy and water conservation in temperate-zone mammals and birds (Lyman et al. 1982; Hosken and Withers 1997; Thomas and Geiser 1997; Boyer and Barnes 1999; Geiser 2004), tropical and subtropical regions are viewed as thermally too benign to require energy to be conserved via a substantial reduction of  $T_b$ , as that achieved during torpor. It has even been argued that hibernation especially (sequence of multiday bouts of torpor, interspersed by periodic arousals) is impossible in tropical/subtropical habitats (Henshaw 1970; McNab 1974).

Webb et al. (1996) have shown that temperatures in the hibernacula of bats range from  $-10$  to  $21^{\circ}\text{C}$ . The higher end of these values are within the climatic averages reported for subtropical (coldest mean monthly  $T_a$   $6$ – $18^{\circ}\text{C}$ ) or tropical (mean monthly  $T_a > 18^{\circ}\text{C}$  for all months) regions and thus torpor should be possible in these regions just from a thermal perspective. Of course, an important consideration with regard to  $T_a$  and torpor is not only  $T_a$  *per se*, but also whether the  $T_a$  in the roost is stable or fluctuating. Many bats in warm climates, as they are not exposed to sub-zero  $T_a$ s, are able to roost in trees or other exposed sites, rather than or in addition to well-insulated caves, mines, or buildings (Kunz and Fenton 2003). At exposed sites they experience substantial daily fluctuations of  $T_a$ , which are considered to be a constraint on employing at least multiday bouts of torpor even at low  $T_a$ s (Henshaw 1970).

Despite these perceptions on limitations for torpor use in tropics/subtropics, new data on thermal biology and torpor use by tropical and subtropical mammals (tenrecs and primates) have recently been published and some of these include data showing substantial energy savings even at high  $T_a$  (Dausmann 2008, Lovegrove and Genin 2008; Giroud et al. 2009; Schmid and Speakman 2009). These publications also include results specifically on bats, provided by Don Thomas and co-workers (Audet and Thomas 1997) and others (Stawski et al. 2009; Cory Toussaint et al. 2010; Liu and Karasov 2011). These data as well as older literature mainly from laboratory studies provide quantitative evidence about the expression of torpor by a number of tropical and subtropical bats (Table 1). Because bats are most diverse in the tropics and subtropics (Willig et al. 2003), our aim was to assess (1) how common and taxonomically widespread use of torpor is in tropical and subtropical bats by valuating data for heterothermy in various families, (2) describe patterns expressed by different taxa and in different habitats/climates and, if available, different seasons, (3) synthesize the implications of heterothermy for energetics and long-term survival in bats in general, and (4) scrutinize use of torpor in tropical/subtropical bats in relation to the evolution of endothermy and torpor.

## Methods

Data on thermal biology, use of torpor, and torpor patterns were derived mainly from the primary literature (Table 1) for as many bat families as possible. We also included unpublished work from a recent study on ghost bats (Megadermatidae) because data

on low  $T_b$  in this family are especially scarce. Data on climate of sites where bats occur or the origin of bats and the body mass were used as provided by the original sources. Most data came from individuals living at low elevations; only two species were identified from high elevations. When quantitative field and laboratory data were both available, the field data were preferentially used because laboratory studies often underestimate the ecological significance of torpor use under natural conditions (Geiser et al. 2000). In some of the older literature, low  $T_b$  in bats was induced by exposure to low  $T_a$ . However, most of these studies do not provide data on endothermic rewarming from torpor at low  $T_a$ . Therefore, it is unclear whether bats became hypothermic (i.e., fall in  $T_b$  simply a failure in thermoregulation and bats forced to reduce  $T_b$  because of excessive cold) or whether the bats in fact entered torpor (i.e., the reductions of  $T_b$  and MR were controlled and reversible processes) (see Henshaw 1970; Lyman et al. 1982 for definitions). Thus, data on low  $T_b$  in bats without data on endothermic rewarming were either excluded or were clearly identified. The familial systematics and the number of bat species used here are based on Wilson and Reeder (2005).

## Torpor in tropical and subtropical bats

Torpor has been observed in diverse tropical and subtropical bats both in captivity and under natural conditions (Table 1). Of the total 18 chiropteran families worldwide, 10 include species that express torpor in the tropics/subtropics. Several of the other eight families are either not found in the tropics or subtropics, or there are no data on torpor use in these groups [for example: New-World (Thyropteridae) and Old World (Myzopodidae) sucker-footed bats, or leaf-chinned bats (Mormoopidae)]; rather than that heterothermy does not occur. Even without knowledge about these low-diversity families, the total number of species of chiropteran families containing known heterothermic bats from tropical/subtropical regions represents the vast majority. The 10 families containing heterothermic species, which are distributed into the tropics/subtropics number 1079 or 96.7% of the currently recognized 1116 species (Wilson and Reeder 2005). Obviously, not all of these species are likely to be heterothermic, and only  $\sim 35$  species have been confirmed to be, but based on current data a large number of tropical/subtropical bats are likely to employ torpor for conserving energy.

