

Chapter 3

Tropical Heterothermy: Does the Exception Prove the Rule or Force a Re-Definition?

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Abstract Recent interest in heterothermy in the tropics and the subtropics has raised issues with the existing definitions of torpor. The current methods used to distinguish and define patterns of heterothermy are insufficient in face of the numerous forms of torpor expression and high daily variation in normothermic body temperature (T_b) observed in species inhabiting the tropics. Tropical heterothermy often occurs at highly variable ambient temperatures that may lead to a continuum between hibernation, daily torpor and normothermia with no clear distinction between states. While we do not seek to redefine torpor in this review, by listing torpor patterns that fall outside the usual categories (the exceptions to the rule), we discuss these thermoregulatory behaviours in terms of the energetics and evolution of heterothermy under warm climates.

3.1 Defining Heterothermy in Endotherms

Strict homeothermy bears a high energetic cost and, therefore heterothermy has been selected in numerous species in response to harsh environmental constraints such as low temperatures or reduced energy supply (Lyman et al. 1982). Torpor, commonly defined as ‘a physiological state associated with controlled reductions of metabolism and T_b resulting in energy savings compared to defence of

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normothermic T_b' (Geiser 2004), was traditionally thought to be restricted to temperate, cold climate zones, where the energy saved by lowering T_b was high. However, recent studies revealed an increasing number of heterothermic species living in the tropics: bats, birds, echidnas, primates, tenrecs, marsupials (Geiser et al. 2008; Heldmaier et al. 2004; Lovegrove and Genin 2008; McKechnie and Lovegrove 2002; McKechnie and Mzilikazi 2011; Stawski and Geiser 2011). The increasing interest in the study of torpor in tropical and subtropical climates has led to the discovery of more varied patterns of heterothermy than was originally thought possible (Cossins and Barnes 1996; Geiser and Ruf 1995; Lovegrove 2000, 2012; McKechnie and Mzilikazi 2011). Classically, daily torpor was defined as short shallow torpor bouts, generally lasting less than 24 h, with body temperatures remaining slightly elevated above ambient temperatures (T_a). Hibernation involves multiday torpor bouts that may last as long as several days with T_b decreasing to a degree or two above T_a (Geiser and Ruf 1995).

Recent reviews have questioned the accuracy of the current definitions of torpor arguing that they are often arbitrary in application and that the lines between daily variation in T_b and torpor are often blurred (Angilletta et al. 2010; Boyles et al. 2011a; Brigham et al. 2011). Similarly, not only can the definitions of torpor be unclear, but also the degree to which it is expressed. Thus, whether an animal is classed as a daily heterotherm or as a hibernator remains vague, all the more so when torpor patterns appear to be governed largely by environmental temperatures (McKechnie and Mzilikazi 2011). Torpor in the tropics, often uncoupled from low ambient temperatures, provides some of the most clear-cut examples of the failings of the current terminology.

Here, we argue that the current definitions for torpor, daily heterothermy and hibernation are not appropriate to all heterotherms, especially those in the tropical and subtropical habitats. By listing the current methods used to define torpor and reviewing the species that fall outside the usual categories, we hope to illustrate the problems that can occur using current definitions. We wish to call for a systematic review of current terminology and seek to caution the inference of various states (active, resting, torpid) from T_b patterns alone.

3.2 Current Methods for Determining Torpor Expression

The most accurate method for determining torpor expression would be to measure metabolic rate (MR) in free-ranging animals over long time periods. Unfortunately, the complicated logistics of measuring MR in the field has led the vast majority of studies to use T_b as a proxy. Furthermore, as measuring core T_b involves the use of invasive methods (surgery), skin temperature (T_{sk}) is often used instead. Whereas T_{sk} has been shown to approximate T_b over a wide range of activity states and body temperatures (Barclay et al. 1996; Dausmann 2005), it is most accurate when an animal is resting at stable T_a and can be inaccurate when observing active animals in changing thermal environments (Willis and Brigham 2003).

