

MINI-SERIES

The importance of temporal heterothermy in batsC. Stawski^{1,2}, C. K. R. Willis³ & F. Geiser²¹ Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland² Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW, Australia³ Department of Biology and Centre for Forest Interdisciplinary Research, University of Winnipeg, Winnipeg, Canada**Keywords**

bat; chiroptera; disease; heterothermy; hibernation; reproduction; torpor; white-nose syndrome.

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Abstract

Animals must balance their energy budgets even when confronted with periodic food shortages and/or adverse environmental conditions. Especially, small endothermic animals require large amounts of energy to maintain high and stable body temperatures (T_b) via endogenous heat production. To deal with energetic challenges, many small endotherms are heterothermic, abandon regulation of high T_b and enter a state of torpor resulting in large energy savings. Torpor is used by many bat species because they are small, have high rates of heat loss and rely on fluctuating food resources (e.g. insects, fruit, nectar). Many bats use torpor all year, but the expression of temporal heterothermy can be strongly seasonal especially for temperate and subtropical species, which may hibernate for long periods. Recent advances in our understanding of torpor expression in bats have been made using temperature telemetry for remote data collection of T_b in free-ranging wild individuals from all climate zones. This new knowledge on free-ranging bats has revealed the importance of torpor expression not only for energy conservation but also for other benefits, such as reduction of extrinsic mortality (e.g. predation). On the contrary, dense clustering during hibernation, important for minimizing energy and water loss, may also expose bats to infectious disease. An emerging, cold-tolerant fungal pathogen of bats causes a new disease called white-nose syndrome (WNS), which is devastating populations of multiple species in eastern North America. Given the importance of temporal heterothermy to their biology, and links between torpor expression and mortality from WNS, it is becoming increasingly important to understand the ecology and physiology of torpor in this largely understudied and cryptic mammalian group. Here, we review past and current literature to summarize the importance and evolution of heterothermy in bats.

Introduction

Critical to any organism's survival and fitness is balancing energy acquisition and expenditure so all necessary functions of life and reproduction can be maintained. Inter-annual, seasonal and unpredictable changes in environmental conditions create challenges for both the intake and the expenditure sides of this energy budget (Nagy, Girard & Brown, 1999; Tattersall *et al.*, 2012). Cold winters and droughts can significantly reduce food availability, resulting in a mismatch between energy uptake and energy expenditure. As a result, selection has favoured a range of adaptations that help maintain energy balance in the face of changing environments. Endothermic animals benefit from the ability to remain active for energy acquisition across a broad range of conditions. However, they require large amounts of energy for heat production to regulate high and relatively stable body temperatures (T_b)

(Speakman & Thomas, 2003). Especially for small species with a large relative surface area, this energy use can exceed that of similar-sized ectotherms by 30–100 times, especially at low ambient temperatures (T_a) (Nagy *et al.*, 1999; Speakman & Thomas, 2003). Many small mammals and birds therefore use torpor, also referred to as temporal heterothermy, which is a reduction of T_b and metabolic rate (MR) to conserve energy and also water (Ben-Hamo *et al.*, 2013; Geiser, 2013). These mammals and birds are thus heterothermic endotherms that are capable of regulating a high T_b , but are also able to thermo-conform over a wide temperature range (Speakman & Thomas, 2003; Geiser, 2013).

Bats are one taxon that is especially likely to exhibit torpor. The vast majority of bat species are small and weigh <25 g and nearly half weigh <10 g (Willis, Turbill & Geiser, 2005). Their high rates of heat loss to the environment due to small size are further exaggerated by their highly vascularized flight mem-

branes (Lyman, 1970; Yalden & Morris, 1975). As bats have high maintenance and thermoregulatory energy requirements together with the energetically expensive activities of flying and echolocation (Fenton, 1983; Neuweiler, 2000; Shen *et al.*, 2010), they need to manage their energy prudently.

Although many bats tend to express torpor, they are likely to exhibit a range of thermoregulatory strategies, simply because they are so diverse (Table 1). With *c.* 1100 species, bats represent about 20% of mammalian species and are found in virtually all terrestrial ecosystems (Brunet-Rossinni & Austad, 2004; Wilson & Reeder, 2005; Monadjem *et al.*, 2010; Wang, Walker & Poon, 2011). Bats inhabit many climate zones, including highly seasonal cold-temperate and warm tropical climates, and roost in varying microclimates, from thermally stable caves to thermally unstable leaves (Brunet-Rossinni & Austad, 2004; Kunz *et al.*, 2011).

Depending on climate and roosts, patterns of temporal heterothermy vary among species (Table 1). Some species only appear capable of daily torpor (i.e. short and shallow bouts), whereas others hibernate during winter with the typical pattern of deep multi-day bouts of torpor interspersed by short periodic arousals (Geiser & Ruf, 1995). The majority of bats inhabit warm climates and many of these express short bouts of torpor, although some species can hibernate (Geiser & Stawski, 2011). The number of bats inhabiting temperate regions is much smaller and all of these species are exclusively insectivorous (Davis, 1970; Willig, Patterson & Stevens, 2003; Geiser & Stawski, 2011). While some temperate bats are known to migrate to avoid energetically demanding winters (Stones & Wiebers, 1965; Davis, 1970; McGuire & Boyle, 2013), most do not migrate long distances (i.e. >500–1000 km) but hibernate, some with extremely long bouts of torpor and very low T_b (Hock, 1951; Thomas & Geiser, 1997; Speakman & Thomas, 2003; Geiser, 2006; Jonasson & Willis, 2012).