**Table 1** Heterothermy and torpor in subtropical (ST) and tropical (T) bats

Family species (climate)	Body mass (g)	Minimum $T_b$ or $T_{skin}$ ( $^{\circ}$ C)	Torpor bout duration (d)	Measurement	Source
<b>Pteropodidae</b>					
Long-tongued fruit bat, <i>Megaloglossus woermanni</i> (T)	12	26.2		Laboratory	Kulzer and Storf (1980)
Common blossom-bat, <i>Syconycteris australis</i> (ST)	18	17.2 18.9	0.32 0.23	Laboratory (S) Laboratory (W)	Geiser et al. (1996) Coburn and Geiser (1998)
Northern blossom-bat, <i>Macroglossus minimus</i> (T)	16	23.1	0.34	Laboratory	Bartels et al. (1998)
Tube-nosed bat, <i>Nyctimene albiventer</i> (T)	28	25.5		Laboratory	Bartholomew et al. (1970)
Eastern tube-nosed bat, <i>Nyctimene robinsoni</i> (T)	50		<1	Laboratory	Hall and Pettigrew (1995)
Bare-backed fruit bat, <i>Dobsonia minor</i> (T)	74	26		Laboratory	McNab and Bonaccorso (2001)
<b>Rhinolophidae</b>					
Eastern horseshoe bat, <i>Rhinolophus megaphyllus</i> (T <sup>a</sup> )	8	16		Laboratory	Kulzer et al. (1970)
<b>Hipposideridae</b>					
Orange leaf-nosed bat, <i>Rhinonictes aurantius</i> (T)	7	23.6		Laboratory	Kulzer et al. (1970)
Trident leaf-nosed bat, <i>Asellia tridens</i> (ST)	15	27		Laboratory	Kulzer (1965)
Formosan leaf-nosed bat, <i>Hipposideros terasensis</i> (ST)	60	16.5	19	Field (W)	Liu and Karasov (2011)
<b>Megadermatidae</b>					
Asian false vampire bat, <i>Megaderma lyra</i> (T)	26	30		Laboratory	Kulzer (1965)
Ghost bat, <i>Macroderma gigas</i> (T)	100	32		Laboratory	Geiser, Stawski, Pavey unpublished data
<b>Rhinopomatidae</b>					
Mouse-tailed bat, <i>Rhinopoma hardwickei</i> (ST)	10	16		Laboratory	Kulzer (1965)
Mouse-tailed bat, <i>Rhinopoma microphyllum</i> (ST)	19	23		Laboratory	Kulzer (1965)
<b>Emballonuridae</b>					
Dog-faced bat, <i>Peropteryx macrotis</i> (T)	5	24		Laboratory	Genoud et al. (1990)
Coastal sheath-tail bat, <i>Taphozous australis</i> (T)	23	16		Laboratory	Kulzer et al. (1970)
Tomb bat, <i>Taphozous melanopogon</i> (T)	26	27		Laboratory	Kulzer (1965)
<b>Phyllostomidae</b>					
Long-tongued bat, <i>Glossophaga soricina</i> (T)	10	21	0.7	Laboratory (L)	Kelm and von Helversen (2007)
White-lined bat, <i>Vampyrops helleri</i> (T)	15	28.5		Laboratory	Rasweiler (1973)
Yellow-shouldered bat, <i>Sturnira lilium</i> (T)	17	23		Laboratory	Audet and Thomas (1997)
Leaf-nosed bat, <i>Carollia perspicillata</i> (T)	20	22		Laboratory	Audet and Thomas (1997)
Vampire bat, <i>Desmodus rotundus</i> (ST high?)	30	25		Laboratory	Lyman (1970)
<b>Natalidae</b>					
Funnel-eared bat, <i>Natalus tumidirostris</i> (T)	5	23		Laboratory	Genoud et al. (1990)
<b>Molossidae</b>					
Little northern freetail bat, <i>Mormopterus loriae</i> (T)	8.5	10		Laboratory	Kulzer et al. (1970)
Egyptian free-tailed bat, <i>Tadarida aegyptiaca</i> (ST high)	16	6.2	9	Field (W)	Cory Toussaint et al. (2010)
Angolan free-tailed bat, <i>Mops condylurus</i> (ST)	23	16 12		Laboratory Field (W)	Maloney et al. (1999) Vivier and van der Merwe (2007)
<b>Vespertilionidae</b>					
Eastern forest bat, <i>Vespadelus pumilus</i> (ST)	4	14.5	0.25	Field (S)	Turbill et al. (2003)
White-winged serotine, <i>Neoromicia (Pipistrellus) tenuipinnis</i> (T)	5		>1	Laboratory	Eisenraut (1956)
Large-footed myotis, <i>Myotis adversus</i> (T <sup>a</sup> )	7.8	8	8	Laboratory	Kulzer et al. (1970)
Lesser long-eared bat, <i>Nyctophilus geoffroyi</i> (T <sup>a</sup> )	7.8	19.8	0.4	Field (W)	Geiser et al. (2011)
Northern long-eared bat, <i>Nyctophilus bifax</i> (ST)	9	16 9.4	0.9 5.4	Field (S) Field (W)	Stawski and Geiser (2010b) Stawski et al. (2009)
Large bentwing bat, <i>Miniopterus schreibersii</i> (T <sup>a</sup> )	15	10.5		Laboratory	Kulzer et al. (1970)
Yellow bat, <i>Lasiurus intermedius</i> (ST)	22	9		Laboratory	Genoud (1993)
House bat, <i>Scotophilus mhlangani</i> (ST)	28	18.2	0.7	Field (A)	Jacobs et al. (2007)
Yellow house bat, <i>Scotophilus dinganii</i> (ST)	29	18.5	0.6	Field (A)	Jacobs et al. (2007)

