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Non-Torpid Heterothermy in Mammals: Another Category along the Homeothermy–Hibernation Continuum

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Running Title: Non-torpid heterothermy and energetics in mammals

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Synopsis: Variability in body temperature is now recognized to be widespread among whole-body endotherms with homeothermy being the exception rather than the norm. A wide range of body temperature patterns exists in extant endotherms, spanning from strict homeothermy, to occasional use of torpor, to deep seasonal hibernation with many points in between. What is often lost in discussions of heterothermy in endotherms are the benefits of variations in body temperatures outside of torpor. Endotherms that do not use torpor can still obtain extensive energy and water savings from varying levels of flexibility in normothermic body temperature regulation. Flexibility at higher temperatures (heat storage or facultative hyperthermia) can provide significant water savings while decreases at cooler temperatures, even outside of torpor, can lower the energetic costs of thermoregulation during rest. We discuss the varying uses of the terms heterothermy, thermolability, and torpor to describe differences in the amplitude of body temperature cycles and advocate for a broader use of the term "heterothermy" to include non-torpid variations in body temperature.

Introduction

Whole-body endothermy, the capacity to use endogenous means of heat production to regulate core body temperature (body temperature hereafter), allowed mammals and birds to inhabit a wide range of climates and represents a significant step in the evolution of these two groups (Crompton et al. 1978; Bennett and Ruben 1979; Lovegrove 2012). Yet, the maintenance of high and relatively stable body temperatures comes at a significant cost both in terms of energy and of water needs. There is now considerable evidence that the relatively high level of homeothermy observed in many extant mammals and birds derived from more thermally labile ancestors (Grigg et al. 2004; Lovegrove 2012). As we have continued to collect data from animals inhabiting warm environments, we have observed a wider range of thermoregulatory phenotypes, ranging from highly variable (i.e. a form likely closer to the ancestral state) to relatively constant (i.e. an apparently more derived state) body temperatures (Lovegrove 2012; Boyles et al. 2013). Variability in body temperatures is observed not just at the level of torpor expression (see Nowack, Stawski, et al. 2023) but also at body temperatures that could still be considered normothermic. Deviations from strict homeothermy can provide significant energy savings at cold temperatures as well as water savings at higher ambient temperatures (Cooper et al. 2009; Levesque and Lovegrove 2014; Gerson et al. 2019). In large mammals, heterothermy, in the form of small normothermic deviations (1-5°C), has long been recognized as a common response to low energy or water availability (reviewed in Hetem et al. 2016) However, until very recently (Geiser 2021), in smaller endotherms the conversation around heterothermy has largely focused on the use of torpor, i.e. substantial energy savings via a controlled reduction in metabolic rate and a decrease in the body temperature-ambient temperature differential observed in some species of mammals and birds, in its varying forms (Ruf and Geiser 2015; Nowack et al. 2020). This dichotomy of focus has led to a disparate definition of ‘heterothermy’ between researchers who study large mammals versus those who study small endotherms. For example, Ruf and Geiser (2015) define a ‘heterothermic endotherm’ as follows: “An organism that is capable of homeothermic thermoregulation, but at certain times of the day or the year enters a state of torpor.” This definition would preclude the entirety of what has been considered heterothermy in large mammals as it focuses solely on torpor and not on changes in the level and variability in the daily amplitude of body temperatures (Hetem et al. 2016). We support the most recent definition found in Geiser (2021) which states : “Heterothermic organisms also can be considered as those that show large daily fluctuations of body temperature, such as some large birds and mammals that do not enter torpor". Reconciling earlier disparate definitions of heterothermy is an important step towards facilitating discussions around the evolution of endothermy and appreciating nuanced differences observed in extant endotherms. Doing so would allow one to muse the ecological significance of smaller variations in body temperatures that, although they may have energetic consequences, have often been overlooked. Reconciling these disparate definitions of heterothermy enables us to understand the full range of physiological responses, allowing us to more thoroughly contextualize the evolution of endothermy and its diversity in extant endotherms. In this paper we discuss means of assessing and comparing heterothermy in torpid and non-torpid endotherms, both free-ranging and captive, how to separate them, and provide a framework for assessing the phenotypic plasticity in body temperature in endotherms.