Metabolism and thermal physiology of normothermic and torpid bats are also influenced by body mass. As for all endotherms, large bats have lower mass-specific resting MRs at low T_a in comparison to small bats. However, even under thermo-neutral conditions, bats, particularly vespertilionids, have a lower basal MR than other mammals of similar size (McNab, 1982; Hosken & Withers, 1997; Willis *et al.*, 2005). The vast differences in body size and ecology of bats, among other factors, will result in differences in thermal energetics and torpor expression (Table 1).

Climate change already appears to be linked to the recent extinction of at least one bat species (i.e. the Christmas Island pipistrelle *Pipistrellus murrayi*; Martin *et al.*, 2012). Along with global warming and habitat loss, the ongoing mass mortalities of bat species due to wind turbines (Baerwald *et al.*, 2008; Cryan & Barclay, 2009) and white-nose syndrome (WNS) (Frick *et al.*, 2010) highlight the urgency of understanding the physiology and ecology of bats. Since Speakman & Thomas's (2003) comprehensive review of the physiological ecology and thermal biology of bats, knowledge of torpor expression in bats, especially in the field, has substantially expanded. More recent reviews on the topic have focused specifically on torpor use in tropical and subtropical bats (Geiser & Stawski, 2011) or in Australian bats (Geiser, 2006).

Our aim therefore was to summarize current information on temporal heterothermy in bats worldwide in relation to reproductive status, diet and environmental factors specific to their habitats. We first reviewed the available information on torpor in bats in the context of phylogenetic groups and geography (Table 1) and discussed the evolution of heterothermy in bats. We then highlighted a number of examples illustrating fundamental connections between use of torpor by bats and other aspects of their natural history with an emphasis on reproduction and disease. These examples can inform key questions about ecology and evolution in heterothermic endotherms, but are also relevant to bat conservation. In general, the available data strongly support the importance of temporal heterothermy to the survival of individual bats and the persistence of bat populations, and we review the examples that highlight this importance.

Torpor in relation to phylogeny, geography and evolution

Traditionally, bats were grouped into two suborders: the microchiropterans and the megachiropterans. Recent molecular studies suggest an alternative grouping: (1) Yinpterochiroptera, which includes all members of the Pteropodidae (i.e. megachiropterans, old world fruit bats) and the Rhinolophidae (historically considered microchiropterans, horseshoe bats); and (2) Yangochiroptera, which includes all remaining microchiropterans (Teeling *et al.*, 2005; Teeling, 2009).

Yinpterochiroptera

Temperate

Rhinolophid bats that inhabit temperate regions are known to hibernate (Davis, 1970). In particular, *Rhinolophus ferrumequinum* expresses torpor bouts of up to 2 weeks during the hibernation period (Park, Jones & Ransome, 2000) and even longer torpor bouts have been recorded in *Rhinolophus hipposideros* (Harmata, 1987). Torpor has also been recorded in the South African *Rhinolophus capensis* (Brown & Bernard, 1994). Australian temperate rhinolophids are known to use torpor, but there are only few data and more work is needed.

Tropical/subtropical

Pteropodids are entirely restricted to tropical/subtropical areas of the old world. The widely held view in the past was that all members of this family are strictly homeothermic (Morrison, 1959; Henshaw, 1970; Lyman, 1970; Ransome, 1990). This interpretation was supported by laboratory studies, which did not observe torpor in a number of species of medium and large pteropodids (80–1100 g) (Bartholomew, Leitner & Nelson, 1964; McNab, 1989). Free-ranging eastern tube-nosed bats *Nyctimene robinsoni* also did not use torpor, but the work was conducted in a tropical area when environmental conditions were mild and food was abundant (Riek, Körtner & Geiser, 2010).

Table 1 Summary of thermal physiology of each bat family; taxonomy from Wilson & Reeder (2005)

