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Modelling mammalian energetics: the heterothermy problem

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Abstract

Global climate change is expected to have strong effects on the world's flora and fauna. As a result, there has been a recent increase in the number of meta-analyses and mechanistic models that attempt to predict potential responses of mammals to changing climates. Many models that seek to explain the effects of environmental temperatures on mammalian energetics and survival assume a constant body temperature. However, despite generally being regarded as strict homeotherms, mammals demonstrate a large degree of daily variability in body temperature, as well as the ability to reduce metabolic costs either by entering torpor, or by increasing body temperatures at high ambient temperatures. Often, changes in body temperature variability are unpredictable, and happen in response to immediate changes in resource abundance or temperature. In this review we provide an overview of variability and unpredictability found in body temperatures of extant mammals, identify potential blind spots in the current literature, and discuss options for incorporating variability into predictive mechanistic models.

Keywords: Endothermy, Torpor, Heterothermy, Mechanistic models, Body temperature, Hibernation, Mammal,

Background

Global climate change has provided a sense of urgency to the importance of understanding the interactions between organisms and environmental temperatures. As we seek to improve the accuracy of predicting organismal responses to changes in climate, emphasis is being placed on mechanistic models that rely on an in-depth understanding of the thermoregulatory physiology and energetics of a species [1–6]. To date, however, the bulk of these models have been built and tested on ectothermic organisms [7–9], while research on endotherms has lagged behind [10]. This is partly due to deficiencies in understanding the mechanisms of the relationship between environmental temperatures and energy metabolism in endotherms [8, 11–13]. With a few notable exceptions (eg. [14]), ectotherms predominantly rely on external sources of heat production and therefore have a relatively consistent, and thus predictable, relationship between ambient temperature (T_a) and body temperature (T_b) [9, 15, 16]. By contrast, endotherms can generate heat using metabolism and as such T_b is generally independent of T_a [17].

From its conception, the comparative study of endothermic thermoregulation has been based on the assumption that T_b is maintained at a constant and elevated level [7, 18]. One of the most common ways to quantify the relationship between T_b and T_a in mammals, and in endotherms in general, is the Scholander-Irving model [18]. Also called thermal profiles, the Scholander-Irving model requires measuring resting metabolic rate (preferably from fasted, non-reproductive individuals, during their rest-phase) over a series of environmental temperatures to identify the range of T_as over which metabolic rate remains minimal, referred to as the thermoneutral zone (TNZ) [18]. At temperatures below the lower critical limit of the TNZ, thermal conductance (the rate at which heat is lost from the body, and the inverse of insulation) is at a minimum and energetically costly means of heat production (primarily shivering and non-shivering thermogenesis) are used to maintain T_b. Similarly, as temperatures increase above the upper critical limit, where thermal conductance is maximised, metabolism increases as energetically costly means of evaporative cooling (panting and sweating) are employed to maintain a stable T_b [16].

Existing mechanistic models have incorporated the Scholander-Irving model, and its assumptions, into a set

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of predictive equations used to calculate the costs of thermoregulation under various environmental conditions [13, 19–21]. However, these models present a somewhat simplistic version of mammalian energetics in relation to climate. Often, it is assumed that the animal is actively defending a set T_b, and therefore the models do not take into account the potential effects of variable T_b (but see [22], for a notable exception). Strict homeothermy (a constant, often elevated T_b) is not the norm and, as we will demonstrate in this review, many endotherms vary their T_b considerably. While some species only show slight daily changes, with higher T_b during activity than at rest, others employ larger decreases in T_b during the rest phase [23–27], or thermoconform, which is accompanied by a decrease in metabolism, by either reducing T_b, (torpor, [28–30]) or increasing T_b (hyperthermia, reviewed in [31]). When environmental temperatures rise above T_b, evaporative cooling is often the only means of maintaining a stable T_b. To conserve water and avoid dehydration, some endotherms employ facultative hyperthermia (also referred to thermoconforming or heat storage) at high T_a and increase their T_b to sublethal temperatures [31–33]. Increases in T_b reduces both the energetic and water costs of cooling mechanisms [32, 34, 35].