Towards a more practical definition of heterothermy

"Heterothermy: The pattern of temperature regulation in a tachymetabolic species in which the variation in core temperature, either nychthemerally or seasonally, exceeds that which defines homeothermy (Gk. hetero—different; therme—heat)." (IUPS Thermal Commission 2003)

The definition above, provided in the International Union of Physiological Sciences' "Glossary of terms for thermal physiology" (IUPS Thermal Commission 2003) cannot in any way be considered a practical or useful definition. The accompanying definition of homeothermy is equally vague referring to 'arbitrarily defined limits' in variability. It is therefore not surprising that either (or both) of these terms have been used to describe various body temperature patterns over the years. Circadian patterns in body temperature regulation in endotherms are well known and have been studied for decades (Aschoff 1963; Refinetti 2010; Maloney et al. 2019). Most species, especially those with a strict daily activity pattern will have, independent of activity, an increase in body temperature during the active phase and a decrease during the resting phase. These endogenous changes are regulated by the circadian clock and differ between species according to activity patterns (diurnal, nocturnal, crepuscular, etc.) and habitat, as well as the energetic status of the animal (Maloney et al. 2019; Refinetti 2020). Take for example two species of small mammal from the tropical rainforests in Borneo: the nocturnal tarsier

(*Cephalopachus bancanus*) and the diurnal large treeshrew (*Tupaia tana*, Figure 1). The nocturnal tarsier is out of phase with daily amplitudes in ambient temperature and has a relatively low active body temperature (~35°C) resulting in very little variability between active and resting body temperatures in free-ranging animals (~0.6°C, Welman et al. 2017). The diurnal treeshrew, on the other hand, has a higher normothermic body temperature (~39°C) and is active during the hottest parts of the day and resting during the coolest, thus displaying a high daily variation in normothermic body temperatures (~3.5°C, Levesque et al. 2018). Even higher variability can be seen in so called 'thermolabile' species, such as naked mole-rats (*Heterocephalus glaber*) who living in subterranean burrow systems and can show skin temperatures varying between 23.7- 35.4°C (Holtze et al. 2018). The difference in the level of precision in body temperature regulation seen between these species illustrates the type of heterothermy that is often ignored in studies on mammalian energetics in favor of focusing on quantifying torpor.

What has been made clear from the various debates and controversies over the years is that the point at which the rest-phase decrease in body temperature switches from normothermy to torpor is difficult to define (Schleucher and Prinzinger 2006; McKechnie et al. 2007; Willis 2007; Boyles et al. 2011; Brigham et al. 2011; Canale et al. 2012). Torpor use is generally seen as active suppression of thermogenesis or metabolism that typically decreases the body temperature-ambient temperature differential and we commonly differentiate between hibernation (multiday torpor bouts associated with a period of extended inactivity) and daily torpor (short bouts of less than 24 hours, Ruf and Geiser 2015). Metabolic rates during daily torpor and hibernation differ substantially even under comparable ambient conditions, body temperature, and torpor bout duration suggesting that these are distinct metabolic states (Staples 2016; Currie et al. 2022; Geiser and Ruf 2023). Yet, the variety of torpor use phenotypes in extant mammals (reviewed in Nowack et al. 2020; Nowack, Stawski, et al. 2023) is vast, with some species falling between categories (such as those who use prolonged torpor lasting several days) or hibernators seemingly switching from one torpor type to another (from short torpor bouts for less than 24 hours, to prolonged torpor or hibernation) depending on the environmental conditions (Geiser and Mzilikazi 2011; Turner et al. 2012; Levesque et al. 2014; Boyles et al. 2017), provoking discussions about clear classifications. Many mammals may also show short and shallow bouts of torpor with only a small decrease in body temperature (i.e. body temperature above 30°C) that despite being associated with noteworthy levels of energy savings (Levin et al. 2012; Olson et al. 2017; Nowack, Mzilikazi, et al. 2023), are often ignored in mammals when only a body temperature decrease below an arbitrary threshold (often 30-33°C) is classified as torpor (Boyles et al. 2011; Canale et al. 2012; Nowack, Mzilikazi, et al. 2023). Although it is worth noting that a similar phenomenon referred to as 'nocturnal hypometabolism' in birds has also received considerable attention, perhaps because the abundance of diurnal species with large rest-phase reductions in body temperature makes it more evident (Schleucher 2004; Schleucher and Prinzinger 2006; Noakes et al. 2013).

Most, if not all, of the issues with defining torpor stem from the fact that body temperature alone is not enough of a diagnostic characteristic (Willis 2007; Canale et al. 2012; Boyles et al. 2020; Currie et al. 2022). A single body temperature measurement can represent different underlying physiological states depending on whether the animal is heating, cooling, suppressing thermogenesis or actively suppressing metabolic rate below basal metabolism, not to mention uncontrolled pathologies impacting thermoregulation such as disease, parasites, or overall body condition and health (Thomas et al. 2010; Robar et al. 2011; Cézilly et al. 2013; Rey et al. 2017). Concurrent measures of either metabolism or heart rate assist in the diagnosis of entry into torpor or in differentiating torpor from hypo- or even hyperthermia, yet these measures are not as readily obtainable as body temperature (Willis 2007; Currie et al. 2014; O'Mara et al. 2017). Therefore, body temperature alone is often used to assess the energetic state of an animal. However, regardless of whether or not torpor - in the strictest sense *i.e.* a reduction in metabolism below a defined threshold (sometimes as little as 25% below resting rates, Hudson and Scott 1979) is employed, flexibility in body temperature conserves significant energy compared to strict homeothermy (here referring to body temperature regulated with only minimal circadian variation despite variable ambient conditions). For example, in the large treeshrew (*Tupaia tana*) (Figure 1) modal body temperature during activity (~39°C) is higher than the body temperatures of the average mammal (36.8°C according to Clarke and O'Connor 2014), yet body temperature routinely decreases to ~35.9°C during the nighttime rest-phase. Measurements of resting metabolism and body temperature taken from individuals under ambient temperatures similar to their usual nighttime temperatures (~25°C) indicate that these animals are resting at the lower end of thermoneutrality (below which metabolic rate increases to defend normothermy; Figure 2; Levesque et al. 2018) and are decidedly not torpid. A hypothetical strictlyhomeothermic treeshrew resting at 25°C with a body temperature of 39°C instead of 36°C (assuming a Q_{10} temperature coefficient of ~2-3 for metabolic rate) would have a basal metabolic rate of 1.23-1.39 times higher than measured. Although this difference is not as extreme as the costs of normothermy compared with torpor, the energy savings are still substantial.

