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Saving energy via short and shallow torpor bouts

Julia Nowack [a,b,*], Nomakwezi Mzilikazi [c], Kathrin H. Dausmann [b]

[a] School of Biological and Environmental Sciences, Liverpool John Moores University, Byrom Street, Liverpool, United Kingdom
[b] Department of Biology, Institute of Cell and Systems Biology of Animals, Functional Ecology, University Hamburg, Hamburg, Germany
[c] Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa

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ABSTRACT

Maintaining a high and stable body temperature as observed in most endothermic mammals and birds is energetically costly and many heterothermic species reduce their metabolic demands during energetic bottlenecks through the use of torpor. With the increasing number of heterotherms revealed in a diversity of habitats, it becomes apparent that triggers and patterns of torpor use are more variable than previously thought. Here, we report the previously overlooked use of, shallow rest-time torpor (body temperature >30 °C) in African lesser bushbabies, *Galago moholi*. Body core temperature of three adult male bushbabies recorded over five months showed a clear bimodal distribution with an average active modal temperature of 39.2 °C and a resting modal body temperature of 36.7 °C. Shallow torpor was observed in two out of three males ($n = 29$ torpor bouts) between June and August (austral winter), with body temperatures dropping to an overall minimum of 30.7 °C and calculated energy savings of up to 10%. We suggest that shallow torpor may be an ecologically important, yet mostly overlooked energy-saving strategy employed by heterothermic mammals. Our data emphasise that torpor threshold temperatures need to be used with care if we aim to fully understand the level of physiological plasticity displayed by heterothermic species.

1. Introduction

The regulation of a stable body temperature (T_b) is generally thought of as a key characteristic of endothermic animals. But not all endothermic species maintain homeothermy throughout their life and so-called heterothermic species can abandon regulation of T_b on a constant level, enabling them to save energy and water, via the use of torpor (Geiser, 2004; Heldmaier et al., 2004). Historically, two distinct types of heterothermic responses were differentiated: daily torpor, a moderate reduction of metabolic rate for less than 24 h, and hibernation, i.e. long phases of reduced metabolic rate and a T_b often reflecting ambient temperature (T_a). Hibernation usually lasts up to several weeks or even months, and torpor bouts are usually interspersed by regular, short periodic arousals (Ruf and Geiser, 2015). Although subject to an ongoing debate, it is widely assumed that daily heterotherms and hibernators represent two distinct adaptations to energetic bottlenecks (Ruf and Geiser, 2015), with daily torpor currently seen as the more ancient form (Lovegrove, 2012; Ruf and Geiser, 2015).

However, with the recent advances in biologging techniques and the subsequent increase in the availability of long-term datasets from free-ranging animals from various regions of the world and a diversity of habitats, we begin to see that physiological responses of heterotherms to challenging ambient conditions are more flexible than previously thought. The use of heterothermy can vary between individuals of one population or between populations of one species (e.g. Kobbe et al., 2011). There is growing evidence that individuals may adjust their expression of torpor in relation to environmental conditions (Reher et al., 2022a), and intermediate expressions of torpor are prevalent (Dausmann et al., 2020; Nowack et al., 2020). Several hibernating species can also employ short opportunistic bouts of torpor with T_b patterns similar to daily torpor found in daily heterotherms (Levesque et al., 2016). Furthermore, prolonged torpor, i.e. an intermediate form of torpor lasting over several days, has been recognised as opportunistic energy and water-saving option for hibernators in comparison to the often static months-long hibernation (Boyles et al., 2017).

Notably, most of these discoveries have been made on heterothermic species from warm tropical or arid habitats, for which torpor patterns and triggers generally seem to be more flexible than previously known (Levesque et al., 2016; Nowack et al., 2015; Stawski et al., 2015). This may have implications for the way we define torpor. Current definitions

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* Corresponding author. School of Biological and Environmental Sciences, Liverpool John Moores University, Byrom Street, Liverpool, United Kingdom.
E-mail address: j.nowack@ljmu.ac.uk (J. Nowack).