3.2.1 Threshold T_b

When using T_b or T_{sk} , the most common method for determining torpor expression is via the use of a threshold value differentiating torpid T_b from normothermic T_b (Barclay et al. 2001; Boyles et al. 2011a; Willis 2007). While there are numerous theoretical and logistical limitations of using this method (see Boyles et al. 2011a) it remains the simplest way to determine the number, depth and duration of torpor bouts. Whereas some studies have provided clear reasons for selecting a particular T_b threshold a large number simply select an arbitrary T_b , usually 30°C, and provide little or no justification for the choice (Barclay et al. 2001). The most common, reliable but underused methods for empirically determining cut-off T_b s are:

- (1) *The bi-, multi-modal frequency distribution of T_b measurements* (McKechnie et al. 2007). Ideally torpid and normothermic T_b distributions form clear more or less normally distributed groupings, and cut-off temperature can be determined using the lesser used transitional temperatures (see Geiser and Mzilikazi 2011 for a good example of this). This method works best when T_a is stable and thus has no effect on T_b distribution.
- (2) *Recording MR during entry into torpor and calculating the T_b at which MR decreases below basal metabolic rate (BMR)*. Willis (2007) described this method in detail and calculated a general equation taking into account the effects of T_a and body mass on threshold T_b . Unfortunately, there has been little success in establishing the use of either the method or the equation.
- (3) *Active T_b .* Barclay et al. proposed that the threshold T_b could be calculated using the lowest T_b recorded immediately prior to an animal exiting its rest site. This method proved controversial as bats and birds leave roosts while still in a semi-torpid state and rely on heat generated by flight muscle activity to complete the final stages of rewarming (Willis and Brigham 2003) and many daily heterotherms rearm with using T_a well before the start of their activity periods (Geiser et al. 2004). A more accurate application of this concept could be achieved using daily profiles of locomotor activity recorded either by a receiver in the laboratory or movement sensors in the field and to identify the threshold T_b under which locomotor activity rapidly declines (Canale et al. 2011).

3.2.2 Metrics

Recently, the concept of using metrics to quantify the level of heterothermy has been proposed. The primary advantage being the inclusion of homeotherms and the potential benefits they gain from circadian changes in T_b (Boyles et al. 2011b; Gordon 2009). The first proposed that the absolute differential in daily body temperatures can be used to calculate the instability of circadian rhythms, in species with regular variation in T_b (Gordon 2009). However, this method highly

underestimated the level of heterothermy in boreal and arctic hibernators (Boyles et al. 2011b) as they maintain a low and constant T_b during these periods (Gordon 2009). Moreover, it is only accurate for species that maintain precise and regulated circadian T_b rhythms. A second metric, the heterothermy index (HI), has been proposed for comparison among individuals and species (Boyles et al. 2011b) by estimating the magnitude of the heterothermic response, i.e. the time spent away from normothermic T_b over any time frame. The limitations of this method have been presented in greater detail elsewhere (see review by Brigham 2011), but perhaps the most important of those listed is that the HI places species with shallow, long-duration torpor bouts and species with deep, short-duration bouts on the same scale, despite the fact that these responses are obviously different in terms both of energy savings and the adaptive value of heterothermy.

3.2.3 Thermoregulating Versus Thermoconforming

While not explicitly stated as such, the majority of studies on animals hibernating at high and variable T_a have used $T_b - T_a$ differentials to determine torpor expression (Dausmann et al. 2005; Kobbe et al. 2011; Lovegrove and Genin 2008). Thus when an animal's T_b is only slightly above T_a , and tracks T_a as it changes, it is in torpor, and it is normothermic when T_b is independent of T_a (Arlettaz et al. 2000). However, such methods underestimate the potential occurrence of torpor at T_b s below normothermic levels but higher than T_a and are only applicable when the animal is thermoconforming and not in cases where they defend a set torpid T_b above T_a (Barclay et al. 2001).

