Chapter 10
The Other Functions of Torpor

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Abstract Although energy conservation by cold-climate adult endotherms in winter is often viewed as the main function of torpor, recent evidence suggests that this may not always be the case. We examined whether other functions of torpor may be equally or even more important in some instances. Torpor enhances fat storage during migration, apparently permits prolonged female sperm storage in bats, allows reproduction with limited or fluctuating food supply, and delays parturition until more favorable periods. Torpor appears to increase the efficiency of energy and nutrient use during development. Further, torpor reduces water requirements, appears to permit persistence during droughts, reduces the load of some parasites, permits co-existence of competing species, and also reduces the risk of predation and mammalian extinctions. Thus, the functions of torpor are complex and some of these appear to be not just proximate.

10.1 Introduction

It remains a widely held view that the ultimate function of torpor is energy conservation to increase the probability of survival despite limited food availability in winter by adult, non-reproductive mammals and birds living in cold climates (Lyman et al. 1982). To some extent this paradigm is related to the regions where

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most of the classical work on torpor was conducted (northern Europe and North America) and where torpor often occurs predictably in winter when food availability decreases and ambient temperatures (T_a) are low (e.g. Hall 1832; Horvath 1878; Eisentraut 1929; Kayser 1939; Jaeger 1948; Lyman 1948).

The physiological variables measured in the context of torpor such as heart rate, rate of oxygen consumption, or carbon dioxide production that are often used as proxies for energy metabolism are variables relatively easy to measure. Their substantial decline during torpor is consistent with energy conservation being the ultimate function of torpor. In contrast, perceived proximate effects of torpor use such as predator avoidance, a prolonged life span, or other life history traits are often more obscure and therefore difficult to quantify, especially for animals under natural conditions. Nevertheless, evidence has emerged in recent years which taken together suggests that the functions of torpor may not be as straight forward as commonly thought. In some instances, the data suggest that energy conservation during torpor might in fact be a proximate, rather than the ultimate effect. Torpor is now known to occur in many mammals and birds including tropical and subtropical species (Dausmann et al. 2005; Stawski et al. 2009). Torpor is also used by reproductively active individuals as well as developing young. While many heterothermic species enter torpor mainly or only when energetically challenged (Wang 1978; Christian and Geiser 2007; Landry-Cuerrier et al. 2008) others display torpor in summer or in situations where they have access to food and exhibit no obvious energetic stress (Hill 1975; Geiser and Baudinette 1987; Nicol and Andersen 2002; Rimbaldini and Brigham 2008; Bieber and Ruf 2009; Stawski and Geiser 2010). This suggests that torpor likely has other functions besides energy conservation during periods of severe energy shortage or that animals have no reason to not use torpor. Our review is an attempt to synthesize what is known about some of these other functions and to examine whether these functions are more than simply proximate effects.

10.2 Torpor and Migration

An important difference in how small birds and terrestrial mammals deal with adverse conditions in winter often identified in text books is that because birds can fly, they commonly employ a behavioral option and migrate to avoid winter conditions. In contrast, because small terrestrial mammals cannot migrate long distances, they more often use a physiological option and employ torpor, characterized by pronounced reductions in metabolism and body temperature (T_b), to survive the winter. Clearly, the situation is more complex as bats can fly but many do not migrate and hibernate instead. Further, one of the first identified ‘new functions of torpor’ stems from evidence that migrating hummingbirds enter torpor not simply to reduce metabolic rate when energetically challenged, but as a means to enhance fat storage at night during the period of migration (Carpenter and Hixon 1988; Hiebert 1993). A free-ranging migratory hummingbird (*Selasphorus rufus*) used torpor for most of the night while roosting although it had enough stored fat to remain normothermic (Carpenter and Hixon 1988). Captive individuals of the same species enter the longest and most frequent bouts of spontaneous torpor during the autumnal migration period, the time of the year when they are at their greatest body mass and have amassed fat stores up to 50% of lean body mass. Such fat stores would easily allow for regulation of normothermic T_b in the cold (Hiebert 1993). These observations strongly suggest that torpor use is not simply an acute response to an energetic challenge, but rather a predictive strategy that anticipates a likely future energy-demanding event.