Variable T_b is widespread in mammals, and both habitat and evolutionary history have a large influence on the thermoregulatory characteristics of endotherms [10, 29, 36]. Energy usage in relation to climate is further affected by phylogeny, activity level, microclimate selection, reproductive status, and energy availability [13, 21, 37–40]. Due to fundamental differences in thermoregulation between mammals and birds, we will focus predominantly on mammals in this review (but see [32, 35, 41] for a discussion on birds). The complexities of predicting metabolism, or even T_b, in relation to differences in T_a affect the accuracy of predictive mechanistic models. In this review we seek to provide an overview of the variability of thermoregulatory patterns of extant mammals, demonstrate how this variability can complicate predictive mechanistic models, and outline some potential avenues for improvement.

Daily variability in mammalian T_b

Many of the existing models that seek to explain species distributions or responses of endothermic animals to climate change are based on the assumption that endotherms maintain a high, relatively stable T_b throughout a variety of habitats and climatic conditions [18, 42, 43]. Although, when compared with ectothermic species, endotherms generally have significantly reduced variability in T_b, many species show marked differences between active-phase and rest-phase T_b (Fig. 1) [39, 44, 45]. Mean normothermic T_b of eutherian mammals lies between 36 and 38 °C (range 30.5–40.7 °C) [46], whereas marsupials and monotremes are generally considered to have lower T_bs (mean 35.3 °C, range 30.8–37.4 °C) [46–48]. While some species, such as the golden hamster (*Mesocricetus auratus*) [49] or the swamp rat (*Rattus lutreolus*; Fig. 1a) only decrease their T_b 2–3 °C during normothermic resting, others, such as treeshrews (*Tupaia* sp.), show more pronounced 24 h amplitudes in T_b (Fig. 1b) [45]. Marsupials, generally have larger daily T_b amplitudes, and T_b can vary from between 32 and 34 °C during normothermic resting, to above 40 °C during activity, this despite their average T_bs being listed at around 35 °C (Fig. 1c) [46, 50, 51]. Basoendotherms (*sensu* [36]) such as tenrecs (Fig. 1d) and echidnas show the highest level of variability with rest-phase T_b closely following T_a during most times of the year [52–56].

The cost of endothermy, usually measured via metabolism, varies greatly depending on a number of factors including body size, habitat, resource availability, climatic conditions, and activity patterns [57–59]. A strictly nocturnal activity pattern is the ancestral condition in mammals, and is efficient in warm climates, as it allows animals to save both water and energy [55, 60, 61]. This is especially true for small mammals with low normorthermic T_bs (~32–35 °C), as a relatively high T_b is maintained passively during the day-time rest-phase, and activity can offset most of the potential thermoregulatory costs at night [38, 55, 61]. Conversely, in colder climates where most small-bodied species rest in thermally insulated burrows, diurnal activity can reduce overall energy expenditure by lowering the need for thermogenesis during the active period [13, 62]. The relative energetic costs and benefits of a nocturnal or diurnal activity pattern have so far mostly been discussed in single species studies, or in hypotheses about the evolution of endothermy [40, 61, 63–65]. Unfortunately, nocturnal and diurnal species, as well as those that do not fit clearly in either category, are usually lumped together in meta-analyses despite facing vastly different environmental conditions.

Daily amplitude changes in T_b are not solely the result of differences in activity, but appear to be under some level of circadian control, persisting even during continuous rest [39, 66]. Interestingly, while differences in resting metabolic rates between the active-phase and rest-phase were commonly measured in older studies [67, 68], the recent trend toward focusing on the importance of measuring basal metabolism has meant that the energetics of resting during the active-phase is largely ignored. Basal metabolism is measured under a set of restrictive, and often ecologically irrelevant conditions; the animals must be post-absorptive, non-reproductive and not growing [57, 69]. For species with pronounced, T_a-dependent, decreases in T_b during normothermic