The temperature traces of the treeshrew and the tarsier demonstrate the advantage of multiple diagnostic metrics. Although it appears as though the treeshrew is the more heterothermic of the two species in the wild (Figure 1), because of the amplitude of the daily maxima and minima, this is not the case and under controlled-standardized laboratory conditions it is the tarsier that shows a higher degree of heterothermy (Figure 2, Welman et al. 2017; Levesque et al. 2018). The degree of variability in body temperature and metabolism that an animal is capable of during their rest-phase is directly affected by the ambient temperatures during that period as well as other factors such as microclimate and body mass (Refinetti 1997). If, during the rest-phase, ambient temperatures should approach body temperatures, which occurs more frequently in the tropics and sub-tropics, the smaller thermal gradient (i.e. between the animal's core and the environment) can limit the extent to which animals can lower their body temperature, dampening their degree of thermal flexibility as seen in the tarsier (Canale et al. 2012; Levesque et al. 2014; Lovegrove et al. 2014). Cold can also limit variability in body temperature, for example desert-dwelling ungulates routinely display higher absolute temperatures resulting in larger daily amplitudes during summer compared to winter (Hetem et al. 2009, 2010). Cooler temperatures during winter result in the continuous need for thermogenesis which can elevate body temperature at the low end, which, combined with a reduction in hyperthermic heterothermy, reduces the overall daily range of body temperatures measured (Thompson et al. 2019; Græsli et al. 2020). Thus free-ranging temperature patterns are useful in describing what occurs under natural conditions (with the caveats mentioned above about our abilities to diagnose phenotypes from body temperatures alone in mind) but a more consistent approach is needed to be able to compare a species' fundamental ability to harness flexibility in body temperature. One may argue that a more standardized approach could be the solution, but whether what is currently in use sufficiently encapsulates the thermoregulatory variability of species must first be considered.

Scholander-Irving Curves as a Means of Assessing Capacity for Non-Torpid Heterothermy?

One commonly used standard approach has been to measure metabolism at rest over a range of ambient temperatures under laboratory or field laboratory conditions. These measurements can be used to construct Scholander-Irving (SI) Curves, or thermal profiles, and are considered a standardizable means of characterizing thermoregulation in endotherms (Huey et al. 2012; Riek and Geiser 2013; Khaliq et al. 2017). These curves illustrate the relationship between ambient temperature and metabolic rate and often include readily comparable characteristics such as the lower limit of thermoneutrality and the thermoneutral zone (a species-specific range of ambient temperature over which metabolic rate remains constant- *i.e.* basal). By contrast, defining the upper limit of thermoneutrality has proven more difficult and the determining factor typically varies between either increases in metabolism (Riek and Geiser 2013; Wolf et al. 2017) or increases in evaporative water loss (IUPS Thermal Commission 2003; Withers et al. 2016). This inconsistency illustrates one of the major complications with the use of SI curves over the years: metabolism is not the sole actor in temperature balance. Evaporative water loss plays an equal, if not greater, role in thermoregulation in endotherms, especially at high ambient temperatures. It is also worth noting that many endotherms live at temperatures either below (Humphries and Careau 2011) or above (Mitchell et al. 2018) their thermoneutral zone and are therefore routinely expending either energy or water to maintain normothermic body temperatures. Many species also change either body mass, insulation, or both, between seasons resulting in different parameters depending on the season (Pauls 1981; Lovegrove 2005; Kobbe et al. 2014).