In non-migratory birds, torpor use, in addition to dealing with food shortages in winter, has been suggested to represent a key adaptation for maintaining a year round home range (Körtner et al. 2000). Tawny frogmouths (*Podargus strigoides*), an insectivorous species that has to deal with a substantial seasonal reduction of food and low T_a, regularly enter torpor in winter and remain in almost the identical part of the forest. Therefore, unlike migrating birds, they do not need to re-establish a new home range for breeding in early spring, which, as in hibernating terrestrial mammals, is likely to increase fitness.

10.3 Torpor and Reproduction

Although many endotherms undergoing reproduction appear to avoid torpor (Brigham 1992; Kissner and Brigham 1993; Barnes 1996; Mzilikazi and Lovegrove 2002), many others have been observed using torpor during various parts of the reproductive cycle. These include torpor during periods when females store sperm, during pregnancy, and during lactation. Sperm storage in female vertebrates is longest in ectothermic reptiles (up to several years) and up to 225 days in bats (Wimsatt 1960; Racey 1979; Birkhead and Møller 1993; Wang et al. 2008). In other mammals, sperm storage typically is 0.5–10 days, although 30 days has been reported in hares (*Lepus europaeus*) (Birkhead and Møller 1993). In bats, the longest periods of sperm storage (>100) days have been observed in cold-climate hibernating species (Racey 1979; Birkhead and Møller 1993; Wang et al. 2008). However, even in warm-climate species, including tropical bats, sperm storage lasting from several weeks to around 2 months have been observed (Wang et al. 2008). The enormous difference in duration of successful sperm storage in female bats in comparison to other mammals is likely related to some aspect of the extensive use of torpor. Bats frequently display torpor, including multiday torpor, even in tropical/subtropical areas (Stawski et al. 2009; Cory Toussaint et al. 2010; Liu and Karasov 2011), whereas most other mammals in which sperm storage is <1 month (Birkhead and Møller 1993) are homeothermic and a few (small marsupials and rodents) use daily torpor exclusively (Geiser and Ruf 1995).

Prolonged sperm storage in female bats has several implications (Racey 1979; Birkhead and Møller 1993). It often allows separation of the male and female reproductive cycle and likely facilitates optimal timing of reproduction. Female sperm storage represents insurance against not finding a partner in spring and enables females to synchronize births. So while the main function of torpor is likely to allow winter survival, it nevertheless also permits bats to cope with having to fertilize eggs soon after winter with enough time for the development of young, which can be critical especially in cold regions. Synchronization of births likely decreases predation and increases fitness.

Aside from enhancing sperm storage, torpor is also important after fertilization. Torpor during pregnancy has been recorded in echidnas (*Tachyglossus aculeatus*; Geiser 1996; Morrow and Nicol 2009), small marsupials (Frey and Fleming 1984; Geiser et al. 2005), tenrecs (*Microgale* spp.; Stephenson and Racey 1993), and vespertilionid and pteropodid bats (Racey 1973; Audet and Fenton 1988; Grinevich et al. 1995; Geiser 1996; Turbill and Geiser 2006; Stawski 2010). In many species, torpor during pregnancy is shorter and shallower than in non-reproductive females, but this is not always the case (Turbill and Geiser 2006). Although torpor during pregnancy appears to be mainly expressed during energetic stress, some mammals appear to use it to enhance fat storage (Geiser 1996). Pregnant mulgaras (*Dasycercus cristicauda/blythi*) enter spontaneous torpor (food available) under thermally mild conditions in captivity (Geiser and Masters 1994). During the period when torpor is expressed females increase body mass substantially. This is not due to the mass of the developing young because entire neonate marsupial litters weigh <0.5% of their mothers' body mass (Geiser and Masters 1994). Female mulgaras remain normothermic for a few days before giving birth and also do not enter torpor while lactating, which in marsupials is the energetically most demanding reproductive period. Although data are limited, female mulgaras in the wild in central Australia appear to use the same approach as captive animals with extensive use of torpor during pregnancy in winter (much deeper and longer than males at the same time of year) and homeothermy during lactation (Körtner et al. 2008). Thus, like for migration, it appears that torpor is not always a response to acute energy shortage or thermal stress, but rather an anticipatory strategy to reduce energy loss and enhance fat storage for future energy-demanding events.