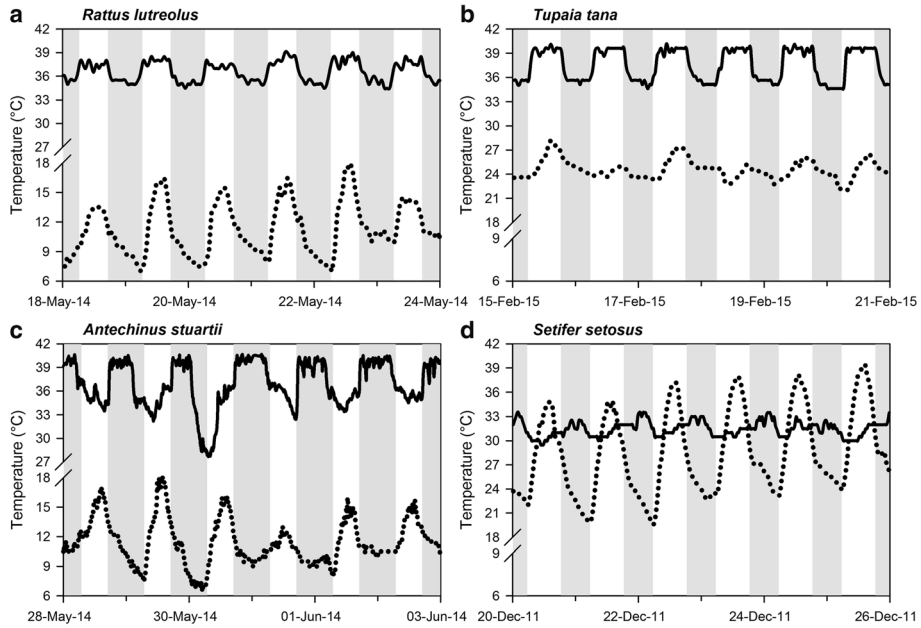

Fig. 1 Sample body temperature traces (*solid lines*) of a single free-ranging individual from several mammal species over a period of 6 days. Also shown are ambient temperature traces (*dotted lines*) and the nocturnal period is represented by the grey bars and daytime by the white bars. The mammals represented are: (**a**) an Australian diurnal homeotherm with small daily amplitudes in T_b (*Rattus lutreolus*, Order: Rodentia, Stawski, Körtner, Nowack and Geiser unpublished data); (**b**) a diurnal homeotherm from Borneo with large daily T_b amplitude (*Tupaia tana*, Order: Scandentia, Levesque, Tuen and Lovegrove unpublished data); (**c**) an Australian nocturnal daily heterotherm shown with a torpor bout, low resting T_b, and high active T_b (*Antechinus stuartii*, Order: Dasyuromorphia, Stawski, Körtner, Nowack and Geiser unpublished data); and (**d**) a nocturnal basoendotherm from Madagascar (*Setifer setosus*, Order: Afrosoricida, data from [55])

rest, measuring resting metabolism during the rest-phase only could grossly underestimate the total baseline energy and water budgets. Pronounced normothermic decreases in rest-phase T_b have received considerable attention in the avian literature [41, 70, 71], where decreases in T_b of >5 °C are common, but have been largely ignored in mammals [16].

A major factor that can be overlooked when relying on simplistic mechanistic models is the potential for phenotypic plasticity [6, 72]. Individuals of one species, or even of one population, can respond differently to an environmental challenge often depending on the condition of the individual. The daily amplitude of T_b is not a fixed trait, and can change based on various external factors such as water and energy availability, or competition [25, 73–75]. Camels (*Camelus dromedarius*) for example maintain a near stable T_b with only little T_b variation (≤2 °C) and use evaporative cooling when water is available, but increase daily amplitudes in T_b to more than 6 °C to conserve water when water stressed [34]. Similarly, Arabian oryx (*Oryx leucoryx*) show a higher amplitude in daily T_b during warm dry periods than during periods where water was readily available, which is attributed to low water availability [6]. Flexible increases in T_b amplitudes by thermoconforming are also employed by small desert mammals in response to high T_a during the active phase [33]. Some bats in the Australian arid-zone are known to tolerate T_a up to 48 °C, with corresponding skin temperatures up to 45.8 °C [76]. In general, however, our capacity to model mammalian responses to high T_a is hindered by a general lack of understanding of upper limits in T_a tolerance and how flexible they are [2, 8, 12, 77]. We have been much better at collecting lower limits of the TNZ than upper (204 versus 93) [78]. Specifically, while increases in T_b at high T_a have been shown to reduce the energetic costs and increase the efficiency of evaporative cooling in birds and some small desert mammals [32, 33, 79, 80], the interplay between water loss, T_b and T_a at the upper limits of the TNZ are largely unknown in mammals. Additionally, very little has been done to equate upper limits measured in the lab to conditions experienced by the animals under natural conditions (but see [42, 81]).