Family	No. of species	Distribution	Diet	Roost type	Patterns of heterothermy	References
Pteropodidae	186	Subtropical, tropical	Frugivorous, nectarivorous	Trees, leaves, caves, rock crevices, buildings	Smaller species in this family are known to use daily torpor throughout the year. Larger species appear to be homeothermic.	Bartholomew <i>et al.</i> (1970); Kulzer & Storf (1980); Hall & Pettigrew (1995); Geiser <i>et al.</i> (1996); Bartels <i>et al.</i> (1998); Coburn & Geiser (1998); McLab & Bonaccorso (2001); Kulzer <i>et al.</i> (1970); Park <i>et al.</i> (2000)
Rhinolophidae	77	Temperate, subtropical, tropical	Insectivorous	Trees, leaves, caves, buildings	Known to hibernate in temperate regions and to use short bouts of torpor in tropical regions	Kulzer (1965); Liu & Karasov (2011)
Hipposideridae	81	Subtropical, tropical	Insectivorous	Trees, caves, buildings	Hibernate in a subtropical region; short torpor bouts have also been recorded	Kulzer (1965); Geiser & Stawski (2011)
Megadermatidae	5	Tropical	Insectivorous, carnivorous	Trees, caves, rock crevices, buildings	Only small reductions in T_b have been recorded	Kulzer (1965); Geiser & Stawski (2011)
Rhinopomatidae	4	Subtropical, tropical, arid	Insectivorous	Caves, rock crevices, buildings	Hibernate at high T_a ; short shallow torpor bouts have also been recorded	Kulzer (1965); Levin <i>et al.</i> (2010); Levin <i>et al.</i> (2012)
Craseonycteridae	1	Tropical	Insectivorous	Caves	Thermal biology not known	Kulzer (1965); Kulzer <i>et al.</i> (1970); Genoud, Bonaccorso & Arends (1990)
Emballonuridae	51	Warm temperate, subtropical, tropical	Insectivorous	Trees, leaves, caves, rock crevices, buildings	Express shallow daily torpor bouts	Kulzer (1965); Kulzer <i>et al.</i> (1970); Genoud, Bonaccorso & Arends (1990)
Nycteridae	16	Subtropical, tropical	Insectivorous, carnivorous	Trees, caves, buildings	Shallow torpor in <i>Nycteris thebaica</i>	Cory Toussaint & McKechnie (2012)
Myzopodidae	1	Tropical	Insectivorous	Leaves	Thermal biology not known	Daniel (1979); Sedgely (2001); Christie & Simpson (2006)
Myzacinidae	2	Temperate	Insectivorous, frugivorous	Trees	Reduced winter activity. Individuals did not emerge from their roost for up to 13 days, suggesting they hibernate.	
Phyllostomidae	160	Subtropical, tropical	Insectivorous, carnivorous, sanguivorous, frugivorous, nectarivorous	Trees, leaves, caves, rock crevices, buildings	Short and shallow bouts of torpor	Lyman (1970); Rasweiler (1973); Audet & Thomas (1997); Kellm & von Helversen (2007)
Mormoopidae	10	Subtropical, tropical	Insectivorous	Trees, caves	Appear to be strict homeotherms, no torpor found in four species	Bonaccorso <i>et al.</i> (1992)
Noctilionidae	2	Tropical	Insectivorous, carnivorous	Trees, rock crevices	Thermal biology not known	
Furipteridae	2	Tropical	Insectivorous	Caves, buildings	Thermal biology not known	
Thyropteridae	3	Tropical	Insectivorous	Leaves	Thermal biology not known	
Natalidae	8	Tropical	Insectivorous	Caves	Limited data, shallow torpor bouts recorded	Genoud <i>et al.</i> (1990)
Molossidae	100	Temperate, subtropical, tropical, arid	Insectivorous	Trees, caves	Hibernate with multiday torpor bouts and low T_b during winter and also express short torpor bouts in temperate, subtropical and arid regions	Kulzer <i>et al.</i> (1970); Maloney <i>et al.</i> (1999); Arlettaz <i>et al.</i> (2000); Marom <i>et al.</i> (2006); Vivier & van der Menve (2007); Cory Toussaint <i>et al.</i> (2010); Bondarenco <i>et al.</i> (2013)
Vespertilionidae	407	Temperate, subtropical, tropical, arid	Insectivorous, carnivorous	Trees, leaves, caves, rock crevices, buildings	Heterothermy is very common in this family in species from all regions. Short torpor bouts are expressed throughout the year in all regions. Typical winter hibernation patterns in temperate species with T_b near/below 0°C; multiday torpor bouts during winter also occur in the subtropics.	Eisenbraut (1956); Kulzer <i>et al.</i> (1970); Audet & Fenton (1988); Genoud (1993); Hosken (1997); Hosken & Withers (1997); Turbill <i>et al.</i> (2003); Willis <i>et al.</i> (2005); Turbill (2006); Jacobs <i>et al.</i> (2007); Rambaldini & Brigham (2008); Turbill & Geiser (2008); Stawski <i>et al.</i> (2009); Daniel <i>et al.</i> (2010); Dunbar & Brigham (2010); Stawski & Geiser (2010b); Geiser, Stawski, Bondarenco, & Pavey (2011); Jonasson & Willis (2012); Stawski & Geiser (2012); Czenze <i>et al.</i> (2013)

In contrast, laboratory studies have established that, especially when food is restricted, several small pteropodid species express daily torpor with T_b as low as 17.2°C (Bartholomew, Dawson & Lasiewski, 1970; Kulzer & Storf, 1980; Hall & Pettigrew, 1995; Bartels, Law & Geiser, 1998; Coburn & Geiser, 1998; McNab & Bonaccorso, 2001; Geiser, 2006). All heterothermic pteropodids were <50 g and it therefore may be correct that the larger species are homeothermic (Bartholomew *et al.*, 1964; McNab, 1989; Geiser & Stawski, 2011). Interestingly, while torpor use is more pronounced during the cool winter period in most species, the Australian subtropical pteropodid *Syconycteris australis* shows an increase in torpor duration during summer, most likely due to the decreased availability of flowering plants and thus nectar (Coburn & Geiser, 1998). This emphasizes the importance of food availability on the energy partitioning of bats and therefore its influence on the use of torpor by bats.

The rhinolophid *Rhinolophus megaphyllus*, from a tropical habitat in Australia, reduced its T_b to a minimum of 16°C under laboratory conditions, confirming that members of this family may also use torpor in a mild climate (Kulzer *et al.*, 1970).