In hoary bats (*Lasiurus cinereus*), entry into torpor by pregnant females during cold spells in spring appears to have an important function aside from energy conservation (Willis et al. 2006). Hoary bats use multiday torpor not only for survival, but also to slow embryonic growth which delays parturition until conditions are favorable for lactation and neonatal survival. Torpor has long been known to reduce growth rates and to prolong gestation in bats (Racey 1973), but this was typically viewed in a negative rather than a positive context.

Torpor during lactation is used by marsupial dunnarts (*Sminthopsis crassicaudata*; Morton 1978), sugar gliders (*Petaurus breviceps*; Geiser et al. 2008) and vespertilionid bats (Audet and Fenton 1988; Grinevich et al. 1995). Whereas in some bats, torpor during lactation appears to be shallower than during pregnancy, this is not the case in long-eared bats (*Nyctophilus* spp.; Turbill and Geiser 2006). In sugar gliders (*Petaurus breviceps*) torpor appears to be used exclusively during lactation and not pregnancy (Geiser et al. 2008). While it is known that torpor may be used during lactation, functions that go beyond simply saving energy to deal with limited food supply have not been identified, although conservation of water (see below) may be an important reason.

10.4 Torpor and Development

Many endotherms are altricial at hatching or birth. Altricial young lack insulation, are small, often uncoordinated, have a low capacity for heat production and a limited ability for physiological thermoregulation. Because they are well below adult size (in marsupials as little as $\sim 0.1\%$ or less) they have to continue to grow using imported nutrients, which are typically supplied by parents, and must use these efficiently. The largely poikilothermic thermoregulatory response (or perhaps better hypothermic response because heat loss exceeds heat production that is, however, well above that in ectotherms, Hill 1976) during early development permits the more or less exclusive investment of nutrients into growth. However, when the developing young becomes able to metabolically defend their T_b at low T_a at about 1/3 or 1/2 of adult size (or even at smaller sizes when huddling in nests or exposed to high T_a, Hill 1976) they face the problem of excessive heat loss that has to be compensated for by increased internal heat production via combustion of fuels to maintain a constant high T_b. It is likely that to minimize energy loss and to permit survival during adverse conditions or when parents are unable to supply enough food, some developing altricial young use torpor. Although this facet of torpor use has not received nearly enough scientific attention (it has not even been investigated in precocial young, which also face heat loss problems because of relatively large surface areas), it is currently known for five birds (chats *Ephthianura tricolor*, martins *Delichon urbica*, swifts *Apus apus*, mousebirds *Urocolius macrourus*, strom-petrels *Oceanodroma furcata*), four marsupials (dunnarts *Sminthopsis macroura*, antechinus *Antechinus stuartii*, *A. flavipes* and kowaris *Dasyuroides byrnei*), and three placental mammals (shrews *Crocidura russula*, hamsters *Phodopus sungorus*)(reviewed in Geiser 2008), and bats, *Eptesicus fuscus* (Hollis and Barclay 2008). In addition, reductions in core T_b by >5°C and even more in peripheral tissues have also been reported in developing king penguins (*Aptenodytes patagonicus*; Eichhorn et al. 2011). Torpor during development appears to have two major functions. The first is the traditionally accepted acute response permitting survival during adverse conditions and limited energy availability as for many adult heterotherms. However, torpor in developing young, although it likely slows growth, also has the potential to be used for diverting nutrients to enhance growth when the young are again normothermic (Giroud et al. 2012). Currently evidence supporting the hypothesis that this function of torpor is limited to a single study, but it certainly warrants further work.

10.5 Torpor and Water Conservation

Torpor is widely used by arid zone mammals and birds (Serventy and Raymond 1973; Warnecke et al. 2008; Doucette et al. 2011, 2012; Levy et al. 2011a). Lovegrove (2000) suggested that the unpredictability of food in environments such as deserts may be the reason for its extensive use, particularly on a daily basis.