Regardless of seasonality, most mammals spend their lives outside of thermoneutrality which highlights the fact that the thermoneutral zone and its limits are not an indication of thermal tolerance, although they have occasionally been mistaken as such (reviewed in Mitchell et al. 2018; Levesque and Marshall 2021). Therefore, similar to the caveats above on relying solely on body temperature measurements, measuring metabolic rate alone is not enough to gain a holistic understanding of the characteristics of thermoregulation in a species. For example, species like treeshrews maintain a surprisingly large thermoneutral zone (spanning >10°C) for their body mass (reviewed in Thonis et al. 2020) likely due to the fact that they reduce body temperature by ~4°C within the thermoneutral zone. The aforementioned example illustrates a core problem with comparing SI curves between species, which is that Scholander *et al*. (1950) did not measure body temperature in their original publication and considered body temperature to be a constant and relatively non-adaptive trait in endotherms (Scholander, Hock, Walters, and

Irving 1950; Angilletta Jr et al. 2010). This oversight has led to a number of misinterpretations over the years including the belief that the relationship between ambient temperature and resting metabolic rates in endotherms can be modelled using first principles and Newton's Laws of Cooling, and that when a line is drawn through metabolism below the thermoneutral zone it extrapolates to body temperature at y=0. Although this might be the case for some of the more (rare) homeothermic mammals, it does not hold for species with even minor differences between active and resting body temperatures (reviewed in Boyles et al. 2019). A major flaw in these assumptions is that body temperature is assumed to be held constant whereas in reality body temperature in small mammals in particular often follows a curvilinear pattern, decreasing within the thermoneutral zone, increasing slightly below it as thermogenesis is engaged producing excess heat, and finally decreasing again when approaching lethal temperatures (reviewed in Lovegrove et al. 1991). Yet, the degree of this variability in body temperature, or precision in body temperature regulation, does vary between species (Figure 2, Figure 3) and even between seasons in a single species (Haim et al. 1991; Glanville and Seebacher 2010; Levesque and Tattersall 2010; Thiel et al. 2019) and therefore body temperature changes measured during thermal profile experiments can be diagnostic of a species' ability to vary body temperature in a comparable way (Figure 3; Breit 2023).

Fundamental vs Realized Dimensions of Heterothermy

What we have presented above are two means of assessing heterothermy in mammals: body temperature traces of free-ranging animals and body temperature measurements under steady-state conditions. The first, body temperature traces of free-ranging animals can give an idea of what body temperatures animals are experiencing in the wild. Although these can be used to gain a rough estimate of energetic states over time, they cannot accurately reflect the energetic state of the animal nor do they necessarily give an indication of the capacity of the species to employ heterothermy, either via torpor or thermolability. Body temperatures of free-ranging animals are often, but not always, indicative of the animal's propensity or willingness to employ heterothermy. There are instances where warm ambient temperatures preclude obvious reductions in body temperature but the animal is torpid (O'Mara et al. 2017; Reher et al. 2018), furthermore there are also instances where it may be too costly (from an ecological sense) to enter torpor (Nowack et al. 2010). Thus, body temperatures alone are not guaranteed to be a reliable indicator of the physiological capacity of the animal to use torpor (i.e. how low the hypothalamic body temperature setpoint can be regulated before active thermoregulation is required). Similar arguments apply to non-torpid heterothermy, although the costs (along with the energy savings) will be less than those of torpor. It should be noted that the benefits of non-torpid heterothermy have been discussed when it comes to highly thermolabile species (basoendotherms *sensu* Lovegrove 2012) such as marsupials, molerats, echidnas and tenrecs (*e.g.* Withers et al. 2000; Grigg et al. 2004; Boyles et al. 2012; Levesque et al. 2014) but we have been lacking the language to adequately account for lesser levels of non-torpid heterothermy such as that observed in the treeshrews.

The second means of assessing a species' capacity or proclivity for non-torpid heterothermy, body temperature measured under steady-state conditions (such as during experiments to establish the SI-curve), and usually at rest, can give a better idea of a species' baseline level of thermolability, but not an indication of how frequently it will be employed in the wild. Although it should be noted that, at least when it comes to torpor use, some species have been found to be reluctant to enter torpor in the laboratory and are more homeothermic than under free-ranging conditions (Geiser et al. 2000, 2007). Heterothermy outside of torpor has not been compared in the same way therefore whether there will also be differences between the lab and the field has yet to be established. It is important when comparing between and even within a species to consider whether or not the conditions are reflective of the species' true capacity, the fundamental physiological niche (*sensu* Landry-Cuerrier et al. 2008), or simply the potentially limiting conditions of its environment or physiology. Thanks to advancements in data-logger technology, it is now possible to obtain concurrent body temperature and heart rate (a common proxy for metabolic rate) of even small-bodied endotherms (Hetem et al. 2016; Chmura et al. 2018). This combination of physiological variables would provide a more reliable representation of the animals' thermoregulatory state *in situ* but would still require validation using field metabolic rate if the end-goal was to quantify the animals' total energy expenditure. Nevertheless, based on the simple principle that endogenous heat production must increase to defend body temperature at an increasing gradient with the environment, even slight reductions in body temperature, whether due to torpor or non-torpid heterothermy, will convey energy conservation benefits due to a reduction in endogenous heat production needed to combat heat lost from the body.