3.3 The Exceptions that (Dis)prove the Rule

Whereas the above methods have their advantages, their application can be complicated in certain situations. A growing number of novel patterns of torpor expression, many at high ambient temperatures have been described in the last few decades that question classical definitions.

3.3.1 Continuum Between Daily Torpor and Hibernation?

The most clear-cut of these exceptions are species with levels of torpor expression intermediate to daily torpor and hibernation. In these species, torpor expression appears to be highly flexible in response to current environmental conditions. Whereas many of these species appear capable of long-term hibernation, thus allowing them to be classified as hibernators sensu Geiser and Ruf (1995), torpor

expression can vary within and between individuals to such an extent that a strict delineation between daily torpor and hibernation can be difficult. This has been demonstrated in a wide range of species such as echidnas (*Tachyglossus aculeatus*, Brice 2009), bats (*Nyctophilus bifax*, Stawski et al. 2009) and many Afrotropical species including elephant shrews (*Elephantulus edwardii*, *Elephantulus myurus*, Geiser and Mzilikazi 2011; Mzilikazi and Lovegrove 2004), Egyptian free-tailed bats (*Tadarida aegyptiaca*, Cory Toussaint et al. 2010) and mouse lemurs (*Microcebus murinus*, *Microcebus griseorufus* (Kobbe et al. 2011; Schmid and Ganzhorn 2009; see McKechnie and Mzilikazi 2011 for a full review). One of the clearest examples of individual flexibility in thermoregulation has been observed in *Microcebus griseorufus* exhibiting different energy saving strategies influenced by ambient temperatures. *M. griseorufus* showed daily torpor bouts and also long-term hibernation. Individuals have been observed to enter daily torpor from the early morning until they warmed up with the rising T_a , with an absolute minimal T_{sk} of 7°C. The longest hibernation phase without arousals lasted 45 days and the lowest T_{sk} observed was 6.5°C (Kobbe et al. 2011). It is unclear whether these patterns are truly distinct intermediates between daily heterothermy and hibernation or simply indicative of the high degree of physiological flexibility in torpor expression selected in response to unpredictable anomalies in rainfall associated with the El Niño Southern Oscillation, widespread in Afrotropical, Australasian and Indomalayan zones (Canale and Henry 2010; Kobbe et al. 2011; Lovegrove 2003).

3.3.2 Continuum Between Normothermy and Torpor?

In addition to increasingly blurred lines between daily torpor and hibernation, the lines between circadian changes in T_b and torpor expression are continually under contention (Angilletta et al. 2010; Boyles et al. 2011b). This debate has been more predominant in birds, where the delineation between nocturnal hypothermia (controlled yet non-torpid nocturnal reductions in T_b) and torpor has been highly contested (Lovegrove and Smith 2003; McKechnie and Lovegrove 2002; Schleucher and Prinzing 2006). As with the use of a threshold T_b , the distinction between the two states is often arbitrary with studies considering reductions of up to 50% of BMR as circadian changes in MR and not torpor (Lovegrove and Smith 2003).

It is becoming increasingly apparent that T_b alone is not indicative of the physiological state of the animal. Many species show a rather large overlap between active and resting body temperatures (see Boyles et al. 2011a for a review). Multiple species have been shown to be active, and perform optimally, at T_b close to or $<30^\circ\text{C}$, the most commonly used cut-off T_b (Brice et al. 2002). For example, a recent paper shows that torpid planigales (*Planigale gilesi*) move to basking sites with T_b as low as 13.8°C (Warnecke and Geiser 2009). The distinction between the two states is especially difficult in baso- and meso-endotherms (sensu Lovegrove