Note. S = summer, W = winter, A = autumn, L = laboratory-bred, high = high elevation.

<sup>a</sup>Wide distribution in addition to tropical/subtropical.

### Pteropodidae

Contrary to a widely held view in the past that 'megabats' are strictly homeothermic (Hock 1951), torpor has been reported for several small pteropodids with a body mass ranging from 12 to 74 g (Table 1). This is at the lower end of body masses of 'fruit bats' within this family which range up to 1.6 kg (Nowak 1999). Heterothermic species include the small long-tongued fruit bats from Africa and blossom-bats from Australia and south-eastern Asia, which are among the smallest members of this family. However, larger tube-nosed bats from Australia and New Guinea and a small fruit bat from New Guinea also have been observed to be heterothermic in captivity. Free-ranging tube-nosed bats (*Nyctimene robinsoni*) did not enter torpor in tropical Queensland in winter when food was abundant. However, they reduced  $T_b$  from about 38°C to a minimum of 32.6°C during the day and also had low  $T_b$  on moon-lit nights when they appeared to be less active, perhaps to avoid predation (Riek et al. 2010). Thus, all current information on torpor physiology in this family is based on laboratory investigations and all pteropodids studied to date are small daily heterotherms that displayed shallow, daily torpor exclusively, usually for several hours during the daytime resting period. The minimum  $T_b$  recorded in this family was 17.2°C (normothermic  $T_b$  ranged from ~35 to 39°C) and the minimum MR during torpor was ~40% of the basal MR (BMR) (Coburn and Geiser 1998). Large pteropodids measured in the laboratory remained homeothermic (Morrison 1959; Kulzer et al. 1970).

Information on seasonal changes in use of torpor by pteropodids is limited, but interesting. Blossom bats (*Syconycteris australis*) show deeper and longer daily torpor in summer than in winter (Table 1), which is the opposite of what is usually observed in cold-climate species, and appears to mainly reflect reduced availability of nectar in summer (Coburn and Geiser 1998). The only other species known to express more pronounced torpor in summer than in winter, likely to conserve water, is the desert-dwelling golden spiny mouse (Levy et al. 2011).

### Rhinolophidae

Horseshoe bats are well known hibernators from temperate regions (Ransom 1990; Park et al. 2000). However, even *Rhinolophus megaphyllus* in tropical Australia were found lethargic in a cave at a  $T_a$  of about 23°C (Kulzer et al. 1970). Individual *R. megaphyllus* originating from tropical Australia also substantially reduced  $T_b$  when exposed to low  $T_a$  in the

laboratory, similar to individuals from a temperate region.

### Hipposideridae

Leaf-nosed bats are mainly found in tropical and subtropical regions of Africa, Asia, and Australia (Nowak 1999) and, in the past, data were restricted to captive individuals suggesting that these bats are highly sensitive to cold, but may display shallow torpor (Kulzer 1965; Kulzer et al. 1970; Baudinette et al. 2000). However, recent field work in subtropical Taiwan revealed that the large (60 g) cave-dwelling Formosan leaf-nosed bat, *Hipposideros terasensis*, hibernates in the wild (Liu and Karasov 2011). Although  $T_b$  during torpor ( $T_b$  16.5–24°C) and the  $T_a$  of the caves (mean  $T_{roost}$  14.3–22.3°C) were well above those commonly observed in hibernating temperate zone bats, a sequence of multiday torpor bouts of up to 19 days, such as those seen during classical hibernation, occurred during winter from December to early March (Liu and Karasov 2011).