Conclusions: Non-torpid heterothermy an under-quantified yet useful physiological characteristic of endotherms

Although we do not yet have an easy means of quantifying the impacts of the true capacity for a species to employ non-torpid heterothermy, nor any clear prescriptions as to how important it is, we wish to stress the importance of considering the full breadth of the homeothermic-heterothermic continuum in mammals. Strict thresholds can delineate between the type of torpor used by a species (such as daily torpor or hibernation) along what is obviously an evolutionary gradient in the physiological capacity among endothermic species to employ shorter or longer bouts of torpor. We recognize that there are various schools of thought regarding heterothermy and how best to define it, prompting disagreement between researchers, however, decades of focusing on defining thresholds (daily torpor, hibernation etc) along the heterothermic continuum, while important in characterizing those distinct states, has resulted in the loss of some potentially important nuances. Even very small levels of heterothermy (0.5-5°C; from shallow torpor or non-torpid heterothermy) can provide savings over strict homeothermy and changes in the level of heterothermy over time can be indicative of an energetic imbalance, reproductive status, or other important stage changes in an animal's life (reviewed in Hetem et al. 2016; Maloney et al. 2017). We argue that heterothermy should no longer be used synonymously with torpor but broadened to include non-torpid body temperature variation and that greater care should be taken when evaluating torpor use to include the potential benefits of non-torpid heterothermy. Although the differentiation between shallow torpor and the lower end of normothermy will be challenging, it is important to consider both as part of a continuum of energy saving options. We have presented two means with which to access both the fundamental as well as realized use of thermolability in endotherms, but suspect that more will be developed as technology continues to open new doors and we continue to find new dimensions and points along the mammalian heterothermic-homeothermic continuum.

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Data availability

No new data were generated for this perspectives paper.

References

Angilletta Jr MJ, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology in endotherms. Front Biosci 2:861–81.

Aschoff J. 1963. Comparative physiology: Diurnal rhythms. Annu Rev Physiol 25:581–600.

Bennett AF, Ruben JA. 1979. Endothermy and activity in vertebrates. Science 206:649–54.

Boyles JG, Bennett NC, Mohammed OB, Alagaili AN. 2017. Torpor patterns in Desert Hedgehogs (*Paraechinus aethiopicus*) represent another new point along a thermoregulatory continuum. Physiol Biochem Zool 90:445–52.

Boyles JG, Johnson JS, Blomberg A, Lilley TM. 2020. Optimal hibernation theory. Mammal Rev 50:91–100.

Boyles JG, Levesque DL, Nowack J, Wojciechowski MS, Stawski C, Fuller A, Smit B, Tattersall GJ. 2019. An oversimplification of physiological principles leads to flawed macroecological analyses. Ecol Evol 9:12020–25.

Boyles JG, Smit B, McKechnie AE. 2011. A new comparative metric for estimating heterothermy in endotherms. Physiol Biochem Zool 84:115–23.

Boyles JG, Thompson AB, McKechnie AE, Malan E, Humphries MM, Careau V. 2013. A global heterothermic continuum in mammals. Glob Ecol Biogeogr 22:1029–39.

Boyles JG, Verburgt L, McKechnie AE, Bennett NC. 2012. Heterothermy in two mole-rat species subjected to interacting thermoregulatory challenges. J Exp Zool Part Ecol Genet Physiol 317:73–82.

Breit AM. 2023. Comparative energetics of mammalian thermoregulatory physiology. University of Maine (PhD).

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 36:376–79.

Canale CI, Levesque DL, Lovegrove BG. 2012. Tropical heterothermy: Does the exception prove the rule or force a re-definition? In: Ruf T, Bieber C, Arnold W, Millesi E, editors. Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations Heidelberg: Springer Berlin. p. 29–40.

Cézilly F, Favrat A, Perrot-Minnot M-J. 2013. Multidimensionality in parasite-induced phenotypic alterations: ultimate versus proximate aspects. J Exp Biol 216:27–35.

Chmura HE, Glass TW, Williams CT. 2018. Biologging physiological and ecological responses to climatic variation: new tools for the climate change era. Front Ecol Evol 6:92.

Clarke A, O’Connor MI. 2014. Diet and body temperature in mammals and birds. Glob Ecol Biogeogr 23:1000–1008.

Cooper CE, Withers PC, Cruz-Neto AP. 2009. Metabolic, ventilatory, and hygric physiology of the gracile mouse opossum (*Gracilinanus agilis*). Physiol Biochem Zool 82:153–62.

Crompton AW, Taylor CR, Jagger JA. 1978. Evolution of homeothermy in mammals. Nature 272:333–36.

Currie SE, Körtner G, Geiser F. 2014. Heart rate as a predictor of metabolic rate in heterothermic bats. J Exp Biol 217:1519–24.

Currie SE, Körtner G, Geiser F. 2022. Pronounced differences in heart rate and metabolism distinguish daily torpor and short-term hibernation in two bat species. Sci Rep 12:21721.