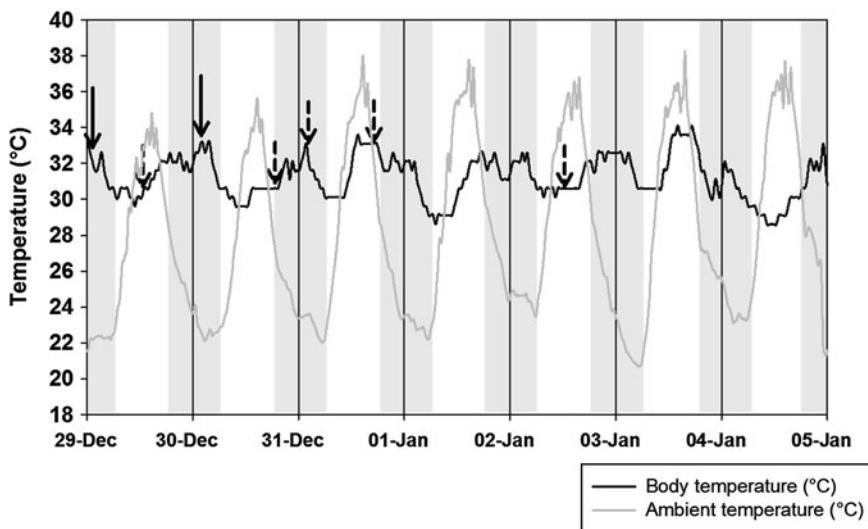


Fig. 3.1 Body temperature of a nocturnal free-ranging male *Setifer setosus* over the course of 7 days during the rainy (breeding season). Arrows indicate times which the animal was located and found to be active (solid) or *dashed* (resting). On two occasions, the 31-December and the 4-January, T_b was highest when the animal was in the nest site resting and decreased when the animal became active. Grey horizontal bars indicate the dark phase and the horizontal lines midnight

2012). These species, most commonly found in the tropics and semi-tropics, have high variations in normothermic T_b and have highly variable torpor patterns. Data on free-ranging echidnas in the hot dry climate of south-west Queensland showed that resting animals had higher T_b s than active animals (Brice et al. 2002). The authors in this study took a novel and cautious view of torpor expression and defined it as occurring when an individual had remained in a rest site for greater than 24 h and had lower T_b than other individuals in similar situations.

Similar difficulties in differentiating torpor from highly variable normothermic T_b patterns have been found in free-ranging greater hedgehog tenrecs (*Setifer setosus*—Levesque and Lovegrove unpublished data). Free-ranging T_b s from the active season (Fig. 3.1) illustrate the caution necessary when interpreting states of activity, rest and torpor from T_b alone. During a 7-day period of T_b measurement from an adult male during the breeding season, higher resting T_b s than active T_b s was observed on two occasions and the lowest recorded T_b (28.6°C) occurred during what may have been a torpor bout (thermoconforming) that was cut short by a rise in T_a . A lack of knowledge on the activity patterns of this species could have led to the false belief that the initiation of activity occurred during the high T_b s shown in late afternoon. However, this animal is strictly nocturnal and, in one case, was in the same rest location from 02:00 to 18:03. The animal became active sometime after T_b had reached its maximum and T_b decreased during activity.

Such species possessing a high range in active and normothermic T_b can also complicate the use of an MR threshold for torpor expression, since it is nearly impossible to measure BMR or calculate a thermal neutral zone. Echidnas (Brice, Levesque and Grigg unpublished data), streaked tenrecs (*Hemicentetes semispinosus*, Stephenson and Racey 1994) and hedgehog tenrecs (*Setifer setosus*, Levesque and Lovegrove unpublished data) all show a high degree of heterothermy and the T_b of resting, but not torpid, animal changes dramatically with ambient temperature making it impossible to determine MR from T_b alone.

3.3.3 Thermoconforming Versus Change in T_b Set Point

One of the clearest exceptions to the classical patterns of torpor expression is the fat-tailed dwarf lemur (*Cheirogaleus medius*, Dausmann et al. 2005). In this species, hibernation occurs in often poorly insulated arboreal nests which are subject to high variation in T_a (from 9.3 to 35.9°C). Thus even if the animal lowers its T_b set point it cannot maintain a continuous low T_b , but rather thermo-conforms throughout the hibernation period. This pattern has subsequently been observed in several species of mouse lemurs from the same family (Kobbe and Dausmann 2009; Kobbe et al. 2011; Schmid and Ganzhorn 2009), as well as another Malagasy heterotherm, the lesser hedgehog tenrec (*Echinops telfairi*, Lovegrove and Genin 2008). Interestingly, whereas individuals in poorly insulated nests did not show the spontaneous arousals common to most hibernators, those in well-insulated nests, in which T_a did not rise above 30°C, actively rewarming. Similar patterns have also been observed in captive *E. telfairi* held under various T_a regimes (Wein 2010).