### Megadermatidae

Most literature about the family of false vampires suggests that they are homeothermic (e.g. Leitner and Nelson 1967). However, we observed a wide range of  $T_b$  (32–39°C) in large (100 g) captive *Macroderma gigas* held at  $T_a$  ~20°C overnight (Geiser et al., unpublished data). This is not the first observation of a reduction of  $T_b$  below normothermic values in members of this family. Kulzer (1965) measured a reduction of  $T_b$  from 39.3 to ~30°C in the much smaller (23 g; a low body mass for this species) Indian *Megaderma lyra* when they were exposed to rather high  $T_a$ s of approximately 25°C. These data suggest that work on free-ranging individuals will reveal that some members of this family employ torpor for the conservation of energy.

### Rhinopomatidae

The original information on torpor in two species of mouse-tailed bats is based on laboratory investigations of individuals from North Africa (Kulzer 1965). Both *Rhinopoma* species entered torpor when exposed to  $T_a$  between 12 and 20°C in the laboratory. The larger species, *R. microphyllum*, defended its  $T_b$  during torpor at 23°C, whereas for the smaller species, *R. hardwickei*, minimum  $T_b$  recorded was 16°C. When both species were exposed to  $T_a$  below their minimum  $T_b$ , they regulated  $T_b$  at higher values approximating the normothermic resting  $T_b$  of ~34°C. Recent data from Israel show that

*R. microphyllum* select warm ( $\sim T_a$  20°C) caves for winter hibernation and do not emerge from these for 5 months (Levin et al. 2010).

### Emballonuridae

Many sheath-tailed bats are fast-flying and largely insectivorous species from tropical and subtropical regions. Currently, data on torpor are available only from laboratory work. *Taphozous australis* originating from tropical Australia reduced  $T_b$  to a minimum of 16°C when exposed to a  $T_a$  of  $\sim 14^\circ\text{C}$ . In one individual, a  $T_b$  of 12°C was measured when it was exposed to  $T_a$  10°C, but this bat was unable to rewarm (Kulzer et al. 1970). Consequently, this individual was hypothermic with a  $T_b$  below its species-specific minimum  $T_b$  that is regulated during torpor, but not during hypothermia. *Peropteryx macrotis* from Venezuela exhibited torpor in the laboratory; its  $T_b$  fell to 24°C and MR to  $\sim 50\%$  of that in normothermic resting bats. Because MR increased in torpid bats at  $T_a < 20^\circ\text{C}$ , it appears these bats defend  $T_b$  at this relatively high value (Genoud et al. 1990). Tomb bats (*Taphozous melanopogon*) from India had a minimum  $T_b$  of 27°C at  $T_a$ s between 15°C and 20°C; at lower  $T_a$ ,  $T_b$  was regulated at higher values (Kulzer 1965).

### Phyllostomidae

New World leaf-nosed bats from tropical and subtropical regions of mainly South and Central America feed on insects, fruit, nectar, and also blood. This is another family that was considered to be homeothermic (Hock 1951), but clearly is not (Audet and Thomas 1997; Kelm and von Helversen 2007). Even when frugivorous *Carollia perspicillata* and *Sturnira lilium* in Costa Rica were held under mild conditions ( $T_a$  of 21°C and free access to food), both species entered shallow torpor with a minimum  $T_b$  of  $\sim 22^\circ\text{C}$  (Audet and Thomas 1997). Free-ranging bats equipped with radio-transmitters did not employ torpor (Audet and Thomas 1997), but data were limited to a few days, and  $T_a$  during measurements was around 28°C, thereby providing little scope for reduction in  $T_b$ . The other species that has been investigated in regard to torpor use is the long-tongued nectarivorous bat *Glossophaga soricina*, captive-bred from individuals originating from Jamaica (Winter 1998; Kelm and von Helversen 2007). *Glossophaga* entered short bouts of torpor when food availability was reduced; the minimum  $T_b$  measured was 21°C, the lowest MR measured during torpor was only  $\sim 9\%$  of BMR, and the longest bout lasted for 17 hours

(Kelm and von Helversen 2007). Captive white-lined bats (*Vampyrops helleri*) from Trinidad lowered  $T_b$  to a minimum of 28.5°C after food deprivation (Rasweiler 1973). Similarly, captive vampire bats (*Desmodus rotundus*) from low (270 m) and high (2400 m) elevations in Mexico could rewarm when  $T_b$  was as low as 25°C (Lyman 1970).