In general, endotherms with flexible control over normothermic T_b (i.e. thermolabile species) can maximize energy and water use efficiency in response to unpredictable conditions [7, 33, 72, 82]. An extreme example can be found in basoendotherms. In these species, the thermoneutral zone (TNZ) can be difficult to distinguish as T_b often closely tracks T_a, which also blurs the lines between normothermy and torpor [63, 83–85]. What these basoendotherms demonstrate, is that by allowing

T_b to decrease along with T_a they reduce the $T_b - T_a$ gradient, which allows for lower rates of heat loss as well as a widening of the range of T_a over which minimum rates of metabolism are measured. Such flexible thermoregulation usually corresponds with a parallel ability to be active over a larger range of T_bs [55, 86–89] and is seen to a lesser degree in other endothermic species with high thermolability, but requires more study [7, 77, 90, 91] (Levesque, Lovegrove and Tuen unpublished data). Thermolability, and by extension the characteristics of the TNZ, is not fixed seasonally, however. For example, the reddish-gray mouse lemur (*Microcebus griseorufus*) not only hibernates during the winter period, but also increases the breadth of their normothermic TNZ during the colder period of the year [92]. In this species the lower critical temperature of the TNZ decreases by 7.5 °C from summer to winter, which allows the species to keep its energy demands during normothermia constant despite colder T_as during winter [92]. This is a relatively common phenomenon in non-hibernating mammals, but most studies focus on change in insulation rather than change in T_b as an energy saving mechanism [93–95]. A large body of work exists assessing the evolution of thermal flexibility in ectotherms (reviewed by [15]), but similar approaches have yet to be applied systematically to endotherms [10, 11].

Seasonality and unpredictability of mammalian T_b

In addition to daily changes in T_b, many mammalian species show changes in their T_b between seasons. The most extreme example are the so called 'heterothermic' mammals [29] which can temporarily abandon normothermia and reduce T_b and metabolic rate in a state of torpor. Definitions of torpor, and therefore heterothermy, vary throughout the literature. Although most agree that torpor occurs when rest-phase decreases in T_b are large enough for metabolism to drop below basal levels, the distinction between the two states can sometimes be unclear [52, 91, 96]. In practice, however, torpor is often defined using arbitrary T_b cut-offs which can underestimate energy saved by T_b reductions above the torpor cut-off T_b (see [91], for an in-depth discussion). Similar to the vast differences in the daily T_b amplitudes, torpor patterns are highly variable both among and within species (Fig. 2) [10, 29, 36, 53, 97, 98]. However, a decrease in T_b during winter can not only be observed in heterothermic species, but also, to a lesser degree, in homeothermic species. The homeothermic, European red squirrels (*Sciurus vulgaris*), for example, lower their T_b slightly during the winter [99]. This has also been observed in large mammals, such as the red deer (*Cervus elaphus*) [27] or the Przewalski horse (*Equus ferus przewalskii*) [100]. Lower T_b combined with