3.4 (Re)-Defining Torpor?

Tropical heterothermy is widespread enough to be more than just a single exception to the previously defined patterns of heterothermy. In fact, Lovegrove (2012) argues that heterothermy evolved in the tropics prior to the Cenozoic. However, quantifying it can be extremely difficult, especially with the methods currently available. The concept of a cut-off T_b under which the animal is considered torpid cannot be used in a species where T_b passively follows T_a . Difficulties therefore arise both in the calculation of a threshold T_b and in its application. Frequency distributions of T_b from tropical heterotherms do not show the bi- or multi-modal distributions usually seen in mammalian heterotherms making clear distinctions between thermoregulatory states nearly impossible (Lovegrove and Génin 2008). Identical T_b can be observed in animals that are resting, active and torpid (Brice et al. 2002). Similarly, the concept of active T_b , as proposed by Barclay et al. (2001) is not applicable in these cases. High rest-phase

ambient temperatures can lead to a decrease in T_b at the onset of activity, in stark contrast to the increase usually observed in temperate climates. Metrics used to evaluate heterothermy usually assume that changes in T_b are controlled by the animal, and whereas tropical heterotherms might lower the T_b set point, highly variable T_a makes low T_b impossible to obtain for long periods of time. Thus a metric might underestimate the use of torpor at temperatures that would be considered normothermic in an active animal.

The method that has so far had the most success in the tropics, thermoconformity, requires accurate measurements of the T_a experienced by the animal and is not applicable in defining most torpor that occurs in temperate zones. Thus we are faced with the dilemma of whether to let the exceptions support the traditional views or to force us to reconsider the original definitions.

3.5 Tropical Heterothermy: Benefits Without Cost?

Is tropical hibernation better at overcoming energetic constraints than temperate hibernation? Torpor is a well-known mechanism that reduces energy expenditure during seasonal energetic bottlenecks in both high and low latitudes. However, the physiological flexibility of torpor in tropical species allows them to rapidly adjust their energy expenditure, and thus overcome sudden energetic limitations in shorter time frames. This flexible, aseasonal use of daily torpor in response to rapid environmental changes confers high energetic benefits even during the reproductive season (Canale et al. 2012; Daniel et al. 2010; Geiser 1996; Stawski and Geiser 2010).

Torpor and hibernation at high and variable T_a provide an excellent opportunity to study the benefits conferred by warmth on torpor expression. Tropical and subtropical climates with high daily variation in T_a could confer to species greater energy savings than similar time spent torpid in arctic and temperate species. Frequent passive, often daily, exposures to high ambient temperatures are more energy efficient than costly arousals, obligatory to hibernation in cold environments (Carey et al. 2003; Humphries et al. 2003). Stripe-faced dunnarts (*Sminthopsis macroura*) can reduce the cost of arousals threefold through the use of exogenous passive heating (Lovegrove et al. 1999a). Periodic arousals in hibernating fat-tailed dwarf lemurs are much less costly with MR increasing by 40% instead of by 1000% as seen in temperate hibernators (Dausmann et al. 2009). In addition, the ability to completely forgo periodic arousals would limit the high level of oxidative stress resulting from the increased production of reactive oxygen species during active rewarming (Giroud et al. 2009). Furthermore, the negative effects of extreme metabolic suppression and long-term hypothermia could be limited at variable T_a . Short bouts of hypometabolism associated with T_b close to high T_a might allow sleep during a semi-torpid state, ensuring brain function and memory consolidation, in contrast to arctic species that suffer a sleep debt (Roth et al. 2010). Moreover, rapid rewarming tracking T_a might allow reactivation of the immune system faster than that of pathogens. Passive thermal responses