### Natalidae

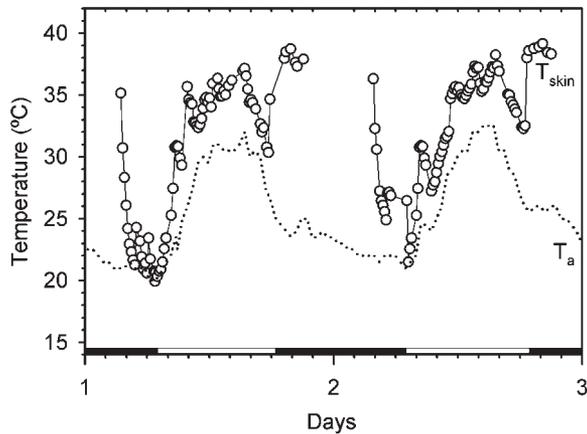
Information on insectivorous funnel-eared bats is limited to a single study on captive *Natalus tumidirostris* from Venezuela (Genoud et al. 1990). Individuals reduced  $T_b$  from 32.2°C during normothermia to  $\sim 23^\circ\text{C}$  during torpor and this minimum  $T_b$  was regulated by an increase in MR (Genoud et al. 1990). Minimum MR during torpor fell only slightly below BMR, but at  $T_a$  10–20°C it was  $\sim 50\%$  of the resting MR of normothermic bats.

### Molossidae

Historically, the widely accepted view was that free-tailed bats cannot hibernate or are poor hibernators (Lyman 1970). However, recent work has shown that *Tadarida teniotis* hibernates in the European Alps, although its minimum  $T_b$  was higher ( $\sim 10^\circ\text{C}$ ) and bouts of torpor were shorter than in temperate zone vespertilionids (Arlettaz et al. 2000). In subtropical regions, prolonged torpor in free-ranging bats is only known for *Tadarida aegyptiaca*, which displays multi-day bouts of torpor in Pretoria (elevation  $\sim 1300$  m) in winter. Individuals residing in a house displayed both short and prolonged bouts lasting up to 9 days and the minimum  $T_b$  recorded was 6.2°C (Cory Toussaint et al. 2010). Other studies on thermal biology of free-tailed bats were conducted in captivity on an Australian tropical species (*Mormopterus loriae*), which lowered its  $T_b$  to 10°C (Kulzer et al. 1970). A South African species from a subtropical coastal region (*Mops condylurus*) lowered its  $T_b$  (measured rectally) in the field during winter mornings to a minimum  $T_b$  of 12°C (Vivier and van der Merwe 2007); captive bats had a minimum  $T_b$  of 16°C and an astonishing tolerance of high  $T_b$  (up to 43°C) (Maloney et al. 1999). Captive *M. condylurus* also displayed shallow torpor ( $T_b$  26.7°C) in summer when exposed to natural  $T_a$  (Vivier and van der Merwe 2007).

### Vespertilionidae

Vespertilionids are by far the largest chiropteran family with 407 species currently recognized and



**Fig. 1** Skin temperatures ( $T_{\text{skin}}$ ) of free-ranging long-eared bat *Nyctophilus geoffroyi* (body mass 7.8 g) and ambient temperature ( $T_a$ ) over 2 days in winter in tropical Australia. Black horizontal bars indicate the time between sunrise and sunset. Note the partial passive rewarming with  $T_a$  in the morning and the second drop of  $T_{\text{skin}}$  in the late afternoon before active rewarming. Data from Geiser et al. (2011).