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are often based on the historic view of torpor as a winter-survival mechanism by animals living in cold and highly seasonal habitats with a clearly visible and pronounced reduction in metabolic rate and T_b. Furthermore, most studies use a more or less arbitrary threshold based on a cut-off temperature and a minimum duration of metabolic depression to differentiate between normothermic resting and torpor use (e.g. Brigham, 1992; Christian and Geiser, 2007; Nowack et al., 2010). By focusing on those thresholds, we may risk overlooking ecologically important energy- and water-saving strategies, such as the recently discovered micro-torpor bouts (<20 min) of a Malagasy bat species (Reher et al., 2018) that would not have been detected under many of the commonly used torpor definitions. In addition to such variation in torpor duration, we can also assume torpor depth to vary as non-Holarctic species in arid, tropical or subtropical habitats are often subject to higher daily minimum temperatures than their temperate and arctic counterparts.

The African lesser bushbaby, *Galago moholi*, is a small, nocturnal primate exposed to high seasonal variations in temperature, water, and food availability in its natural habitat. While the species is able to undergo torpor ($T_b < 30$ °C) in response to adverse environmental conditions, deep torpor seems to be only used by a fraction of the population as a last-resort strategy (Nowack et al., 2010, 2013a, 2013b). We present data of shallow T_b reductions ($T_b > 30$ °C) in the African lesser bushbaby and discuss whether shallow reductions in T_b should be considered as torpor-like energy savings strategies in mammals.

2. Methods

2.1. Ethics

Animals were captured under permit no. CPM-002-00003, issued by the Department of Economic Development, Environment and Tourism, Limpopo Province/South Africa. All procedures complied with the "Principles for Animal Care", publication no. 86–23, revised 1986 (National Institute of Health) and the "Code of Ethics for Animal Experimentation" manual adopted by the Nelson Mandela Metropolitan University (Animal Ethics Clearance No. A09-SCI-ZOO-001).

2.2. Capture and data collection

The African lesser bushbaby, *G. moholi*, is a small nocturnal primate (adult weight~170–200 g) distributed throughout Southern Africa. We measured core T_b of African lesser bushbabies over the cold-dry period in Nylsvley Nature Reserve in South Africa (S 24.6548, E 28.691). In autumn 2010 and 2011, a total of six animals (5 males, 1 female) were captured with self-built walk-in live traps baited with bananas, honey and peanut butter and implanted with temperature loggers (3 g, thermochron iButtons/DS1922, Dallas Semiconductor, USA; coated in Elvax; sample frequency every 30 min; calibrated in a water bath). Loggers were implanted into the peritoneal cavity under inhalation anaesthesia (isoflurane in oxygen; induction and maintenance 2%; flow rate ca. 0.5 L*min^{-1}) and individuals released at the capture site after recovery. Details about surgical procedures can be found in Nowack et al. (2013a). Loggers were programmed to start recording 1 week after the surgery. Three adult males (all >180 g) were recaptured, and the data loggers were explanted following the same protocol as described above (logger resolution set to 0.5 °C for longer recording time for two individuals and to 0.0625 °C for one individual). The three retrieved data sets span from March to August 2010 (n = 148 days), March to June 2010 (n = 86 days) and April to August 2011 (n = 129 days). These data sets have already been part of the data reported in Nowack et al. (2013a) but were previously only analysed in the context of daily torpor defined as $T_b < 30$ °C for more than 2 h.

Ambient temperature (T_a) within the individuals' home ranges was recorded every 30–60 min at ca. 1.5–2 m height on the shady side of a tree (Hygrochron Ibutton/DS1923, Dallas Semiconductor, USA; resolution 0.0625 °C). Temperature data (minimum/maximum T_a) for time spans between field seasons (in this case mid-June to early July 2010) as well as data on rainfall were provided by the local weather station at Nylsvley Nature Reserve.