Yangochiroptera

Temperate

Bats from the families Vespertilionidae and Molossidae from high-latitude temperate regions are known to hibernate (Davis, 1970; Lyman, 1970; Ransome, 1990; Arlettaz *et al.*, 2000). Hibernation by the little brown bat *Myotis lucifugus*, which ranges over much of North America, has received considerable attention (Hock, 1951; Matheson, Campbell & Willis, 2010; Jonasson & Willis, 2012; Reeder *et al.*, 2012; Czenze, Park & Willis, 2013). However, other species from other regions have also been examined in detail (e.g. Lausen & Barclay, 2003; Willis, Brigham & Geiser, 2006; Solick & Barclay, 2007; Wojciechowski, Jefimow & Tęgowska, 2007; Becker *et al.*, 2013; Klug & Barclay, 2013). Most insectivorous bats in temperate regions typically show the traditional hibernation pattern throughout winter, with multi-day torpor bouts interspersed by periodic and short arousals (Henshaw, 1970; Turbill, 2006; Hope & Jones, 2012; Jonasson & Willis, 2012). Although it has been claimed that some hibernating bats may express longer torpor bouts than most other hibernators (Menaker, 1964; Brack & Twente, 1985), this has only recently been confirmed using temperature telemetry in the field with torpor bouts of up to ~48 days in *M. lucifugus* (Jonasson & Willis, 2012). Despite these long torpor bouts, these small bats require fat reserves that are large relative to their body size to survive the prolonged hibernation season. Although bats have to fly, restricting the extent of fat they can store, their mass can be 30% higher at the beginning of hibernation than when they emerge in spring (Davis, 1970; Yalden & Morris, 1975; Speakman & Racey, 1989; Kunz, Wrazen & Burnett, 1998; Koteja, Jurczyszyn & Wołoszyn, 2001; Jonasson & Willis, 2011).

In milder temperate climates, some insectivorous bats arouse throughout winter and do not immediately re-enter torpor, but forage during warm spells when insect activity presumably increases. In some of these temperate species, activity in winter appears to be routine (Ransome, 1968; Avery, 1985; Hays, Speakman & Webb, 1992; Wojciechowski *et al.*, 2007; Turbill & Geiser, 2008; Hope & Jones, 2012). Those insectivorous bats that forage during winter show less pronounced seasonal changes in body mass and consistently synchronize periodic arousals from torpor with photoperiod (Turbill & Geiser, 2008; Hope & Jones, 2012). On the contrary, *M. lucifugus* hibernating in cold climates, where insects are unavailable for many months, synchronize arousals with conspecifics with no circadian pattern to arousal (Czenze *et al.*, 2013).

Temperate bats from both Northern and Southern Hemispheres appear to show similar patterns of torpor and thermal physiology during winter and are strongly influenced by roost microclimate (Geiser & Brigham, 2000). However, because thermal conditions in much of the Southern Hemisphere inhabited by bats are less severe, more southern bats roost in trees for the entire year in comparison to northern bats (Turbill & Geiser, 2008). Northern bats, especially those living at high latitudes, often require substantial refugia such as caves, which are well buffered from environmental conditions, to survive the winter. These differences in roost selection are reflected in patterns of hibernation. Tree roosts will allow hibernating bats to track weather changes and time arousals when conditions favour foraging to replenish fat stores (Dunbar & Tomasi, 2006; Turbill, 2008; Turbill & Geiser, 2008). Many such species are opportunistic hibernators that will remain torpid during adverse conditions and arouse to forage when conditions improve (Stawski & Geiser, 2010a). This is favoured also by the fluctuating T_a of tree roosts, which enable passive or partially passive rewarming reducing the energetic cost of arousals (Chruszcz & Barclay, 2002; Turbill, Körtner & Geiser, 2008). Conversely, caves tend to be spacious, open-air environments and with little opportunity for bats to alter the microclimate via heat production, at least in winter (Jonasson & Willis, 2012). This could help explain the energetically conservative hibernation patterns of some northern temperate vespertilionids and the strong tendency of many bat species to roost in clusters, which could trap metabolic heat locally (Davis, 1970; Kurta, 1985; Vivier & van der Merwe, 2007; Boyles, Storm & Brack, 2008; Jonasson & Willis, 2012).

Many temperate bats hibernate for much of the winter, but are also known to exhibit short bouts of torpor during summer, typically after returning from foraging in the morning (Lyman, 1970; Solick & Barclay, 2006, 2007; Turbill, 2006). In summer, these species often arouse largely passively in the middle of the day with increasing T_a and then re-enter torpor in the afternoon until the evening arousal (Turbill, Law & Geiser, 2003; Willis & Brigham, 2003; Turbill, 2006). Interestingly, metabolic data suggest that in hibernating bats the short torpor bouts expressed in summer are physiologically similar to the deep, prolonged torpor bouts seen during the hibernation period and differ substantially from the pattern of

exclusively daily torpor expressed by the small pteropodids (Hock, 1951; Lyman, 1970; Geiser & Brigham, 2000; Turbill *et al.*, 2008; Matheson *et al.*, 2010).

Tropical/subtropical/arid

The diversity of tropical and subtropical bat species is vast and, accordingly, variation in patterns of thermoregulation and energy balance among these species are large (Lyman, 1970). While it was previously assumed that all tropical bats are homeothermic (Henshaw, 1970), many tropical and subtropical yangochiropterans from the families Hipposideridae, Megadermatidae, Rhinopomatidae, Emballonuridae, Phyllostomidae, Natalidae, Molossidae and, especially, Vespertilionidae are in fact heterothermic (Geiser & Stawski, 2011). While most of the data on torpor for these bats are on captive individuals, some are now available for free-ranging individuals of several species studied in the field.

In contrast to the prevailing view that subtropical species do not hibernate, multi-day torpor bouts during winter have now been recorded. Three species of subtropical insectivorous bats entered torpor bouts of 5–19 days at T_a between 4 and 25°C (Stawski, Turbill & Geiser, 2009; Cory Toussaint, McKechnie & van der Merwe, 2010; Liu & Karasov, 2011). These data show that saving energy by employing torpor is important not only to bats in cold climates. Even in tropical areas, frequent use of short bouts of torpor in winter has now also been recorded in some free-ranging insectivorous bats and torpor bouts of longer than a day have also been observed (Geiser *et al.*, 2011; Stawski & Geiser, 2012).