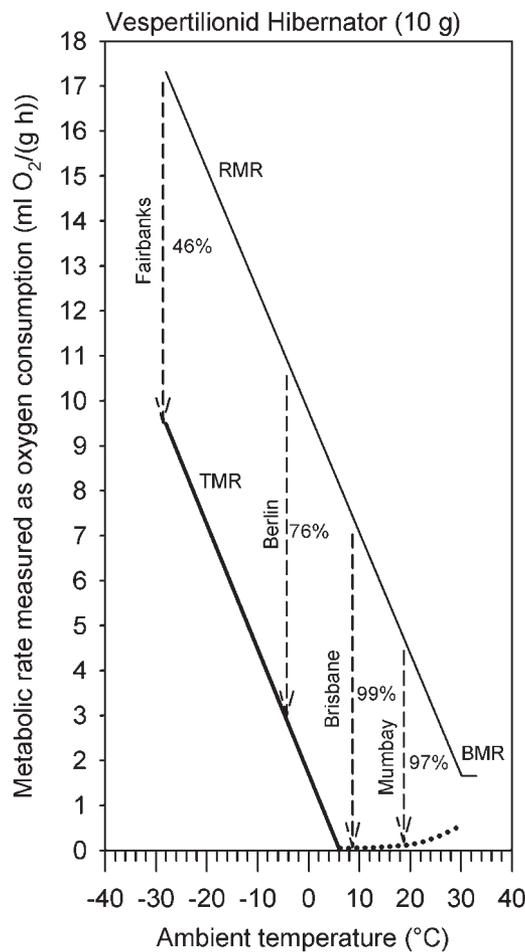
occurring over most of the world (Wilson and Reeder 2005). Most are insectivorous and small (mean body mass of 191 species =  $11.2 \pm \text{SD } 9.1$  g) and many species from northern latitudes are known to hibernate (Hock 1951; Pohl 1961; Brigham 1987; Thomas 1995; Chruszcz and Barclay 2002; Humphries et al. 2002; Willis and Brigham 2003; Willis et al. 2006; Boyles et al. 2007; Wojciechowski et al. 2007; Dunbar and Brigham 2010). Recent field data collected during the subtropical winter show that tree-roosting Australian *Nyctophilus bifax*, despite strong daily fluctuations in  $T_a$ , enter multiday torpor similar in duration to chipmunks and golden hamsters (Stawski et al. 2009). Short bouts of torpor have been observed in the relatively large free-ranging South African house bats (*Scotophilus* spp.) in autumn in a subtropical area (Jacobs et al. 2007). Even in the subtropical summer and the tropical winter, tree-dwelling Australian microbats (*Nyctophilus* and *Vespadelus*) display a high proclivity to enter torpor in the morning, arouse (often passively) about midday, and then re-enter a second bout of torpor, or at least substantially reduce  $T_b$  in the late afternoon (Fig. 1; note that maximum daily  $T_a$  is  $\sim 32^\circ\text{C}$ ) before rewarming in the evening prior to their active phase (Turbill et al. 2003; Stawski and Geiser 2010a; Geiser et al. 2011). The exposed roosts allow bats to re-enter torpor and reduce energy expenditure in the afternoon as soon as  $T_a$  begins to decline (Turbill et al. 2008). Nevertheless, the frequent use of torpor by these Australian bats may seem especially surprising because these species were studied when food

appeared to be abundant and thermal conditions were mild (Turbill et al. 2003; Stawski and Geiser 2010; Geiser et al. 2011). As torpor was especially pronounced in bats in good condition, it has been proposed that torpor is not only used to reduce the expenditure of energy, but the low energy requirements allow them to minimize foraging and thus their exposure to predators (Stawski and Geiser 2010a); in turn this would increase annual survival (Turbill et al. 2011). It must be pointed out, however, that hard data on predation risks of bats are virtually non-existent.

Importantly, although bouts of torpor by vespertilionids at high  $T_a$  or in summer often last only for hours, physiologically these bouts appear to differ from those expressed during daily torpor, as, for example, in the Pteropodidae. The MR during short bouts of torpor in the vespertilionids is as low as that in temperate zone hibernators and often falls to  $<5\%$  of BMR (in comparison to the  $\sim 40\%$  of BMR in the pteropodids; i.e., an almost 10-fold difference), or below 1% of the resting MR at the same  $T_a$  (Geiser and Brigham 2000; Willis et al. 2005; Turbill et al. 2008). Thus, it appears that short bouts of torpor in vespertilionids (and likely many other hibernators) are in fact brief periods hibernation and differ physiologically (as shown by the much lower MR) from the daily torpor of the daily heterotherms. Consequently, these brief bouts in hibernators should not be called ‘daily torpor’. This has been recognized in principle some time ago (Hock 1951; Lyman 1970), but is often ignored in the literature.

## Energetics of torpor

The occurrence of torpor in diverse tropical and subtropical bats raises the question of why it is so widely used. It is often assumed that a low  $T_a$  permitting a low  $T_b$  is essential for maximizing conservation of energy during torpor. This is correct to some extent because the lowest MR in bats have been measured in torpid thermo-conforming bats near the minimum  $T_b$ , often a few degrees above  $T_a/T_b$   $0^\circ\text{C}$  (Hock 1951; Pohl 1961; Thomas et al. 1990; Geiser and Brigham 2000). However, MR increases enormously at  $T_a$ s a few degrees below the minimum  $T_b$  because torpid bats and other heterotherms begin to metabolically defend their  $T_b$  (Fig. 2), thereby avoiding damage of organelles and tissues and maintaining the ability to rewarm actively (Lyman et al. 1982; Geiser et al. 1986). Moreover, the relative reduction in MR during torpor is most pronounced at high  $T_b$  because MR in thermo-conforming torpid