Recent experimental data support this interpretation (Munn et al. 2010). However, use of torpor by desert dwellers and species from other regions may also function to reduce water loss. Free-ranging mouse-lemurs (*Microcebus murinus*) reduce rates of water turnover during torpor in comparison to individuals remaining normothermic (Schmid and Speakman 2009). Evaporative water loss of torpid cactus mice (*Peromyscus eremicus*) is only about 40% of that of normothermic individuals at the same T_a (MacMillen 1965). Similarly, for gerbils (*Gerbillus pusillus*) and marsupial dunnarts (*Sminthopsis macroura*) daily torpor reduces evaporative water loss to between 20 and 40% of that in normothermic individuals (Buffenstein 1985; Cooper et al. 2005). Extreme reductions in evaporative water loss of almost 90% have been reported for torpid bats (*Chalinolobus gouldii*) hibernating at T_a 10°C (Hosken and Withers 1997). Further, evaporative water loss of torpid honey possums (*Tarsipes rostratus*) during torpor was so low as to be undetectable (Withers et al. 1990).

Thus, torpor reduces water loss in mammals and is therefore ecologically important. It has been hypothesized that the large diversity of dasyurid marsupials in the arid zone of Australia, all of whom appear to express daily torpor, some on 100% of days in winter (Warnecke et al. 2008; Körtner and Geiser 2009), is one reason why these mammals persist in such a water poor environment. Although direct evidence for the initiation of torpor with the removal or restriction of water is more equivocal than for food restriction (but see Ibuca and Fukumura 1997), more extensive use of torpor in summer than winter in desert spiny mice (*Acomys russatus*; Levy et al. 2011a) suggests that water limitation rather than energy shortage may be the major cue for torpor use in this species in summer and thus the ultimate function of torpor may be for water rather than energy conservation.

10.6 Torpor and Drought

Cold northern winters are not the only periods of reduced food availability and have the advantage of lasting only about 6 months that can be bridged by fat or food storage and/or by appropriate use of torpor. In contrast, droughts, as for example during El Niño events, may last for a year or more, too long for survival on stored fat or food, at least in endotherms.

A recent study on free-ranging Australian owlet-nightjars (*Aegotheles cristatus*) showed for the first time that lack of rainfall in dry years can substantially affect the use and patterns of torpor in the wild (Doucette et al. 2012). In a dry year, owlet-nightjars in semi-arid central Australia used torpor more frequently than in a wet year (61% vs. 27%), torpor bout duration in the dry year was about twice as long as in the wet year and the minimum T_b in the dry year was 3.3°C lower than in the wet year. The variation in torpor variables between years was not strongly related to differences in T_a, but was best explained by availability of biomass (insects), which was less than half in the dry than the wet year because of reduced primary productivity. However, availability of water per se also may have affected torpor use (see above). Thus torpor seems to be an important adaptation to overcome droughts and persistence in areas that are subject to prolonged rather than seasonal shortages of food and water.

10.7 Torpor and Parasites

Although immune function during torpor appears to be suppressed (Prendergast et al. 2002; Boyles and Willis 2010), parasite loads, especially of some gastrointestinal parasites, decrease during hibernation in some animals (Chute 1964). This could be due to low T_b during hibernation being harmful to the parasite, slowed metabolic processes of the parasite, and seasonal changes in the chemical composition of the host because of hibernation that may be detrimental to the parasite (Chute 1964). Data for Alpine marmots (*Marmota marmota*) show that not all parasites respond in the same way (Callait and Gauthier 2000). A cestode (*Ctenotenia marmotae*) leaves the marmot intestine before/during hibernation and overwinters in an intermediate host, a mite. One nematode (*Ascaris laevis*) disappears from the marmot gut during hibernation. The only parasite that remains in the marmot gut during hibernation is a small nematode (*Citellina alpina*). This species, perhaps because of its small size and location in the marmot caecum is the only one known to persist in its host throughout hibernation (Callait and Gauthier 2000). Thus, it is correct that there is a 'self-curing' effect at the onset of hibernation that reduces the parasite load of this mammalian host. In contrast to marmots, all helminths (trematodes, cestodes, and nematodes) survived in the gut of bats (*Myotis lucifugus*) during hibernation (Coggins et al. 1982) even though T_b falls to near 0°C. This does not support the interpretation that parasites cannot cope with low temperatures nor that all parasites are removed during hibernation.

Ectoparasites of the bat *Miniopterus schreibersii*, which include bat flies, mites, and ticks, were present throughout the yearly cycle (Lourenco and Palmeirim 2008). However, these ectoparasites exhibited substantially reduced reproductive activities during the bats' hibernation period likely in response to reduced temperatures. For bats in tropical and subtropical regions where temperatures do not change dramatically with season, ectoparasites appear to reproduce year round (Marshall 1971). In contrast to marmot gut parasites, ectoparasites (mites) appear to increase in number immediately after hibernation when marmots visit other burrows and are more exposed to the mite than in winter because it lives in marmot nests (Arnold and Lichtenstein 1991).