Torpor bouts tend to be of short duration during summer in subtropical bats, such as the Angolan free-tailed bat *Mops condylurus* from South Africa (Vivier & van der Merwe, 2007). Interestingly, in summer, patterns of torpor expressed by subtropical species are similar to those shown by temperate species, with one bout in the morning followed by a second in the afternoon after a period of normothermy around noon (Turbill *et al.*, 2003).

Although temporal heterothermy appears widely spread among the tropical/subtropical yangochiropterans, some appear to be strictly homeotherms. These include four mormoopids that did not enter torpor even at low T_a and were unable to cope with $T_a < 15^\circ\text{C}$ (Bonaccorso *et al.*, 1992). Only a minority of tropical/subtropical bats have been investigated in terms of their thermal biology, and while current data suggest that many of these are likely heterothermic, this will not be universal.

Data on the use of torpor by bats inhabiting arid regions are also scarce. However, several studies have observed torpor use by arid zone bats, perhaps likely due to the unpredictability of rainfall and food availability in deserts (Marom *et al.*, 2006; Daniel, Korine & Pinshow, 2010; Levin *et al.*, 2010; Bondarenko, Körtner & Geiser, 2013). We predict that many desert bats are heterothermic. Torpor use was recorded throughout the year in two insectivorous bat species from the Negev Desert, *Otonycteris hemprichii* and *Tadarida teniotis* (Marom *et al.*, 2006; Daniel *et al.*, 2010). Hibernation at high T_a has been observed in *Rhinopoma microphyllum* (Levin

et al., 2010). Australian arid-zone molossids, *Mormopterus* spp., were also found to enter torpor regularly during summer and employed largely passive arousals for rewarming from torpor (Bondarenko *et al.*, 2013).

Evolution of heterothermy in bats

Many evolutionary studies on bats have focused on the evolution of flight, echolocation or immune function in bats (Teeling *et al.*, 2005; Teeling, 2009; Shen *et al.*, 2010; Zhang *et al.*, 2013). However, the evolution of torpor in bats also has received some attention, and six candidate genes linked to hibernation were found to be positively selected for in the hibernating bat *Myotis davidii*, as in other hibernating species (Zhang *et al.*, 2013). Twente & Twente (1964) hypothesized that heterothermic bats were derived from tropical homeothermic ancestors when bats invaded cooler habitats. More recent studies propose a plesiomorphic evolution of torpor in bats. Molecular studies on the hormone leptin, important for fattening and energy balance, suggest that heterothermy was the ancestral trait in bats and that homeothermy was derived secondarily (Yuan *et al.*, 2011). Given that many small pteropodids use torpor, and assuming that the Yinpterochiroptera are indeed a single group, a plesiomorphic origin of heterothermy in bats appears to be supported by the available data (Geiser & Stawski, 2011). This scenario would suggest that the capacity for heterothermy has been lost in large tropical/subtropical pteropodids and in other homeothermic bats because of their size, favourable climates and an abundant food supply.

Torpor in relation to the natural history of bats

Torpor and reproduction

Mating in many bat species occurs either before they enter hibernation or during hibernation (Oxberry, 1979; Thomas, Fenton & Barclay, 1979; Turbill, 2006; Turbill & Geiser, 2008). Often, this leads to a mismatch in the timing of reproductive investment for male bats (i.e. late summer to early winter) versus females (i.e. spring to mid-summer), and this mismatch appears to influence the energetics of hibernation in some species. Females of hibernating species either store sperm until spring when fertilization occurs, or fertilization occurs before hibernation and implantation of embryos is delayed until females emerge in spring (Oxberry, 1979; Geiser & Brigham, 2012). Offsetting mating from fertilization or implantation will ensure that females give birth early during spring to allow pups sufficient time to develop, grow and accumulate fat reserves for the next winter. Female little brown bats (*M. lucifugus*) enter hibernation with larger fat reserves than males, and also use their fat reserves more slowly than males throughout winter (Jonasson & Willis, 2011). This presumably enables females to emerge in spring with large enough fat stores for initiation and support of early pregnancy (Jonasson & Willis, 2011).

Table 2 Torpor depth and duration in reproductive female bats in comparison to non-reproductive bats