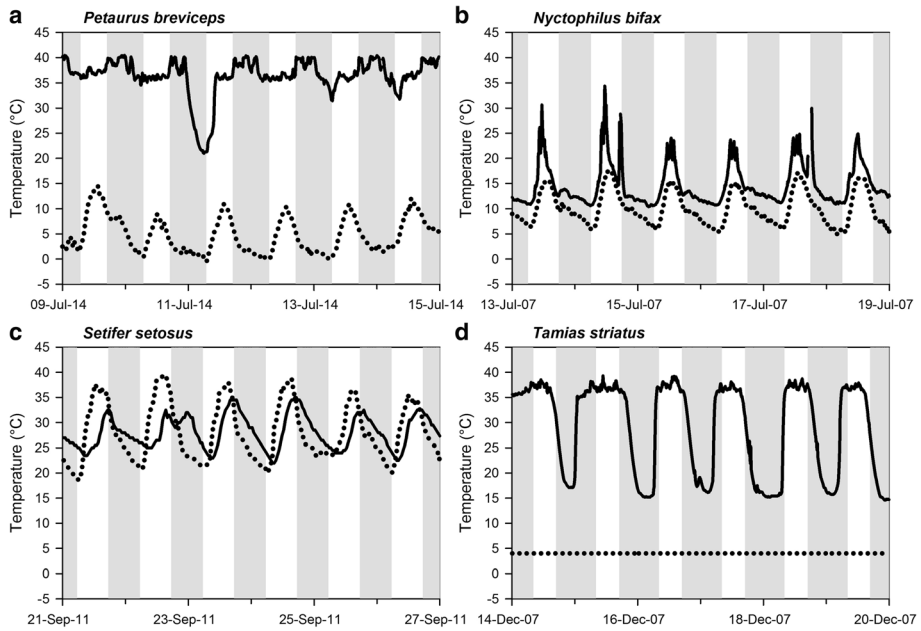

Fig. 2 Examples of variable patterns of torpor expression, defined by reductions in body temperature (*solid lines*). Ambient temperatures are represented by the dotted lines and night and day are illustrated by the grey and white bars, respectively. Shown are: (**a**) an Australian daily heterotherm showing one short torpor bout (*Petaurus breviceps*, Order: Diprotodontia, Nowack unpublished data); (**b**) an opportunistic hibernator from Australia showing a bout of multiday torpor (*Nyctophilus bifax*, Order: Chiroptera, Stawski and Geiser unpublished data); (**c**) a thermo-conforming tropical hibernator from Madagascar during hibernation, the data shown are from a multi-day torpor bout with a single bout of activity occurring the night of the 23rd of September (*Setfier setosus*, Order: Afrosoricida, data from [55]); and (**d**) a food storing hibernator from North America showing multiple single day bouts in the laboratory (*Tamias striatus*, Order: Rodentia, data from [94])

increased fur thickness can already lead to substantial energy savings [101], without suffering the potential negative side-effects of torpor [102–106]. Despite the various benefits, torpor use is also associated with costs, for example, a low T_b interferes with reproduction as it delays fetal development (reviewed in [107]) and hinders spermatogenesis [108, 109]. Further costs include slowed locomotor reactions [89, 110], decreased sensory perception [110] and increased oxidative stress ([111], but see [112]) therefore there is some benefit to avoiding or reducing torpor if resources are abundant [102].

Traditionally, the study of heterothermy in mammals has focused exclusively on strict categorical classifications: *daily heterotherm* (torpor less than 24 h with a relatively high torpid T_b), *hibernator* (multiday torpor bouts at low T_b), or *homeotherm*. However, as thermoregulatory characteristics from more species, especially those from tropical or sub-tropical environments, have been made available, it seems more likely that heterothermy and homeothermy exist on a continuum [36, 53, 113]. Furthermore, by focusing entirely on strict categorical variables, many studies have ignored the potential adaptive benefits to small, non-torpid changes in T_b [7, 91]. It is clear that there exists a high degree of variability in both the level of T_b (often reported as mean T_b or set-point T_b) and the precision with which it is regulated [10, 29, 36, 46]. Furthermore, it is probable that some degree of heterothermy, and likely variable torpor expression, was the ancestral condition in mammals, and that the high degree of homeothermy in extant species evolved via a highly heterothermic ancestor [36, 53, 114]. Interestingly, whether the variability in T_b observed is the result of differences in the level of control over T_b, or the side-effect of differences in metabolism and thermal conductance, remains a topic of debate [58, 67, 115]. After reviewing the T_b of a large number of birds and mammals, Clarke and Rothery [46] came to the conclusion that "… a complex relationship between mass, T_b and resting metabolic rate and leaves open the intriguing question of whether evolution has adjusted resting metabolic rate through changes in T_b or whether T_b is simply a consequence of resting metabolic rate that has evolved for a particular environment and ecology." This confusion illustrates that we still lack a basic mechanistic understanding of effects of T_a on mammalian T_b and metabolism, something which needs to be taken into consideration when attempting large-scale, multi-species, predictions of responses to climate change.