Geiser F. 2021. Ecological physiology of daily torpor and hibernation Springer.

Geiser F, Holloway JC, Körtner G. 2007. Thermal biology, torpor and behaviour in sugar gliders: a laboratory-field comparison. J Comp Physiol [B] 177:495–501.

Geiser F, Holloway JC, Körtner G, Maddocks TA, Turbill C, Brigham RM. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds. In: Heldmaier G, Klingenspor M, editors. Life In The Cold: 11th International Hibernation Symposium Berlin: Springer-Verlag. p. 95–102.

Geiser F, Mzilikazi N. 2011. Does torpor of elephant shrews differ from that of other heterothermic mammals? J Mammal 92:452–59.

Geiser F, Ruf T. 2023. Long-term survival, temperature, and torpor patterns. Sci Rep 13:6673.

Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, McWhorter TJ, Wolf BO. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct Ecol 33:597–607.

Glanville EJ, Seebacher F. 2010. Plasticity in body temperature and metabolic capacity sustains winter activity in a small endotherm (*Rattus fuscipes*). Comp Biochem Physiol A Mol Integr Physiol 155:383–91.

Græsli AR, Thiel A, Fuchs B, Singh NJ, Stenbacka F, Ericsson G, Neumann W, Arnemo JM, Evans AL. 2020. Seasonal hypometabolism in female moose. Front Ecol Evol 107.

Grigg GC, Beard LA, Augee ML. 2004. The evolution of endothermy and its diversity in mammals and birds. Physiol Biochem Zool 77:982–97.

Haim A, Racey PA, Speakman JR, Ellison GTH, Skinner JD. 1991. Seasonal acclimatization and thermoregulation in the pouched mouse *Saccostomus campestris*. J Therm Biol 16:13–17.

Hetem RS, de Witt BA, Fick LG, Fuller A, Kerley GIH, Meyer LCR, Mitchell D, Maloney SK. 2009. Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). Comp Biochem Physiol A Mol Integr Physiol 152:379–88.

Hetem RS, Maloney SK, Fuller A, Mitchell D. 2016. Heterothermy in large mammals: inevitable or implemented? Biol Rev 91:187–205.

Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LCR, Shobrak M, Fuller A, Mitchell D. 2010. Variation in the daily rhythm of body temperature of free-living Arabian oryx (*Oryx leucoryx*): does water limitation drive heterothermy? J Comp Physiol B 180:1111–19.

Holtze S, Braude S, Lemma A, Koch R, Morhart M, Szafranski K, Platzer M, Alemayehu F, Goeritz F, Hildebrandt TB. 2018. The microenvironment of naked mole-rat burrows in East Africa. Afr J Ecol 56:279–89.

Hudson JW, Scott IM. 1979. Daily torpor in the laboratory mouse, *Mus musculus* var. albino. Physiol Zool 52:205–18.

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B Biol Sci 367:1665–79.

Humphries MM, Careau V. 2011. Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. Integr Comp Biol 51:419–31.

IUPS Thermal Commission. 2003. Glossary of terms for thermal physiology - Third edition (Reprinted from the Japanese Journal of Physiology). J Therm Biol 28:75–106.

Khaliq I, Böhning-Gaese K, Prinzinger R, Pfenninger M, Hof C. 2017. The influence of thermal tolerances on geographical ranges of endotherms. Glob Ecol Biogeogr 26:650–68.

Kobbe S, Nowack J, Dausmann K. 2014. Torpor is not the only option: seasonal variations of the thermoneutral zone in a small primate. J Comp Physiol B 184:789–97.

Landry-Cuerrier M, Munro D, Thomas DW, Humphries MM. 2008. Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. Ecology 89:3306–16.

Levesque DL, Lobban KD, Lovegrove BG. 2014. Effects of reproductive status and high ambient temperatures on the body temperature of a free-ranging basoendotherm. J Comp Physiol B 184:1041–53.

Levesque DL, Lovegrove BG. 2014. Increased homeothermy during reproduction in a basal placental mammal. J Exp Biol 217:1535–42.

Levesque DL, Marshall KE. 2021. Do endotherms have thermal performance curves? J Exp Biol 224:jeb141309.

Levesque DL, Tattersall GJ. 2010. Seasonal torpor and normothermic energy metabolism in the Eastern chipmunk (*Tamias striatus*). J Comp Physiol [B] 180:279–92.

Levesque DL, Tuen AA, Lovegrove BG. 2018. Staying hot to fight the heat-high body temperatures accompany a diurnal endothermic lifestyle in the tropics. J Comp Physiol B 188:707–16.

Levin E, Ar A, Yom-Tov Y, Kronfeld-Schor N. 2012. Summer torpor and sexual segregation in the subtropical bat *Rhinopoma microphyllum*. In: Ruf T, Bieber C, Arnold W, Millesi E, editors. Living in a Seasonal World Springer Berlin Heidelberg. p. 167–74.