Thus it appears that hibernation results in the reduction in some intestinal parasites and slows the growth of others. However, overall hibernation does not appear to be an effective approach to remove parasites. A reduction in some parasites is likely a by-product of low T_b during hibernation rather than its primary function.

10.8 Torpor and Inter-Specific Competition

Recent data suggest that torpor use is affected by inter-specific competition and may permit co-existence of competing species. Common spiny mice (*Acomys cahirinus*) in large outdoor enclosures competitively exclude their congener (*A. russatus*; golden spiny mice) from nocturnal activity forcing them to become diurnal (Levy et al. 2011b). This temporal partitioning allows the species to co-exist on a diet of arthropods in summer. In winter, when arthropod levels are low, both species rely on a largely vegetarian diet. Under these conditions, removal of common spiny mice reduced the duration of daily torpor in golden spiny mice whether food was supplemented or not. These results suggest that torpor may allow the co-existence of two competing species during periods of resource limitation and high energetic requirements (Levy et al. 2011b). Further, torpor use and the concomitant energy savings may allow subordinate species to occupy areas dominated by larger competitors. This may also be one reason for the large diversity of sympatric insectivorous/carnivorous marsupials (Dasyuridae) in the Australian arid zone (and perhaps other small desert mammals) despite the limited supply of food and water and the presence of introduced predators.

10.9 Torpor and Mammalian Extinctions

A traditional paradigm is that inactivity and immobility during torpor increase the risk of predation (Armitage 2004). This has been viewed as one of the major costs associated with torpor and selection pressure to minimize use of torpor. Contrary to this, recently published data show that torpor is used under mild conditions in summer without apparent energy stress. Non-reproductive captive dormice (*Glis glis*) in good condition enter a sequence of short torpor bouts in summer often after brief periods of activity following the final arousal from hibernation in spring (Bieber and Ruf 2009). The authors suggested that dormice may use torpor to actually avoid predation which may contribute to their high longevity. Field observations on subtropical bats support this contention. Long-eared bats (*Nyctophilus bifax*) in a subtropical, coastal region enter torpor frequently during summer (85% of observation days) and even do so on 38% of nights during their normal activity period (Stawski and Geiser 2010). Counter to more traditional predictions, bats in good condition (high body condition index) entered torpor more frequently, displayed longer torpor bouts and lower minimum T_bs than bats in poorer condition. Thus, it appears that these bats increased torpor use not because of food shortages or low energy stores, but likely to avoid exposure to predators during foraging when feeding is not required. This is exactly the opposite of what is traditionally predicted.

Predator avoidance may be one of the reasons why opportunistically heterothermic mammals are less threatened with extinctions (Liow et al. 2009) and have suffered fewer extinctions than their homeothermic relatives (Geiser and

Turbill 2009). Of the 61 worldwide confirmed extinctions of mammal species, over the past 500 years (American Museum for Natural History, Committee on Recently Extinct Organisms, http://creo.amnh.org), only four (6.5% of species) were likely heterothermic although the vast majority of these (approximately 85% of species) were within the size range of <10 kg in which deep torpor is expressed. Because only ~15% of extinct mammals weighed >10 kg, it is surprising that almost all extinct mammals (93.5%) were likely homeothermic (Geiser and Turbill 2009). Further, considering that most mammals (approximately 80%) are rodents, bats, insectivores, and marsupials and that many of these are known to be heterothermic, it is astonishing how few of the extinct mammals were likely heterothermic. It has been proposed that extinction risks in heterothermic mammals may be minimized by torpor use due to its enormous scope for adjusting energy requirements. This may allow long-term survival even under adverse environmental conditions and help individuals cope with habitat degradation and avoid introduced or native predators (Geiser and Turbill 2009; Liow et al. 2009). Thus, the use of torpor and the commonly prolonged life span of heterotherms (Turbill et al. 2011; Ruf et al. 2012) appear to have permitted opportunistically heterothermic mammals to deal with anthropogenic disturbances responsible for extinctions better than is the case for most other species.