**Fig. 2** Metabolic rate (MR) measured as rate of oxygen consumption versus ambient temperature ( $T_a$ ) in an average size (10 g) vespertilionid hibernator (mean mass of vespertilionids is 11.2 g). Vespertilionids were used because most data about torpor is available for this family. The graph was constructed using values (minimum  $T_b \sim 6^\circ\text{C}$ ) derived from Geiser and Ruf (1995), MR values/slopes were calculated from equations in Geiser (2004). Vertical arrows indicate the percentage reduction of MR at the average minimum  $T_a$  in winter at the named cities. Solid diagonal lines represent thermo-regulating individuals, the dotted curve is for thermo-conforming individuals. BMR = basal MR, RMR = resting MR, TMR = MR during torpor.

bats is an exponential function of  $T_b$ . In addition, metabolic inhibition (Fig. 2) appears to be employed especially at high  $T_a/T_b$  in species capable of multi-day torpor (Geiser and Brigham 2000; Geiser 2004; Turbill et al. 2008). Because of these relationships, the reduction in MR, in relation to the resting MR of normothermic bats, is much more pronounced in bats displaying torpor at the average minimum  $T_a$  in winter in tropical Mumbai or subtropical Brisbane (97–99% reduction of MR) than in bats in cool-temperate Berlin (76% reduction of MR), or arctic Fairbanks (46% reduction of MR) (Fig. 2), from where bats migrate south before

winter (Humphries et al. 2002). In hibernating bats from Mumbai/Brisbane, the MR during torpor is well below the BMR, but for bats from Berlin, MR during torpor is  $>\text{BMR}$  and would be 5.7-fold that of BMR for bats from Fairbanks (Fig. 2), should they remain there during winter. The main reason for these differences is that torpid tropical/subtropical bats can thermo-conform at the  $T_a$ s they experience, whereas bats from cold climates must thermoregulate to maintain  $T_b$  during torpor above critically low values. These calculations do not even consider increased costs of rewarming and increased frequency of rewarming at low  $T_a$  (Geiser and Kenagy 1988; Buck and Barnes 2000; Humphries et al. 2002). Of course, bats from cold climates may lower their minimum  $T_b$  further to  $0^\circ\text{C}$  or slightly below (Eisentraut 1956), which slightly decreases costs for thermoregulation during torpor, but the scope for a further reduction of  $T_b$  is limited by the freezing point of body water. Moreover, these cold-climate bats, like other mammals, can huddle (e.g., Namekata and Geiser 2009; Jefimow et al. 2011) or select warmer microclimates to some extent to improve energy savings somewhat. However, for example, arctic ground squirrels in Alaska hibernate individually in hibernacula with  $T_a$  as low as  $-25^\circ\text{C}$  (Barnes 1989; Buck and Barnes 2000; Williams et al. 2011). This demonstrates that even well-insulated underground burrows can get awfully cold, and torpid arctic ground squirrels, despite their large size and extremely low minimum  $T_b$ , must increase metabolism substantially to maintain  $T_b$  above a critical level (Barnes 1989; Buck and Barnes 2000; Williams et al. 2011).

In daily heterotherms, such as pteropodid bats, which usually maintain  $T_b$  during torpor  $>15^\circ\text{C}$  (Geiser and Ruf 1995), the situation would be even worse than in hibernating species in temperate and arctic climates because a high minimum  $T_b$  requires metabolic defense of  $T_b$  at high  $T_a$ , thus further compromising energy savings that can be achieved by using torpor. However, all high-latitude bats hibernate and no chiropteran daily heterotherm is known to extend its range into cold regions. In warmer regions, even daily torpor, with relatively high  $T_b$  and MR, is energetically beneficial, and it is therefore of little surprise that both daily and multi-day torpor are used so widely in the tropics and subtropics.

### Torpor and extinctions in bats

Recent analyses have proposed that species capable of using torpor appear less threatened by extinction and

fewer have suffered extinction than obligate homeotherms (Geiser and Turbill 2009; Liow et al. 2009; Canale et al. 2011). Of the 61 worldwide confirmed extinct mammal species over the past 500 years (American Museum for Natural History, Committee on Recently Extinct Organisms, <http://creo.amnh.org>), only 8 (of ~1,100 species) were bats and only 3 of these were likely heterothermic, although the majority of bats most likely use torpor (Geiser and Turbill 2009). This is similar to the number of extinctions in much smaller orders, such as in several marsupial orders, and fewer than in rodents with 26/61 extinctions. Although threatened locally by the white-nose syndrome because they hibernate at low  $T_b$  (Boyles and Willis 2010) and because of other local problems, overall, bats are the only mammalian order of 11 that have suffered extinctions (Geiser and Turbill 2009) with <1% of species becoming extinct.