One potential complication arising from the complex interplay between T_b, conductance, heat storage, water balance and metabolism, is that T_b is rarely a good proxy for energy expenditure. Unlike ectotherms, where differences in metabolic rate at different temperatures are largely the result of Arrhenius effects of temperature on metabolism [116], in endotherms the same T_b can be the result of a number of energetically differing states including, activity, resting, heating, cooling, or torpidity [52, 91, 117]. Furthermore, behavioural thermoregulation is common and many mammals bask to lower energetic needs during rewarming from torpor [118–123] or to reduce energy costs at cold T_as [26]. For example, tree-roosting long-eared bats (*Nyctophilus* spp.) frequently roost under exfoliating bark and in particular on the northern facing side of the tree, which receives more sun than the south side in the southern hemisphere [124]. The roosting site, therefore receives sunlight throughout the day and warms up considerably, allowing bats to passively increase their T_b (Fig. 2b). Indeed, throughout winter the T_b of long-eared bats was found to fluctuate daily between 10–20 °C while remaining torpid. Passive rewarming also allowed bats to save energy on days when they rewarmed to a normothermic T_b [124]. The benefits of basking has also been shown in small marsupials, where in the field it was confirmed that they are able to move at very low T_b (as low as 14.6 °C) to a basking site to further rewarm in the sun [125–127]. The energetic savings of passive rewarming have been confirmed for bats, marsupials, and primates and arousal costs are decreased by up to 66 % in comparison to active arousals [97, 120, 128]. Basking also plays a role in the thermoregulation of large mammals as indicated by the finding of radiant heat-assisted rewarming during winter in a large mammal, the Alpine ibex (*Capra ibex ibex*) [26]. Furthermore, depending on the insulative properties of their resting sites, tropical hibernators, such as tenrecs or lemurs (Fig. 2d), may even undergo long-term hibernation in which their T_b passively tracks T_a, leading to strong daily fluctuations of T_b at a low metabolic cost [52, 55, 64, 97, 129]. The potential for energy and water savings accrued by basking is therefore an important component to energy budgets in species exposed to high T_as or to radiant heat.

For hibernating species the extent of torpor use can also be dependent on body condition or quantity of available food stores [102, 130]. For example, in southern African hedgehogs (*Atelerix frontalis*) and mouse lemurs, only heavy individuals will undergo hibernation during the winter period, whereas individuals with a lower body mass will only use shorter bouts of torpor [98, 131, 132]. Similarly, throughout summer when T_a is mild and insects are abundant, individuals of the Australian subtropical/tropical insectivorous Eastern long-eared bat (*Nyctophilus bifax*) employ more torpor if they are in better body condition in comparison to individuals in poorer body condition [133]. The authors hypothesized that by using torpor bats can reduce their need to forage, hence reducing their exposure to predators [133]. Importantly, individuals in better body condition can continue to employ torpor and save fat reserves, whereas those in

poorer body condition likely need to forage extensively to meet their daily energy requirements [132, 133]. But factors other than energy expenditure, such as low water availability (see above) or the reproductive status of an individual can also influence torpor use. While some species abandon torpor use during pregnancy and lactation [63, 138, 139], others will continue to use torpor to save energy during inclement conditions and even to delay parturition until a more favourable time [107, 140, 141].