2.3. Data analysis

We calculated the mean minimum, mean maximum and modal T_b, as well as daily amplitude of T_b (i.e. the amplitude between daily minimum and maximum T_b), for each individual and month. Plotting the T_b frequency distribution for each individual, we found a bi-modal distribution of T_b for all individuals, with one peak during the resting period ('resting modal T_b') and one peak during the activity period ('active modal T_b'). We also calculated the monthly heterothermy index (HI), as a measure of T_b variability, based on the daily HI for each individual to quantify the amount of variation around the modal T_b (Boyles et al., 2011b):

$$HI = \sqrt{\frac{\Sigma(\text{Tbmodal} - \text{individualTb\_i})^2}{n-1}}$$

using the individual active modal T_b ($T_b$modal) and the minimum T_b recorded for each day (individual $T_{b_}$i) as well as the number of available T_b records per individual (n).

To differentiate between normothermic resting and shallow torpor bouts, we used the resting modal T_b for each individual to define individual normothermic resting T_b. We then focussed on the occurrence of T_b below the individual modal resting T_b, including occurrence, duration and timing, although the latter was only calculated for significant reductions in T_b that were lower than 2 °C below individual resting modal T_b (see results). Duration of bouts was calculated from when T_b dropped below/increased above the individual modal T_b.

To estimate the energetic significance of T_b reductions we calculated metabolic rates based on the continuous measurements of T_b and T_a for the respective day (following Cooper and Withers, 2004) using the following equation:

$$\Delta T_b = 20.1[MR_{calc} – C(T_b – T_a)]/(mb.SH)$$

whereby MR_{calc} is calculated as ml O_2 min^{-1}. ΔT_b is the differential between T_b readings (°C min^{-1}; calculated from subsequent readings every 30 min), at a certain T_a (°C), *C* is the thermal conductance (ml $O_2{}^\circ C^{-1}$ min^{-1}; 0.07 ml O_2 $^\circ C^{-1}$ g^{-1} h^{-1} for male bushbabies (Knox and Wright, 1989)), *mb* is the body mass of the respective individual (180 g), *SH* is the specific heat of animal tissues (3.47 $Jg^{-1}{}^\circ C^{-1}$) and the consumption of 1 ml O_2 is assumed to account for 20.1 J.

2.4. Statistical analysis

Statistical analysis was conducted in R (R Core Team, 2022). We tested whether variations in minimum T_b and daily amplitude were correlated with T_a by running linear mixed effect models corrected for individual ID to account for repeated measures (*lme* in library 'nlme' (Pinheiro et al., 2020)). Normal distribution of residuals was checked visually and by using Shapiro–Wilk tests and non-normally distributed data were boxcox transformed before carrying out the analysis. Influence of T_a on torpor use (yes/no) was tested via a binomial model (*glm* in library 'lme4' (Bates et al., 2014)). Rayleigh tests were used to determine whether circular data (timing of torpor entry and arousal) differed significantly from random distribution (*rayleigh.test* in library 'circular' (Agostinelli and Lund, 2017)).

3. Results

3.1. Ambient conditions

The study period was characterised by pronounced seasonal changes in T_a, with temperature decreasing from March to August and sub-zero night temperatures in June–August 2010 (lowest nightly T_a -3.4 °C in August) and May–August 2011 (lowest nightly T_a -5.1 °C in June) (Table 1). Amplitude between the daily minimum and maximum T_a regularly reached >20 °C, with a maximum daily amplitude of 30.5 °C in August 2010 and 31.3 °C in July 2011. June to August had little to no rainfall in both years (2010: 0 mm; 2011: 0.3 mm in June and 97 mm on one day in August). 2010 and 2011 received 604.3 mm and 504.5 mm of rain before the start of the dry winter months, respectively, but rainfall in the year preceding the data recordings, i.e. 2009, was with 1107.3 mm higher than usual (see Table 2).

3.2. Circadian rhythm and T_a dependency of body temperature

Bushbabies displayed a circadian rhythm in T_b with the highest values during the active period at night and lower values during the diurnal resting phase (Fig. 1). This was reflected in a bimodal distribution, with a modal T_b of 39.2 °C during the active phase and a modal T_b for the resting phase of 36.7 °C, i.e. a 2.5 °C difference between resting and active T_b (Fig. 1, N = 3, n = 509 days). Individual resting modal T_b varied only slightly between the three males (36.7 °C, 36.7 °C and 36.9 °C), while active modal T_b showed more variability ranging from 38.7 to 39.2 °C.