If we examine only the continent of Australia, the situation appears even more clear-cut. Although Australia has suffered almost half of all worldwide mammal extinctions over the past 200 years, the ~75 species of Australian bats, unlike many homeothermic marsupials and rodents, have been almost entirely spared (Johnson 2006; Geiser and Turbill 2009) [although the Christmas Island Pipistrelle, *Pipistrellus murrayi*, probably is now extinct (Lumsden 2010)]. It has been suggested that, in addition to being able to fly, the ability of using torpor with its enormous scope for adjusting energy requirements may allow long-term survival of adverse environmental conditions, habitat modification and degradation, and avoidance of introduced or native predators (Stawski and Geiser 2010a; Geiser et al. 2011), likely to be the major causes of extinctions. Thus, the use of torpor and flight and the resulting prolonged life span appear to have permitted bats to deal with anthropogenic disturbances better than is the case for most other species and, although many may have suffered a reduction in distribution range, these traits appear to have reduced the risk of extinction.

### Evolution of torpor in bats

Use of torpor in diverse tropical/subtropical bats also has implications on the evolution of endothermy in mammals. The evolution of torpor in relation to the evolution of endothermy has been widely debated. Many authors assume that reptilian ectothermy evolved into mammalian homeothermic endothermy by some mysterious manyfold increase in metabolism that went hand in hand with the growth in size and/

or development of fur (Crompton et al. 1978; Ruben 1995). This interpretation seems highly unlikely because a metabolic rate intermediate between that of reptiles and that of homeothermic mammals would not have allowed the regulation of a constant high  $T_b$  during exposure to cold or fluctuating  $T_a$ . However, others have proposed that homeothermy in mammals must have evolved via heterothermy, because this avenue provides a plausible explanation as to how metabolism could have increased gradually over time. Heterothermy would have permitted a low  $T_b$  during cold exposure and passive rewarming from low  $T_b$  before the activity phase would have been possible with a relatively low MR (Geiser et al. 2002; Grigg et al. 2004).

With regard to the evolution of torpor in bats specifically, the oft-mentioned hypotheses are those provided by Twente and Twente (1964). They proposed that: (1) bats evolved from homeothermic gliding insectivores in tropical regions in the hot Cretaceous period, (2) heterothermic bats evolved from homeothermic ancestors in response to dealing with selection of cool microhabitats in the tropics, (3) once heterothermy had evolved, it could be extended into true hibernation upon the cooling of climate, and (4) heterothermy may have given bats a selective advantage and may have been an important factor contributing to their long history and great diversity.

While it is difficult to argue against some, especially the last, of these points, the data we summarized clearly show that use of torpor appears to be common in warm environments and even multiday hibernation is used by free-ranging subtropical bats (Stawski et al. 2009; Cory Toussaint 2010; Liu and Karasov 2011). This suggests that prolonged torpor did evolve in the tropics/subtropics and not after bats invaded temperate climates or were exposed to low temperatures only. The wide diversity of heterothermy in tropical/subtropical bats also suggests that ancestral bats and their ancestors were heterothermic rather than homeothermic and used torpor during the inactive period of the day. Like many extant tropical/subtropical bats they were able to use passive rewarming from low  $T_b$  that only requires a low metabolic rate and saves energy (Lovegrove et al. 1999; Geiser et al. 2002; Turbill et al. 2008). Homeothermic endothermy appears to be a derived trait that evolved secondarily after a heterothermic phase in a few large bats.

### Conclusions

Based on this summary, we argue that torpor is used by a diverse set of tropical and subtropical bats.

We show that knowledge about heterothermy in bats in general has substantially improved in recent years (see Ransome 1990). While the data clearly establish that torpor is employed by species ranging in body mass from 4 to 74 g, the number of species that have been identified remains small, and not even all families have been examined with regard to torpor. Therefore, data on the families Craseonycteridae, Nycteridae, Mormoopidae, Noctilionidae, (Mystacinidae from New Zealand apparently are heterothermic), Furipteridae, Thyropteridae, and Myzopodiade are highly desirable. The quality of data that are available is varied: many of the  $T_b$  values that have been reported are not regulated minima, but simply reflect the  $T_a$  under which bats were measured. Further, data on the duration of bouts of torpor are scarce because often only single rectal  $T_b$ s or a sequence of rectal  $T_b$ s were recorded rather than long-term data derived remotely and without disturbance (e.g., using attached or implanted transmitters or data loggers). Data on metabolic rates during torpor in tropical/subtropical bats are also limited. However, the available data reveal vastly different patterns of heterothermy in tropical and subtropical species and families of bats, that are often more diverse and unpredictable than patterns observed in species from high latitudes. Thus, work on torpor in bats from tropical, subtropical, and other warm climates is one of the new frontiers in thermal biology and future studies are likely to reveal new and perhaps surprising functions for torpor.

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