leading to high T_b would confer an immune advantage for heterothermic hosts (Canale and Henry 2011). Immune activity would regularly return to maximal efficiency and the short arousal periods would give pathogens too short a time to proliferate (Prendergast et al. 2002). With, potentially, such low costs associated, with lower foraging requirements leading to lower risk of predation, it is not surprising that heterothermy is so widespread in the tropics (Geiser and Stawski 2011; Geiser et al. 2011; McKechnie and Mzilikazi 2011). The flexibility in its expression and the relative reduction in the costs are perhaps indicative of a more plesiomorphic form of torpor (Lovegrove 2012).

3.6 Conclusions

It has become apparent that more time and caution is needed when inferring the expression of hypometabolic states from T_b patterns alone, especially those from individuals living in environments with high and variable T_a . T_b recordings should, as much as possible, be accompanied by accurate measurements of T_a , observations on the state of activity and basic knowledge on the species' MR response to constant ambient temperatures (can BMR and the thermal neutral zone be quantified?). The diversity of patterns of heterothermy in endotherms is much larger than was initially believed. There is likely a continuum between daily torpor and hibernation as well as between torpor and normothermy (Heldmaier et al. 2004). During daily torpor the extent of hypometabolism and hypothermia is usually less pronounced as compared to hypometabolism in hibernation (Geiser and Ruf 1995). However, in some species like dormice or elephant shrews, torpid MRs can be as low as minimum MR in hibernation (Lovegrove et al. 1999b; Wilz and Heldmaier 2000). It has been discussed whether daily torpor and hibernation are based on different physiological adaptations. At present no clear qualitative differentiation is known (Heldmaier et al. 2004). The physiological properties of daily torpor and hibernation seem to be very similar. It remains to be determined if differences observed in torpor patterns and thermal physiology are ecological or physiological. The exceptions and mid-points presented above provide excellent case studies for both the adaptive value of heterothermy and the evolution of homeothermy via heterothermy (Angilletta et al. 2010; Grigg 2004; Lovegrove 2012).

As with the reviews cited throughout, this chapter raises more questions than it answers. More work, in both field and in laboratory settings, is needed to fully characterise both the physiology and the energetics of torpor at high and variable ambient temperatures ($>30^\circ\text{C}$). What is happening during the high and variable torpid T_b that allows the animals to forgo the periodic arousals deemed obligatory in cold temperature hibernators? Should the definitions of daily torpor, hibernation and even torpor itself be broadened to include these different forms or do they require their own category?