	Body mass (g)	Min T_b or T_{skin} (°C)	Torpor bout duration (days)	References
Pregnancy				
Pteropodidae				
<i>Syconycteris australis</i> (common blossom-bat)	18	-22 (+4.0)	0.13 (50%)*	Coburn & Geiser (1998); Geiser <i>et al.</i> (2001)
Vespertilionidae				
<i>Myotis myotis</i> (mouse-eared bat)	25		3 (7.3%, W)	Eisentraut (1937); Harmata (1987)
<i>Myotis lucifugus</i> (little brown bat)	6.5–10.8	25.4 (+4.5)*	0.09 (25.7%)*	Dzal & Brigham (2013)
<i>Eptesicus fuscus</i> (big brown bat)	19	14.9 (+13.8, W)*	0.15 (1%, W)*	Hamilton & Barclay (1994); Grinevitch <i>et al.</i> (1995)
<i>Pipistrellus pipistrellus</i> (pipistrelle bat)	6		~ 15.3	Racey (1973)
<i>Lasiurus cinereus</i> (hoary bat)	35.8	5.5	5.6	Willis <i>et al.</i> (2006)
<i>Corynorhinus rafinesquii</i> (Rafinesque's big-eared bat)	8–14	33.9 (+2.6)*	0.08 (30.8%)*	Johnson & Lacki (2013)
<i>Nyctophilus bifax</i> (eastern long-eared bat)	13.8	25.6 (+15.4)	0.07 (10%)	Stawski (2010)
<i>Otonycteris hemprichii</i> (Hemprich's long-eared bat)	16.5–23	18		Daniel <i>et al.</i> (2010)
Mean difference		+8.1 ± 6.0	20.8 ± 18.3%	
Lactation				
Vespertilionidae				
<i>Myotis lucifugus</i> (little brown bat)	6.5–10.8	21.2 (+0.2)*	0.23 (65.7%)*	Dzal & Brigham (2013)
<i>Myotis bechsteinii</i> (Bechstein's bat)	8.9–12.5	31.8 (+8.4)*		Dietz & Hörig (2011)
<i>Myotis daubentonii</i> (Daubenton's bat)	7.1–10.0	33.0 (+10.5)*		Dietz & Hörig (2011)
<i>Eptesicus fuscus</i> (big brown bat)	19	25.8 (+24.7, W)*	0.15 (1%, W)*	Hamilton & Barclay (1994); Grinevitch <i>et al.</i> (1995)
<i>Lasiurus cinereus</i> (hoary bat)	27	23.6*		Klug & Barclay (2013)
<i>Corynorhinus rafinesquii</i> (Rafinesque's big-eared bat)	8–14	32.9 (+1.6)*	0.23 (88.5%)*	Johnson & Lacki (2013)
<i>Otonycteris hemprichii</i> (Hemprich's long-eared bat)	16.5–23	29		Daniel <i>et al.</i> (2010)
Mean difference		+9.1 ± 9.8	51.7 ± 45.4%	

Difference between min T_b/T_{skin} of reproductive and non-reproductive bats is shown in brackets.

Duration of torpor bouts of reproductive bats is shown in brackets as a percentage of the duration of torpor bouts of non-reproductive bats.

All values from non-reproductive bats are from the reproductive season with similar weather patterns as reproductive bats, unless obtained from winter studies and denoted with 'W'.

Where possible, non-reproductive bats are females and if these values were unavailable values from males were used.

Values are the absolute min T_b/T_{skin} or longest torpor bout duration recorded, unless denoted by '**' which indicates mean values were used.

Although torpor and reproduction were considered physiologically incompatible in the past, recent work has shown that it can be used during all reproductive stages in bats and some other heterothermic mammals (Geiser, 1996; McAllan *et al.*, 2012; Dzal & Brigham, 2013; Johnson & Lacki, 2013). However, torpor is generally shallower in pregnant and lactating individuals in comparison to non-reproductive individuals, although the magnitude of this difference varies among species (Table 2). Duration of torpor bouts in pregnant and lactating bats are generally shorter than that in non-reproductive bats, but the difference in duration of torpor bouts also varies greatly among species (Table 2). The use of torpor in pregnant and lactating bats may be surprising, considering that it slows down the development of offspring (Hamilton & Barclay, 1994; Willis *et al.*, 2006; Stawski, 2010; Johnson & Lacki, 2013). However, torpor in reproductive bats has several potential benefits. The most obvious of these is the potential to prevent starvation of both mother and offspring during adverse conditions, as in non-reproductive bats. An added benefit of torpor by pregnant bats could be the delay of

parturition until environmental conditions can promote maximal energetic gains. Supporting this hypothesis, Willis *et al.* (2006) suggested that the multi-day torpor bouts they observed in pregnant hoary bats *Lasiurus cinereus*, a solitary, foliage roosting species, prolonged gestation until after cold weather and snow in spring, allowing the bats to give birth during warm weather and better cope with lactation, the most energetically demanding period of reproduction (Kurta *et al.*, 1989; Wilde *et al.*, 1995). Lactating females appear to avoid torpor use if possible, likely because low T_b slows milk production and low pup T_b will also delay their growth (Racey & Speakman, 1987; Audet & Fenton, 1988; Chruszcz & Barclay, 2002; Lausen & Barclay, 2003; Daniel *et al.*, 2010; Pretzlaff, Kerth & Dausmann, 2010). Lactating bats may also be better able to avoid torpor than pregnant individuals because after parturition, wing loading is dramatically reduced, which likely improves foraging efficiency and the potential to acquire energy (Chruszcz & Barclay, 2002). However, shallow torpor has even been recorded in lactating female bats to possibly save energy in between feeding bouts (Johnson & Lacki,

2013). Reproductive male bats and non-reproductive female bats are often considered as similar in terms of the trade-offs between costs and benefits of heterothermy (Grinevitch, Holroyd & Barclay, 1995; Stawski, 2010). However, depth of torpor bouts in male *Myotis* spp. decreased from early to advanced spermatogenesis (i.e. from spring to autumn), and this change was independent of seasonal change in T_a (Dietz & Hörig, 2011). This suggests that avoidance of torpor at certain times of the annual cycle is also important for reproductive success in males.

In some species, physiological constraints appear to prevent bats from expressing extensive torpor during the reproductive period. For example, in *S. australis* measured in the laboratory, depth of torpor in pregnant females was similar to that of non-reproductive females in the same study, but the duration of torpor was shorter in the former (Geiser, Körtner & Law, 2001), suggesting that there was a physiological change. On the contrary, other bat species appear to use roost selection to promote or avoid torpor use during reproductive periods rather than or in addition to physiological differences. In the wild, reproductive females often roost in clusters (Dwyer & Harris, 1972) and this may enable them to minimize or even avoid torpor use while still saving energy by increasing roost T_a (Hamilton & Barclay, 1994; Cryan & Wolf, 2003; Willis & Brigham, 2007; Pretzlaff *et al.*, 2010). Males, on the contrary, may roost solitarily to promote torpor (Hamilton & Barclay, 1994; Cryan & Wolf, 2003). Laboratory work conducted under the same environmental conditions suggests that torpor patterns are similar between sexes and reproductive states (Turbill & Geiser, 2006), further supporting the view that different roosting preferences are, to a large extent, responsible for the differences in torpor patterns among gender and reproductive states in bats.