Lovegrove BG. 2005. Seasonal thermoregulatory responses in mammals. J Comp Physiol [B] 175:231–47.

Lovegrove BG. 2012. The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. Biol Rev 87:128–62.

Lovegrove BG, Canale CI, Levesque DL, Fluch G, Řeháková-Petrů M, Ruf T. 2014. Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? Physiol Biochem Zool 87:30–45.

Lovegrove BG, Heldmaier G, Ruf T. 1991. Perspectives of endothermy revisited - The endothermic temperature-range. J Therm Biol 16:185–97.

Maloney SK, Goh G, Fuller A, Vesterdorf K, Blache D. 2019. Amplitude of the circadian rhythm of temperature in homeotherms. CAB Rev 14:1–30.

Maloney SK, Marsh MK, McLeod SR, Fuller A. 2017. Heterothermy is associated with reduced fitness in wild rabbits. Biol Lett 13:20170521.

McKechnie AE, Ashdown RAM, Christian MB, Brigham RM. 2007. Torpor in an African caprimulgid, the freckled nightjar *Caprimulgus tristigma*. J Avian Biol 38:261–66.

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. J Anim Ecol 87:956–73.

Mzilikazi N, Lovegrove BG. 2002. Reproductive activity influences thermoregulation and torpor in the pouched mouse, *Saccostomus campestris*. J Comp Physiol [B] 172:7–16.

Noakes MJ, Smit B, Wolf BO, McKechnie AE. 2013. Thermoregulation in African Green Pigeons (*Treron calvus*) and a re-analysis of insular effects on basal metabolic rate and heterothermy in columbid birds. J Comp Physiol B 969–82.

Nowack J, Levesque DL, Reher S, Dausmann KH. 2020. Variable climates lead to varying phenotypes: ‘weird’ mammalian torpor and lessons from lower latitudes. Front Ecol Evol 8:60.

Nowack J, Mzilikazi N, Dausmann KH. 2010. Torpor on demand: heterothermy in the non-lemur primate *Galago moholi*. PLOS One 5:e10797.

Nowack J, Mzilikazi N, Dausmann KH. 2023. Saving energy via short and shallow torpor bouts. J Therm Biol 114.

Nowack J, Stawski C, Geiser F, Levesque DL. 2023. Rare and opportunistic use of torpor in mammals - a ghost of the past? Integr Comp Biol.

Olson MN, Bowman J, Burness G. 2017. Seasonal energetics and torpor use in North American flying squirrels. J Therm Biol 70:46–53.

O’Mara MT, Rikker S, Wikelski M, Ter Maat A, Pollock HS, Dechmann DK. 2017. Heart rate reveals torpor at high body temperatures in lowland tropical free-tailed bats. R Soc Open Sci 4:171359.

Pauls RW. 1981. Energetics of the red squirrel - a laboratory study of the effects of temperature, seasonal acclimatization, use of the nest and exercise. J Therm Biol 6:79–86.

Payne J, Francis C, Phillips K. 1985. A field guide to the mammals of Borneo Kota Kinabalu, Malaysia: The Sabah Society.

Refinetti R. 1997. The effects of ambient temperature on the body temperature rhythm of rats, hamsters, gerbils, and tree shrews. J Therm Biol 22:281–84.

Refinetti R. 2010. The circadian rhythm of body temperature. Front Biosci 15:564–94.

Refinetti R. 2020. Circadian rhythmicity of body temperature and metabolism. Temperature 7:321–62.

Reher S, Ehlers J, Rabarison H, Dausmann KH. 2018. Short and hyperthermic torpor responses in the Malagasy bat *Macronycteris commersoni* reveal a broader hypometabolic scope in heterotherms. J Comp Physiol B 188:1015–27.

Rey B, Fuller A, Mitchell D, Meyer LCR, Hetem RS. 2017. Drought-induced starvation of aardvarks in the Kalahari: an indirect effect of climate change. Biol Lett 13:20170301.

Riek A, Geiser F. 2013. Allometry of thermal variables in mammals: consequences of body size and phylogeny. Biol Rev 88:564–72.

Robar N, Murray DL, Burness G. 2011. Effects of parasites on host energy expenditure: the resting metabolic rate stalemate. Can J Zool 89:1146–55.

Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. Biol Rev 90:891–926.

Schleucher E. 2004. Torpor in birds: Taxonomy, energetics, and ecology. Physiol Biochem Zool 77:942–49.

Schleucher E, Prinzinger R. 2006. Heterothermia and torpor in birds: highly specialized physiologcial ability or just deep “nocturnal hypothermia”? -- The limitations of terminology. Acta Zool Sin 52(Supplement):393–96.

Scholander PF, Hock R, Walters V, Irving L. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol Bull 99:259–71.

Scholander PF, Hock R, Walters V, Johnson F, Irving L. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol Bull 99:237–58.