When attempting to model how a species will respond to changes in climate, it is important to have an understanding of how often, and for how long, they will be able to employ torpor. For a species with readily predictable torpor bout lengths and hibernation seasons of a set length, such as the Holarctic ground squirrels (family Sciuridae, tribe Marmotini, [142]), this would often cover the winter months only (eg. [143]), although this may also change based on latitude or local climate conditions [144, 145]. Such obligate hibernators, must undergo significant pre-hibernation fattening before entering into torpor [30, 105, 146, 147]. However, many species are able to enter torpor opportunistically throughout the whole year, depending on environmental conditions, and therefore, as we will discuss below, their energetic budget can be difficult to predict [133, 148–152]. Further, recent studies have indicated that torpor use increases in response to unpredictable climatic conditions, such as droughts, fires or storms [51, 110, 153, 154].

Variability in T_b, and therefore in energy usage, at both the inter- and intra-specific level poses a complication for predictive models. If an animal increases its $T_{b,}$ rather than shouldering the costs of increased T_a through energetically costly means of defending a set $T_{b,}$ some of the costs of rising T_a may be overestimated. Conversely, in an animal attempting to reduce energy and water usage through torpor, higher T_a can reduce potential savings [64, 155]. In contrast to species that use torpor opportunistically, strict hibernators that are less flexible in their physiological response are likely to face negative consequences when surface temperatures rise. Recent studies have indicated that warmer winter temperatures lead to more frequent arousals during hibernation periods [155–157], imposing the risk for small seasonal hibernators to deplete fat reserves before the end of hibernation [158]. Therefore, to be able to accurately predict mammalian responses to climate change, we need to incorporate a level of predictability in heterothermic responses.

To quantify the prevalence of predictability, or unpredictability, in torpor usage within a species, we coded all of the species found in Table 1 of Ruf and Geiser's [29] recent review of mammalian heterotherms as one of three categories (Fig. 3). The first category, 'predictable', was used to classify species which only employed torpor (either via daily heterothermy or hibernation) in response to seasonal shortages of food or water, or cold temperatures. Species which were shown to employ torpor in a highly variable manner or regardless of time of year or season were classed as 'unpredictable'. Finally, species where all the measurements of T_b were from a single season, or predominantly collected in the laboratory, were classed as 'data deficient'. To date, most species that have been demonstrated to use torpor opportunistically inhabit warmer and more unpredictable habitats (Fig. 3a) [72, 159]. This finding, might be due to the fact that many temperate or arctic species have been only studied in the laboratory or exclusively during the winter season, and the predictability of torpor use for many temperate/arctic species is therefore unknown. Interestingly, a slightly higher proportion of daily heterotherms were unpredictable (57 % versus 46 % for hibernators) but a combined total of 31 % of the species were found to be data deficient. This latter finding indicates the need for further studies on free-ranging animals, which was also one of the results of a large comparison of two heterothermy metrics by Boyles et al. [10]. One of the metrics from that study, the thermoregulatory scope, necessitated only a mean normothermic T_b and a minimum torpid T_b, whereas the second, the heterothermy index, required continuous T_b traces. The former had over ten times the number of species (or measures from different species) than the latter, although the authors admit to only being able to obtain a subset of available T_b datasets. The amount of data we have on heterothermy in mammals is heavily skewed towards laboratory data, which often underestimates torpor use [160]. A large number of the 'data deficient' species were also found at the lower latitudes. This is not surprising, however, because, our knowledge of the physiology of tropical and sub-tropical mammals lags far behind that of temperate species [52, 59, 64].