Costs and benefits of torpor

While torpor results in large energy savings, it entails several possible disadvantages. These include reduced mobility, compromised immunocompetence, accumulation of metabolic wastes and memory loss (Millesi *et al.*, 2001; Prendergast *et al.*, 2002; Humphries, Thomas & Kramer, 2003). One obvious cost of torpor is the dramatically reduced function of skeletal muscle, which can render torpid bats more susceptible to predation. Although this is true at very low T_b , recent data suggest that torpid animals, including bats, are more mobile than is widely assumed, with torpid bats capable of flight at T_b as low as 20°C (Bradley & O'Farrell, 1969; Willis & Brigham, 2003; Rojas, Körtner & Geiser, 2012). Another disadvantage of torpor is reduced immunocompetence during deep torpor (Prendergast *et al.*, 2002), which apparently is possible because growth of bacteria is reduced at low T_b (Bouma, Carey & Kroese, 2010). Moreover, brain function appears to be compromised following arousal from torpor, and while the long-term costs are currently uncertain, experimental evidence suggests that memory may be impaired (Millesi *et al.*, 2001; Thompson, Montiglio & Humphries, 2013). Such costs appear to be the reason why some species use torpor only as a last

resort when energy demands cannot be met because of low food availability (Grinevitch *et al.*, 1995; Humphries *et al.*, 2003; Boyles *et al.*, 2007).

In contrast to bat species that use torpor only during emergency situations, other bats use it regularly without the apparent need to save energy (Stawski & Geiser, 2010b; Geiser & Brigham, 2012). Like any trait, this variation appears to be driven by differences among species in how the balance of costs and benefits of torpor influence reproductive fitness (Angilletta *et al.*, 2010). For example, torpor during summer by subtropical insectivorous bats, a time when T_a is mild and insects are abundant, suggests that torpor has functions beyond energy conservation and that negative effects of torpor for these species are minimal (Bronner, Maloney & Buffenstein, 1999; Turbill *et al.*, 2003; Vivier & van der Merwe, 2007; Stawski & Geiser, 2010b). Subtropical *Nyctophilus bifax* in better body condition during summer used torpor more frequently than those in poorer condition (Stawski & Geiser, 2010b). Similarly, temperate *R. ferrumequinum* foraged during winter only when body condition was poor; fat bats remained in hibernation (Park *et al.*, 2000). This suggests that an additional benefit of torpor, in addition to energy and water savings, could be its potential to reduce exposure to predators by allowing animals to remain inactive in a sheltered roost or hibernaculum (Geiser & Brigham, 2012; Bieber *et al.*, 2013). Although bats are longer-lived than other mammals of similar size, partially attributed to flight, hibernating bats live much longer on average than homeothermic bats, supporting the argument that torpor may reduce mortality from predation and also likely from starvation (Wilkinson & South, 2002; Brunet-Rossinni & Austad, 2004; Munshi-South & Wilkinson, 2010; Turbill, Bieber & Ruf, 2011). Thus, the reduced energy and foraging requirements resulting from torpor may contribute to extending longevity in heterothermic bats (Brunet-Rossinni & Austad, 2004; Munshi-South & Wilkinson, 2010).

Torpor, parasites and pathogens

Parasites are likely a selective force for many bats, especially social species that aggregate in large numbers. In temperate regions, ectoparasites appear to be more prevalent on juveniles and adult female vespertilionid bats in comparison to adult males (Lučan, 2006; Christe *et al.*, 2007; Czenze & Broders, 2011). This could be attributed to the roosting preferences of bats, where reproductive females often roost in clusters and at higher T_a , whereas males and non-reproductive females often roost solitarily and at lower T_a (Hamilton & Barclay, 1994). The roosting preferences of reproductive females could enhance ectoparasite transmission and survival, and ectoparasite infestation rates are higher during the lactation and post-lactation periods and are lower during movement periods (Lučan, 2006; Christe *et al.*, 2007; Czenze & Broders, 2011). Bats with high ectoparasite loads generally have poor body condition (Lučan, 2006), which could affect torpor use either by increasing the use of torpor to conserve energy or by decreasing the use of torpor to increase available foraging times to replenish energy stores. Torpor does appear

to reduce the numbers of some ectoparasites, but this appears to be more prevalent in cold-temperate regions, whereas ectoparasite numbers do not change significantly with season in warm tropical regions (Geiser & Brigham, 2012).

Bats are increasingly being studied from a wildlife disease perspective in part because of their role in a number of high-profile zoonotic disease outbreaks (Turmelle & Olival, 2009; Schinnerl *et al.*, 2011; Wang *et al.*, 2011; Hayman *et al.*, 2013; Luis *et al.*, 2013). The highly social colonial roosting pattern of some bats with high rates of physical contact among individuals, and the dependence on roosts hosting multiple species (e.g. caves and mines), has presumably driven the evolution of a particularly diverse range of pathogens (Luis *et al.*, 2013). Given close links between roosting behaviour, sociality and thermoregulation, knowledge on the use of torpor in bats may have a role to play in our understanding of bat disease and their zoonotic potential. For example, recently, Luis *et al.* (2013) showed that the tendency to express torpor reduces the likelihood that bat and rodent species will host zoonotic viruses, which suggests that torpor may influence pathogen diversity in bats. Additionally, the rate of virus replication may be decreased during torpor bouts as a result of the reduction in T_b and MR (Wang *et al.*, 2011), which suggests that, in addition to possibly reducing the risk of predation, use of torpor could also reduce the risk of pathogen exposure. Links between coloniality, thermoregulation and disease in bats are clearly an important area for future study for both wildlife disease ecology and human public health.