Staples JF. 2016. Metabolic flexibility: hibernation, torpor, and estivation. Compr Physiol 6:737–71.

Tattersall GJ, Sinclair BJ, Withers PC, Fields PA, Seebacher F, Cooper CE, Maloney SK. 2012. Coping with thermal challenges: Physiological adaptations to environmental temperatures. Compr Physiol 2:2151–2202.

Thiel A, Evans AL, Fuchs B, Arnemo JM, Aronsson M, Persson J. 2019. Effects of reproduction and environmental factors on body temperature and activity patterns of wolverines. Front Zool 16:21.

Thomas F, Poulin R, Brodeur J. 2010. Host manipulation by parasites: a multidimensional phenomenon. Oikos 119:1217–23.

Thompson DP, Barboza PS, Crouse JA, McDonough TJ, Badajos OH, Herberg AM. 2019. Body temperature patterns vary with day, season, and body condition of moose (*Alces alces*). J Mammal 100:1466–78.

Thonis A, Ceballos RM, Tuen AA, Lovegrove BG, Levesque DL. 2020. High upper limits and a large thermoneutral zone in a small tropical mammal. Physiol Biochem Zool 93:199–209.

Tomlinson S. 2016. Novel approaches to the calculation and comparison of thermoregulatory parameters: Non-linear regression of metabolic rate and evaporative water loss in Australian rodents. J Therm Biol 57:54–65.

Turner JM, Körtner G, Warnecke L, Geiser F. 2012. Summer and winter torpor use by a free-ranging marsupial. Comp Biochem Physiol -Mol Integr Physiol 162:274–80.

Welman S, Tuen AA, Lovegrove BG. 2017. Searching for the Haplorrhine heterotherm: field and laboratory data of free-ranging tarsiers. Front Physiol 8:745.

Willis CKR. 2007. An energy-based body temperature threshold between torpor and normothermia for small mammals. Physiol Biochem Zool 80:643–51.

Withers PC, Cooper CE, Maloney SK, Bozinovic F, Cruz-Neto AP. 2016. Ecological and Environmental Physiology of Mammals Oxford University Press.

Withers PC, Thompson GG, Seymour RS. 2000. Metabolic physiology of the north-western marsupial mole, Notoryctes caurinus (Marsupialia : Notoryctidae). Aust J Zool 48:241–58.

Wolf BO, Coe BH, Gerson AR, McKechnie AE. 2017. Comment on an analysis of endotherm thermal tolerances: systematic errors in data compilation undermine its credibility. Proc R Soc B Biol Sci 284:20162523.

Figure 1 Body temperature traces (A,C) and frequency distribution histograms of core body temperature (B,D) from two free-ranging endotherms inhabiting a warm environment in the equatorial tropics. The modal temperatures of the active phase are represented by dashed lines in red and the rest phase in blue. A and B represent data collected from the nocturnal Horsfield's tarsier (*Cephalopachus bancanus*, Welman et al. 2017) and C and D the diurnal large treeshrew (*Tupaia tana*, Levesque et al. 2018). Picture credits: Yan Wong (tarsier, phylopic.org) and the treeshrew silhouette was modified from Payne et al (1985).

Figure 2 The subcutaneous (black circles) and body temperature (open circles) for the Horsefield's tarsier (A, *Cephalopachus bancanus*, redrawn from Welman et al. 2017) and the large treeshrew (C, *Tupaia tana*, redrawn from Levesque et al. 2018), and resting metabolic rate (B,D) measured during the rest phase over a range of ambient temperatures. Both species had thermoneutral zones spanning from ~25°C to >35°C and the subcutaneous temperature of the tarsier varied by ~6°C and treeshrew ~ 4°C over that range. The dashed line indicates the lower critical limit of the thermoneutral zone. Picture credits: Yan Wong (tarsier, phylopic.org) and the treeshrew silhouette was modified from Payne et al (1985).

Figure 3: A schematic representation of the thermoregulatory response of a hypothetical small mammal while defending a normothermic body temperature (black), using non-torpid heterothermy (blue), shallow torpor (orange) and deep torpor (red). The vertical black (normothermic) and blue (non-torpid heterothermy) dashed lines represent the lower (L_{CT}) and upper critical limits (U_{CT}) of the thermoneutral zone (TNZ) showing a widening of the thermoneutral zone with the use of thermolability. The dotted diagonal line represents the point at which body temperature equals ambient temperature. In this example only the torpid animal is fully thermoconforming within and below the thermoneutral zone and only the homeothermic animal is thermoregulating above the U_{CT}. Metabolism within and above the thermoneutral zone (TNZ) are omitted for the torpid animals for clarity. Adapted from Scholander et al. (1950), Lovegrove et al. (1991), Tomlinson (2016), Tattersall et al. (2012) with data from Levesque et al. (2018) and Mzilikazi and Lovegrove (2002).