Conclusions: T_b variability, heterothermy, and modelling

Studies on the T_b patterns and thermoregulation of free-ranging animals have illustrated the effects, and sometimes confounding influences, of a number of factors including predation risk [150], presence of conspecifics [145], food availability [130, 161], competition [162] and extreme events [50, 51, 153, 163] on T_b. Yet, robust predictions of responses to climate change require an in-depth understanding of how animals exist in the wild [4, 8]. The level of unpredictability in terms of T_b control in mammals can make predictions more complicated, but not impossible. However, if we are to improve our ability to predict potential responses of mammals to a changing global climate, we need to improve our understanding of endothermic physiology. Large-scale

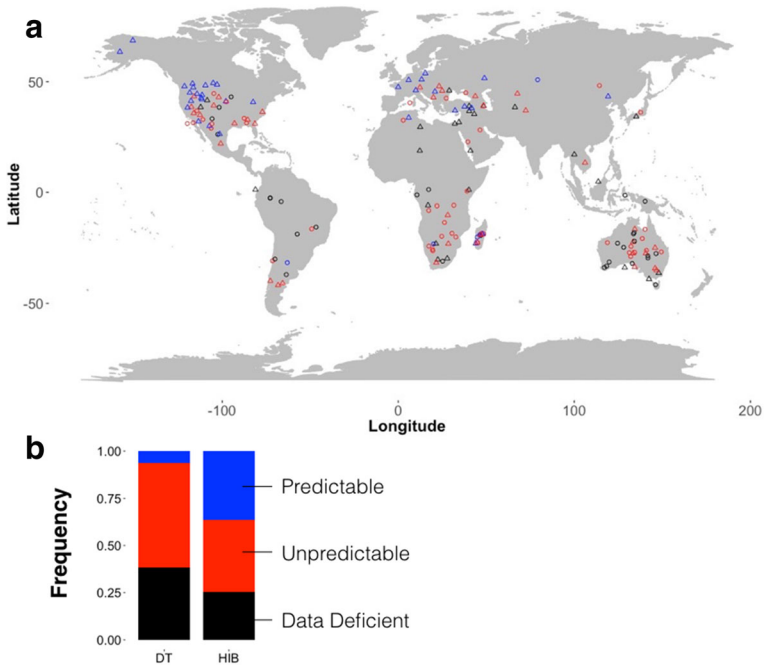

Fig. 3 a A distribution map of the daily heterotherms (DT, circles) and hibernators (HIB, triangles) reviewed in Ruf and Geiser [29]. Latitudes were taken from Table 1 of [29], longitudes from the PanTHERIA database [165], representing the mid-point of the species' range. Heterotherms with strictly seasonal, predictable torpor patterns are depicted in blue, those with unpredictable or spontaneous torpor use are marked in red and those that are data deficient (see text) in black. **b** Frequency distribution of each classification within daily heterotherms and hibernators

predictive models assessing the physiology of endotherms in relation to climate, and therefore their potential to be resilient (or not) in the face of global climate change have lagged behind the literature on ectotherms largely due to this fact. In particular, the lack of data on upper critical limits of the TNZ in mammals, or of thermal tolerance more broadly, as well as how these relate to free-ranging populations, severely hinders our current ability to build accurate models. The comprehensive study of responses to high T_a, both in the laboratory and the field is of pressing importance. Similarly, as extreme events and variability in T_a are expected to increase in the coming decades [35, 164], more effort should be placed on quantifying the level of plasticity in a species response to environmental conditions [72]. To be able to include thermolability into predictive models we must first understand it. We believe that three steps are necessary to achieve this: 1) the level of T_b variability, and its predictability, must be quantified in a range of species; 2) the energy and water costs of strict homeothermy versus any level of variability must be determined; and 3) the potential for variability must be modelled to provide predictions under both low and high variability scenarios. As has been mentioned previously, a first step would be to look to the ectotherm literature, where a large body of work has evaluated the costs and benefits to changing both the level (mean T_b) and the precision (variability) [7, 10, 11], but we need to ensure that we include a variety of species representing different habitats, evolutionary histories, and life-histories. Conceptual and predictive models taking into account the potential for variability, and phenotypic plasticity, will certainly prove to be more robust, and will provide a greater means of understanding endothermic physiology in the face of changing climates.

Abbreviations

T_a: Ambient temperature; T_b: Core body temperature; TNZ: Thermoneutral zone

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Availability of data and material

Data available from the authors on request.

Authors' contributions

DLL conceived the initial idea for the paper. All authors developed, wrote and edited the manuscript, and coded the data. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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