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References

- Angilletta MJJ, Cooper BS, Schuler MS, Boyles JG (2010) The evolution of thermal physiology in endotherms. *Front Biosci E* 2:861–881
- Arlettaz R, Ruchet RC, Aeschimann J, Brun E, Genoud M, Vogel P (2000) Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology* 81:1004–1014
- Barclay RMR, Kalounis MC, Crampton LH, Stefan C, Vonhof MJ, Wilkinson L, Brigham RM (1996) Can external radiotransmitters be used to assess body temperature and torpor in bats? *J Mammal* 77:1102–1106
- Barclay RMR, Lausen CL, Hollis L (2001) What's hot and what's not: defining torpor in free-ranging birds and mammals. *Can J Zool* 79:1885–1890
- Boyles JG, Smit B, McKechnie AE (2011a) Does use of the torpor cut-off method to analyze variation in body temperature cause more problems than it solves? *J Therm Biol* 36:373–375
- Boyles JG, Smit B, McKechnie AE (2011b) A new comparative metric for estimating heterothermy in endotherms. *Phys Biochem Zool* 84:115–123
- Brice PH (2009) Thermoregulation in monotremes: riddles in a mosaic. *Aust J Zool* 57(3–4):255–263
- Brice PH, Grigg GC, Beard LA, Donovan JA (2002) Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Aust J Zool* 50:461–475
- Brigham R, Willis C, Geiser F, Mzilikazi N (2011) Baby in the bathwater: should we abandon the use of body temperature thresholds to quantify expression of torpor? *J Therm Biol* 36:376–379
- Canale CI, Henry PY (2010) Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. *Clim Res* 43:135–147
- Canale CI, Henry PY (2011) Energetic costs of the immune response and torpor use in a primate. *Funct Ecol* 25:557–565
- Canale CI, Perret M, Thery M, Henry PY (2011) Physiological flexibility and acclimation to food shortage in a heterothermic primate. *J Exp Biol* 214:551–560
- Canale CI, Perret M, Henry P-Y (2012) Torpor use during gestation and lactation in a heterothermic primate. *Naturwissenschaften* 99:159–163
- Carey HV, Andrews MT, Martin SL (2003) Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. *Physiol Rev* 83:1153–1181
- 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. *Mammal Biol* 75:466–470
- Cossins AR, Barnes BM (1996) Southern discomfort. *Nature* 382:582–583
- Daniel S, Korine C, Pinshow B (2010) The use of torpor in reproductive female hemprich's long-eared bats (*Otonycteris hemprichii*). *Physiol Biochem Zool* 83:142–148
- Dausmann KH (2005) Measuring body temperature in the field—evaluation of external vs. implanted transmitters in a small mammal. *J Therm Biol* 30:195–202
- Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. *J Comp Physiol B* 175:147–155
- Dausmann KH, Glos J, Heldmaier G (2009) Energetics of tropical hibernation. *J Comp Physiol B* 179:345–357
- Geiser F (1996) Torpor in reproductive endotherms. In: Geiser F, Hulbert AJ, Nicol SC (eds) *Adaptations to the cold, 10th international hibernation symposium*, University of New England Press, pp 81–86

- Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274
- Geiser F, Mzilikazi N (2011) Does torpor of elephant shrews differ from that of other heterothermic mammals? *J Mammal* 92:452–459
- 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, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integr Comp Biol* 51:337–348
- Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) *Life in the cold. Evolution, mechanisms, adaptation, and application*, vol 27. Biological Papers of the University of Alaska, University of Alaska, Fairbanks, pp 199–208
- Geiser F, Christian N, Cooper CE, Körtner G, McAllan BM, Pavey CR, Turner JM, Warnecke L, Willis CKR, Brigham M (2008) Torpor in marsupials: recent advances. In: Lovegrove BG, McKechnie AE (eds) *Hypometabolism in animals: hibernation, torpor and cryobiology*. Interpack Books, Pietermaritzburg, pp 297–306
- Geiser F, Stawski C, Bondarenco A, Pavey CR (2011) Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals? *Naturwissenschaften* 98:447–452
- Giroud S, Perret M, Gilbert C, Zahariev A, Goudable J, Le Maho Y, Oudart H, Momken I, Aujard F, Blanc S (2009) Dietary palmitate and linoleate oxidations, oxidative stress, and DNA damage differ according to season in mouse lemurs exposed to a chronic food deprivation. *Am J Physiol Reg I* 297:R950–R959
- Gordon CJ (2009) Quantifying the instability of core temperature in rodents. *J Therm Biol* 34:213–219
- Grigg GC (2004) An evolutionary framework for studies of hibernation and short term torpor. In: Barnes BM, Carey HV (eds) *Life in the cold. Evolution, mechanisms, adaptation, and application*, vol 27. Biological Papers of the University of Alaska, University of Alaska, Fairbanks, pp 1–11
- Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and daily torpor in mammals. *Resp Physiol Neurobiol* 141:317–329
- Humphries MM, Thomas DW, Kramer DL (2003) The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiol Biochem Zool* 76:165–179
- Kobbe S, Dausmann KH (2009) Hibernation in Malagasy mouse lemurs as a strategy to counter environmental challenge. *Naturwissenschaften* 96:1221–1227
- Kobbe S, Ganzhorn JU, Dausmann KH (2011) Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *J Comp Physiol B* 181:165–173
- Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. *Am Nat* 156:201–219
- Lovegrove BG (2003) The influence of climate on the basal metabolic rate of small mammals: a slow–fast metabolic continuum. *J Comp Physiol B* 173:87–112
- Lovegrove BG (2012) The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biol Rev* 87:128–162
- Lovegrove BG, Genin F (2008) Torpor and hibernation in a basal placental mammal, the Lesser Hedgehog Tenrec *Echinops telfairi*. *J Comp Physiol B* 178:691–698
- Lovegrove BG, Smith GA (2003) Is “nocturnal hypothermia” a valid physiological concept in small birds? A study on Bronze Mannikins (*Spermestes cucullatus*). *Ibis* 145:547–557
- Lovegrove BG, Körtner G, Geiser F (1999a) The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *J Comp Physiol B* 169:11–18
- Lovegrove BG, Lawes MJ, Roxburgh L (1999b) Confirmation of plesiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidae). *J Comp Physiol B* 169:453–460
- Lyman CP, Willis JS, Malan A, Wang LCH (1982) Hibernation and torpor in mammals and birds. Academic Press, New York