In conclusion, our summary shows that torpor has implications for many facets of mammalian and avian biology that go well beyond energy conservation. Use of torpor is known to enhance fat storage during migration, apparently permits prolonged female sperm storage in bats, allows reproduction with limited or fluctuating food supply, and delays parturition until more favorable periods. Torpor also appears to increase the efficiency of energy and nutrient use during development, permits co-existence of competing species and survival of prolonged droughts, and reduce water requirements, parasite loads, and risk of mammalian extinctions. Future work, including data on daily torpor in free-ranging rodents that is currently almost entirely lacking, is likely to identify further ‘other’ functions of torpor.

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References

Armitage KB (2004) Badger predation on yellow-bellied marmots. Am Midl Nat 151:378–387

Arnold W, Lichtenstein AV (1991) Ectoparasite loads decrease the fitness of Alpine marmots (*Marmota marmota*) but not the cost of sociality. Behav Ecol 4:36–39

Audet D, Fenton MB (1988) Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. Physiol Zool 61:197–204

Barnes BM (1996) Relationship between hibernation and reproduction in male ground squirrels. In: Geiser F, Hulbert AJ and Nicol SC (eds) Adaptations to the Cold, 10th international hibernation symposium, University of New England Press, Armidale, pp 71–80

Bieber C, Ruf T (2009) Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. Naturwissenschaften 96:165–171

Birkhead TR, Møller AP (1993) Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds and mammals. Biol J Linn Soc 50:295–311

Boyles JG, Willis CKR (2010) Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? Front Ecol Environ 8:92–98

Brigham RM (1992) Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Physiol Zool 65:457–472

Buffenstein R (1985) The effect of starvation, food restriction, and water deprivation on thermoreguation and average daily metabolic rates in *Gerbillus pusillus*. Physiol Zool 58: 320–328

Callait M-P, Gauthier D (2000) Parasite adaptations to hibernation in Alpine marmots (*Marmota marmota*). In: Heldmaier G and Klingenspor M (eds) Life in the cold. 11th international hibernation symposium, Heidelberg, Springer, pp 139–146

Carpenter FL, Hixon MA (1988) A new function of torpor: fat conservation in a wild migrant hummingbird. Condor 90:373–378

Christian N, Geiser F (2007) To use or not to use torpor? Activity and body temperature as predictors. Naturwissenschaften 94:483–487

Chute RM (1964) Hibernation and parasitism: recent developments and some theoretical consideration. Mammalian hibernation 2. Ann Acad Sci Fenn A, 4 Biol 71:113–122

Coggins JR, Tedesco JL, Rupprecht CE (1982) Seasonal changes and overwintering of parasites in the bat, *Myotis lucifugus* (Le Conte), in a Wisconsin hibernaculum. Am Midl Nat 107: 305–315

Cooper CE, McAllan BM, Geiser F (2005) Effect of torpor on the water economy of an arid-zone marsupial, the striped-faced dunnart (*Sminthopsis macroura*). J Comp Physiol B 175:323–328

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

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. J Comp Physiol B 175:147–155

Doucette LI, Brigham RM, Pavey CR, Geiser F (2011) Roost type influences torpor use by Australian owlet-nightjars. Naturwissenschaften 98:845–854

Doucette LI, Brigham RM, Pavey CR, Geiser F (2012) Prey availability affects daily torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Oecologia. doi:10.1007/s00442-011-2214-7

Eichhorn G, Groscolas R, Le Glaunec G, Parisel C, Arnold L, Medina P, Handrich Y (2011) Heterothermy in growing king penguins. Nat Commun 2:435. doi:10.1038/ncomms1436

Eisentraut M (1929) Beobachtungen über den Winterschlaf der Haselmaus (*Muscardinus avellanarius* L.). Z Säugetierkd 4:213–239

Frey H, Fleming MR (1984) Torpor and thermoregulatory behaviour in free-ranging feathertail gliders (*Acrobates pygmaeus*) (Marsupialia: Burramyidae) in Victoria. In: Smith AP, Hume ID (eds) Possums and gliders. Surrey Beatty and Australian Mammal Society, Sydney, pp 393–401

Geiser F (1996) Torpor in reproductive endotherms. In: Geiser F, Hulbert AJ and Nicol SC (eds) Adaptations to the cold. 10th international hibernation symposium, University of New England Press, Armidale, pp 81–86