White-nose syndrome

In terms of disease, the ability to express long-term torpor is likely beneficial when it comes to evading pathogens because growth of most typical mammalian pathogens (i.e. bacteria and viruses) depends on relatively high T_b (Bouma *et al.*, 2010). This could explain why some bat species (and other hibernators) can afford to significantly down-regulate the immune response during winter (Moore *et al.*, 2013). However, this strategy appears to be failing for many North American bat species. Bat populations in eastern North America are being severely affected by WNS, which is caused by the cold-tolerant fungal pathogen *Geomyces destructans* (Blehert *et al.*, 2009; Warnecke *et al.*, 2012; Lorch *et al.*, 2013). Mortality from WNS was first confirmed during the winter of 2007/2008 and the disease has now spread rapidly throughout the eastern United States and Canada (Blehert *et al.*, 2009). The fungus also occurs on bats in Europe, where it does not cause mass mortality, and experimental evidence suggests that *G. destructans* is a novel, invasive pathogen to North America (Warnecke *et al.*, 2012). The fungus invades the epidermis of infected bats and causes other clinical signs such as electrolyte depletion and emaciation and ultimately death for many individuals (Reichard & Kunz, 2009; Cryan *et al.*, 2013; Lorch *et al.*, 2013; Warnecke *et al.*, 2013).

Although the exact mechanism underlying mortality is uncertain, infected bats arouse up to three times more often than healthy bats during hibernation and are unable to survive the hibernation season due to premature depletion of fat

reserves (Reeder *et al.*, 2012; Warnecke *et al.*, 2012). Infected bats exhibit clinical signs of hypotonic dehydration with reduced plasma electrolyte levels (Na^+ and Cl^-) potentially resulting from fluid loss across fungal lesions in the highly vascularized skin of the wings (Cryan *et al.*, 2013; Warnecke *et al.*, 2013). One explanation for increased arousal frequency, consistent with fluid loss and electrolyte depletion, has been called the dehydration hypothesis (Cryan *et al.*, 2010) and is related to the fact that rates of evaporative water loss and duration of torpor bouts are correlated in hibernators (Thomas & Geiser, 1997). Thus, wing lesions caused by the fungus could lead to increased water loss, which could be the trigger for an increase in arousal frequency and premature fat depletion (Cryan *et al.*, 2010, 2013; Warnecke *et al.*, 2013). WNS affects different bat species disproportionately, with some exhibiting very little response, while in others, mortality rates are very high. Differences in water loss among species are one factor that could influence this variation. Little brown bats (*M. lucifugus*), for example, are particularly affected by WNS and have higher rates of evaporative water loss in comparison to other species, such as European Natterer's bats *Myotis nattereri*, which may be susceptible to *G. destructans* but do not die from WNS (Willis *et al.*, 2011). For some species, hibernacula with the highest humidity appear to have the highest mortality rates (Langwig *et al.*, 2012). One hypothesis to explain this observation is that species and individuals with high intrinsic rates of water loss select the highest humidity environments for hibernation but that these humid environments also favour rapid growth of the fungus. This would explain why these bats, which normally benefit from high humidity environments during hibernation, suffer such high mortality from WNS.

A disease that specifically targets torpid mammalian hibernators is unprecedented and the rapid emergence of WNS has highlighted the importance of more data on basic aspects of hibernation in bats. More information is needed on physiological triggers for arousal, immune function during hibernation, behaviours like clustering and microhabitat selection, anatomy and physiology of wing tissue and links between hibernation physiology, life-history traits and ecology. It is also crucial to determine whether mitigation or management strategies are feasible and to help develop those strategies to deal with WNS.

Conclusions and directions for future research

Many bats are small and have high energetic demands for both activity and maintenance processes. Therefore, torpor has likely been a key survival strategy for the group throughout their evolutionary history (Geiser & Stawski, 2011). By being flexible in their use of torpor, bats can adjust their T_b and MR depending on foraging success and the size of their energy stores (Stawski & Geiser, 2011). While bats with strict hibernation requirements may be negatively affected by climate change and pathogens (Humphries, Thomas & Speakman, 2002; Bouma *et al.*, 2010), those species that are flexible in their use of torpor will likely have an increased

chance of survival (Stawski & Geiser, 2012). Recent evidence suggests that temporal heterothermy is an important long-term survival mechanism and that the majority of mammals that have recently gone extinct were likely unable to use torpor (Geiser & Turbill, 2009; Geiser & Stawski, 2011; Turbill *et al.*, 2011). Data obtained on thermal physiology, reproductive ecology and roosting requirements of bats, in regard to optimal roost temperatures and feeding locations, can be used to develop effective conservation and management plans (Brack, 2007; Encarnação, Otto & Becker, 2012). The crisis for bat conservation resulting from WNS illustrates the importance of more data on the basics of thermal physiology and hibernation ecology of bats to potentially enable informed and effective management responses. The use of torpor is fundamentally linked with many aspects of the ecology and natural history of bats and improved understanding of temporal heterothermy in this diverse group will enhance our understanding of bat ecology and conservation in general.

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