- McKechnie AE, Lovegrove BG (2002) Avian facultative hypothermic responses: a review. *Condor* 104:705–724
- McKechnie AE, Mzilikazi N (2011) Heterothermy in Afrotropical mammals and birds: a review. *Integr Comp Biol* 51:1–15
- McKechnie AE, Chetty K, Lovegrove BG (2007) Phenotypic flexibility in the basal metabolic rate of laughing doves: responses to short-term thermal acclimation. *J Exp Biol* 210:97–106
- Mzilikazi N, Lovegrove BG (2004) Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiol Biochem Zool* 77:285–296
- Prendergast BJ, Freeman DA, Zucker I, Nelson RJ (2002) Periodic arousal from hibernation is necessary for initiation of immune responses in ground squirrels. *Am J Physiol Reg I* 282:R1054–R1062
- Roth TC, Rattenborg NC, Pravosudov VV (2010) The ecological relevance of sleep: the trade-off between sleep, memory and energy conservation. *Philos Trans Royal Soc B Biol Sci* 365:945–959
- Schleucher E, Prinzing R (2006) Heterothermia and torpor in birds: highly specialized physiological ability or just deep “nocturnal hypothermia”? The limitations of terminology. *Acta Zool Sinica* 52:393–396
- Schmid J, Ganzhorn JU (2009) Optional strategies for reduced metabolism in gray mouse lemurs. *Naturwissenschaften* 96:737–741
- Stawski C, Geiser F (2010) Seasonality of torpor patterns and physiological variables of a free-ranging subtropical bat. *J Exp Biol* 213:393–399
- Stawski C, Geiser F (2011) Do season and distribution affect thermal energetics of a hibernating bat endemic to the tropics and subtropics? *Am J Physiol Reg I* 301:R542–R547
- Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat (*Nyctophilus bifasciatus*). *J Comp Physiol B* 179:433–441
- Stephenson PJ, Racey PA (1994) Seasonal variation in resting metabolic rate and body temperature of streaked tenrecs, *Hemicentetes nigriceps* and *H. semispinosus* (Insectivora: Tenrecidae). *J Zool* 232:285–294
- Warnecke L, Geiser F (2009) Basking behaviour and torpor use in free-ranging *Planigale gilesi*. *Aust J Zool* 57:373–375
- Wein J (2010) Effects of ambient temperature on tropical hibernation in the lesser hedgehog tenrec, *Echinops telfairi*. Ph.D. dissertation, Universität Hamburg, Hamburg
- Willis CKR (2007) An energy-based body temperature threshold between torpor and normothermia for small mammals. *Physiol Biochem Zool* 80:643–651
- Willis CKR, Brigham RM (2003) Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. *J Comp Physiol B* 173:379–389
- Wilz M, Heldmaier G (2000) Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*. *J Comp Physiol B* 170:511–521