Geiser F (2008) Ontogeny and phylogeny of endothermy and torpor in mammals and birds. Comp Biochem Physiol A 150:176–180

Geiser F, Baudinette RV (1987) Seasonality of torpor and thermoregulation in three dasyurid marsupials. J Comp Physiol B 157:335–344

Geiser F, Masters P (1994) Torpor in relation to reproduction in the Mulgara, *Dasycercus cristicauda* (Dasyuridae: Marsupialia). J Thermal Biol 19:33–40

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Geiser F, Turbill C (2009) Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften 96:1235–1240

Geiser F, McAllan BM, Brigham RM (2005) Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia). Mamm Biol 70:117–121

Geiser F, Christian N, Cooper CE, Körtner G, McAllan BM, Pavey CR, Turner JM, Warnecke L, Willis CKR, Brigham RM (2008) Torpor in marsupials: recent advances. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: torpor, hibernation and cryobiology, 13th international hibernation symposium, University of KwaZulu-Natal, Pietermaritzburg, pp 297–306

Giroud S, Turbill C, Ruf T (2012) Torpor use and body mass gain during pre-hibernation in late-born juvenile garden dormice exposed to food shortage. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world: thermoregulatory and metabolic adaptations, Springer, Heidelberg

Grinevitch L, Holroyd SL, Barclay RMR (1995) Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. J Zool Lond 235:301–309

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

Hiebert SM (1993) Seasonality of daily torpor in a migratory hummingbird. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) Life in the cold: ecological, physiological and molecular mechanisms. Westview, Boulder, pp 25–32

Hill RW (1975) Daily torpor in *Peromyscus leucopus* on an adequate diet. Comp Biochem Physiol A 51:413–423

Hill RW (1976) The ontogeny of homeothermy in neonatal *Peromyscus leucopus*. Physiol Zool 49:292–306

Hollis L, Barclay RMR (2008) Developmental changes in body temperature and use of torpor by the big brown bat (*Eptesicus fuscus*). In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: torpor, hibernation and cryobiology, 13th international hibernation symposium, University of KwaZulu-Natal, Pietermaritzburg, pp 361–372

Horvath A (1878) Beitrag zur Lehre über den Winterschlaf. Verh phys med Ges Würzburg 12:139–198

Hosken DJ, Withers PC (1997) Temperature regulation and metabolism of an Australian bat, *Chalinolobus gouldii* (Chiroptera: Vespertilionidae) when euthermic and torpid. J Comp Physiol B 167:71–80

Ibuka N, Fukumura K (1997) Unpredictable deprivation of water increases the probability of torpor in the Syrian hamster. Physiol Behav 62:551–556

Jaeger EC (1948) Does the poorwill "hibernate"? Condor 50:45–46

Kayser C (1939) Exchanges respiratoires des hibernants réveillés. Ann Physiol Physicochim Biol 15:1087–1219

Kissner KJ, Brigham RM (1993) Evidence for the use of torpor by incubating and brooding common poorwills, *Phalaenoptilus nuttallii*. Ornis Scand 24:333–334

Körtner G, Geiser F (2009) The key to winter survival: daily torpor in a small arid zone marsupial. Naturwissenschaften 96:525–530

Körtner G, Brigham RM, Geiser F (2000) Winter torpor in a large bird. Nature 407:318

Körtner G, Pavey CR, Geiser F (2008) Thermal biology, torpor and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. Physiol Biochem Zool 81:442–451

Landry-Cuerrier M, Munro D, Thomas DW, Humphries MM (2008) Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. Ecology 89:3306–3316

Levy O, Dayan T, Kronfeld-Schor N (2011a) Adaptive thermoregulation in golden spiny mice: the influence of season and food availability on body temperature. Physiol Biochem Zool 84:175–184

Levy O, Dayan T, Kronfeld-Schor N (2011b) Interspecific competition and torpor in golden spiny mice: two sides of the energy-acquisition coin. Int Comp Biol 51:441–448

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC (2009) Lower extinction in sleep-or-hide mammals. Am Nat 173:264–272

Liu J-N, Karasov WH (2011) Hibernation in warm hibernacula by free-ranging Formosan leaf-nosed bats, *Hipposideros terasensis*, in subtropical Taiwan. J Comp Physiol B 181:125–135