Core T_b of the three study individuals never dropped below 30 °C (Fig. 2), but minimum T_b and daily T_b amplitude were correlated with minimum T_a (amplitude: $F_{1,361} = 176.4$, $p < 0.001$; minimum T_b: $F_{1,361} = 165.8$, $p < 0.001$). Mean daily T_b maxima were relatively stable and varied by only 1.5 °C from 38.7 to 40.2 °C between March and August, with the highest mean maximum T_b and the lowest variability in maximum T_b recorded for July (data of both years: 39.8 ± 0.01 °C; Table 1). The lowest minimum T_bs and highest mean amplitudes were recorded in July (amplitude of 4.4 °C (in both years) versus 2.6 °C in March (only data for 2010); Fig. 3).

3.3. Shallow torpor

Body temperature frequently decreased below individual modal T_b during all months, although the extent differed between individuals (20%–51% of days per animal; N = 3, total n = 61; Fig. 2). Resting $T_b \geq$ 2 °C below modal resting T_b was only observed on 6.9 and 8.1% of days in two of the three animals. These bouts, from now on referred to as “shallow torpor” occurred only during winter (June–August of both years; also indicated by the highest average heterothermy index during those months; Tables 1 and 2) and the T_b patterns during these bouts clearly differed from normothermic resting (Fig. 3; Fig. S1 in the supplementary material). Their occurrence was significantly influenced by minimum T_a ($z = 4.3$, $p < 0.001$), i.e. employed on days with a nightly minimum T_a of <5 °C (N = 2, n = 10 and 19, Fig. 4). Notably, the dataset for the individual that displayed the most stable T_b without evidence of shallow torpor ended at the beginning of the austral winter (early June; Fig. 2b). The largest daily T_b amplitude between active and resting T_b was 9.5 °C with a minimum T_b of 30.7 °C, i.e. 6 °C below modal T_b,

Table 2

Monthly occurrence of body temperature (T_b) below modal resting T_b and shallow torpor bouts (≥2 °C below modal T_b). Data show the occurrence of T_b lower than modal (incl. torpor bouts) and the torpor bouts per month, as well as the year (superscript) and the minimum T_b during torpor. Data are pooled per month from data sets collected in 2010 and 2011. *Individuals* represent the number of individuals for which samples were recorded in a respective month. *Recording days represent* the total number of observations per month.

Month	Individuals	Recording days	Occurrence T_b below modal	Occurrence shallow torpor	Minimum T_b (°C)
March	2	28	1^{2010}	0	–
April	3	90	3^{2010}	0	–
May	3	93	8^{2010}	0	–
June	3	70	$31^{2010,2011}$	$14^{2010,2011}$	32.2
July	2	62	$27^{2010,2011}$	$12^{2010,2011}$	30.7
August	2	24	$10^{2010,2011}$	$3^{2010,2011}$	34.2