Lourenco S, Palmeirim JM (2008) Which factors regulate the reproduction of ectoparasites of temperate-zone cave-dwelling bats? Parasitol Res 104:127–134

Lovegrove BG (2000) Daily heterothermy in mammals: coping with unpredictable environments. In: Heldmaier G and Klingenspor M (eds) Life in the cold: 11th international hibernation symposium, Springer, Heidelberg, pp 29–40

Lyman CP (1948) The oxygen consumption and temperature regulation in hibernating hamsters. J Exp Zool 109:55–78

Lyman CP, Willis JS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Academic Press, New York

MacMillen RE (1965) Aestivation in the cactus mouse *Peromyscus eremicus*. Comp Biochem Physiol 16:227–247

Marshall AG (1971) The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. J Anim Ecol 40:141–154

Morrow G, Nicol SC (2009) Cool sex? Hibernation and reproduction overlap in the echidna. PLoS ONE 4(6):e6070. doi:10.1371/journal.pone.0006070

Morton SR (1978) Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). J Mammal 59:569–575

Munn AJ, Kern P, McAllan BM (2010) Coping with chaos: unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*). Naturwissenschaften 97:601–605

Mzilikazi N, Lovegrove BG (2002) Reproductive activity influences thermoregulation and torpor in pouched mice, *Saccostomus campestris*. J Comp Physiol B 172:7–16

Nicol SC, Andersen NA (2002) The timing of hibernation in Tasmanian echidnas: why do they do it when they do? Comp Biochem Physiol B 131:603–611

Prendergast BJ, Freeman DA, Zucker I, Nelson JR (2002) Periodic arousal from hibernation is necessary for initiation of immune response in ground squirrels. Am J Physiol 282: R1054–R1062

Racey PA (1973) Environmental factors affecting the length of gestation in heterothermic bats. J Reprod Fert Suppl 19:175–189

Racey PA (1979) The prolonged storage and survival of spermatozoa in Chiroptera. J Reprod Fert 56:391–402

Rimbaldini 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

Ruf T, Bieber C, Turbill C (2012) Survival, aging, and life-history tactics in mammalian hibernators. In: Ruf T, Bieber C, Arnold W, Millesi E (eds) Living in a seasonal world: thermoregulatory and metabolic adaptations, Springer, Heidelberg

Schmid J, Speakman JR (2009) Torpor and energetic consequences in free-ranging grey mouse lemurs (*Microcebus murinus*): a comparison of dry and wet forests. Naturwissenschaften 96: 609–620

Serventy V, Raymond R (1973) Torpidity in desert mammals. Aust Wildl Heritage 14:2233–2240

Stawski C (2010) Torpor during the reproductive season in a free-ranging subtropical bat, *Nyctophilus bifax*. J Thermal Biol 35:245–249

Stawski C, Geiser F (2010) Fat and fed: frequent use of summer torpor in a subtropical bat. Naturwissenschaften 97:29–35

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

Stephenson PJ, Racey PA (1993) Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). II. The shrew-tenrecs, *Microgale* spp. Physiol Zool 66:664–685

Turbill C, Geiser F (2006) Thermal biology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*. J Comp Physiol B 176:165–172

Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc Roy Soc B 278:3355–3363

Wang LCH (1978) Energetics and field aspects of mammalian torpor: the Richardsons's ground squirrel. In: Wang LCH, Hudson JW (eds) Strategies in cold. Academic Press, New York, pp 109–145

Wang Z, Liang B, Racey PA, Wang Y-L, Zhang S-Y (2008) Sperm storage, delayed ovulation, and menstruation of the female Rickett's big-footed bat (*Myotis ricketti*). Zool Stud 47: 215–221

Warnecke L, Turner JM, Geiser F (2008) Torpor and basking in a small arid zone marsupial. Naturwissenschaften 95:73–78

Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. Naturwissenschaften 93:80–83

Wimsatt WA (1960) Some problems of reproduction in relation to hibernation in bats. In: Lyman CP, Dawe AR (eds) Mammalian hibernation. Bull Mus Comp Zool, Cambridge, pp 248–270

Withers PC, Richardson KC, Wooller RD (1990) Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. Aust J Zool 37:685–693