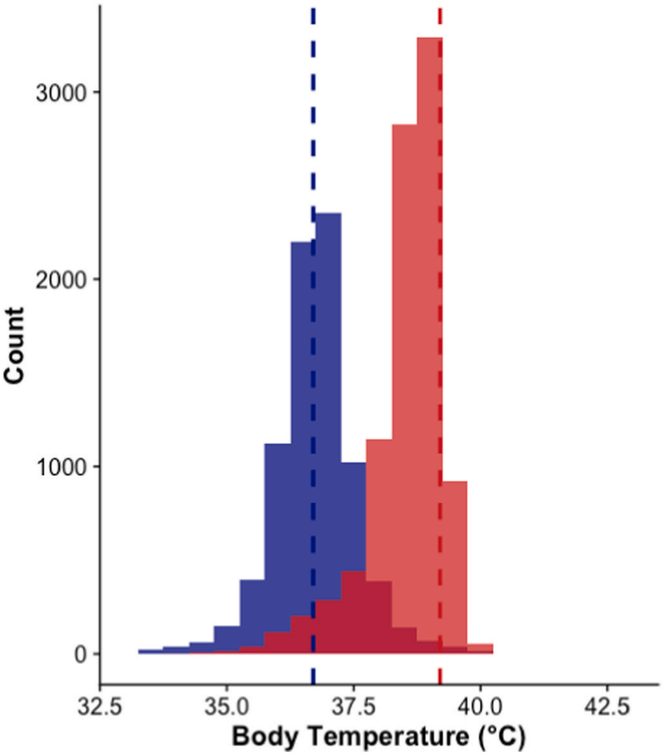

Fig. 1. Body temperature distribution of male *Galago moholi*, South Africa, over spring and winter 2010 and 2011. Body temperatures during the rest phase (day) are depicted in *blue*, body temperatures during the active phase (night) in *red*. The dashed lines represent mean modal temperatures for both distributions (N = 3, n = 509 days). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Body temperature descriptors per month (pooled per month from data sets collected in 2010 and 2011, mean data corrected for individual identity). Shown are monthly minimum ambient temperatures (T_a) for 2010/2011, mean heterothermy index and mean monthly minimum and mean maximum body temperature (T_b). *Individuals* represent the number of individuals for which samples were recorded in a respective month. *Recording days represent* the total number of observations per month.

Month	Individuals	Recording days	Minimum T_a (°C) 2010/2011	Heterothermy index	Minimum T_b (°C)	Maximum T_b (°C)
March	2	28	13.7/no data	1.26 ± 0.08	36.9 ± 0.1	39.5 ± 0.3
April	3	90	10.6/5.6	1.50 ± 0.17	36.3 ± 0.2	39.5 ± 0.2
May	3	93	4.7/-1	1.49 ± 0.22	36.2 ± 0.05	39.6 ± 0.1
June	3	70	-3.2/-5.1	1.67 ± 0.29	35.5 ± 0.3	39.7 ± 0.2
July	2	62	-2.7/-3.1	1.83 ± 0.32	35.4 ± 0.2	39.8 ± 0.01
August	2	24	-3.4/-3.8	1.85 ± 0.11	35.4 ± 0.4	39.6 ± 0.1

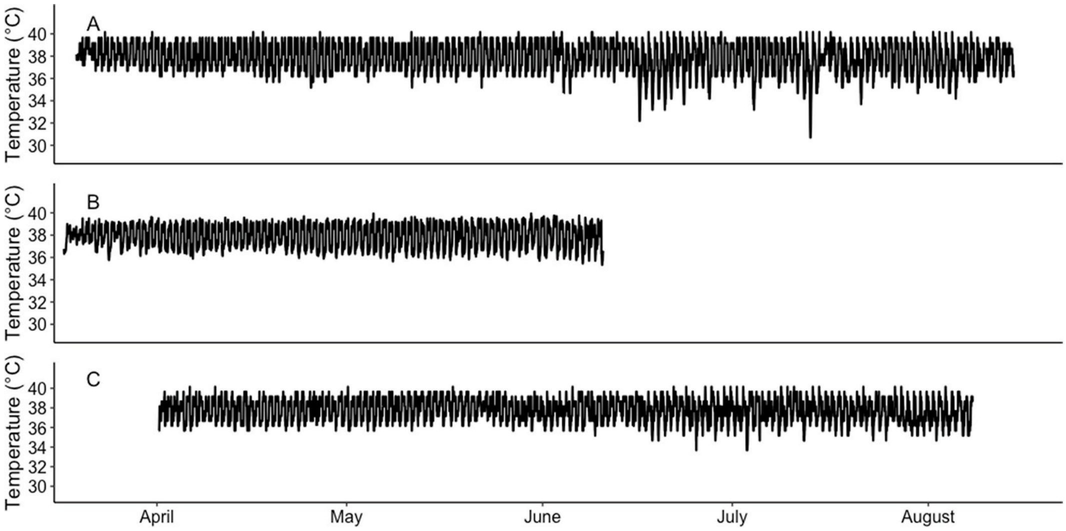

Fig. 2. Body temperature traces for three individuals of South African *Galago moholi*. Panel A and B present data from the same year (2010), whereas the animal in panel C was recorded in the following year (2011).

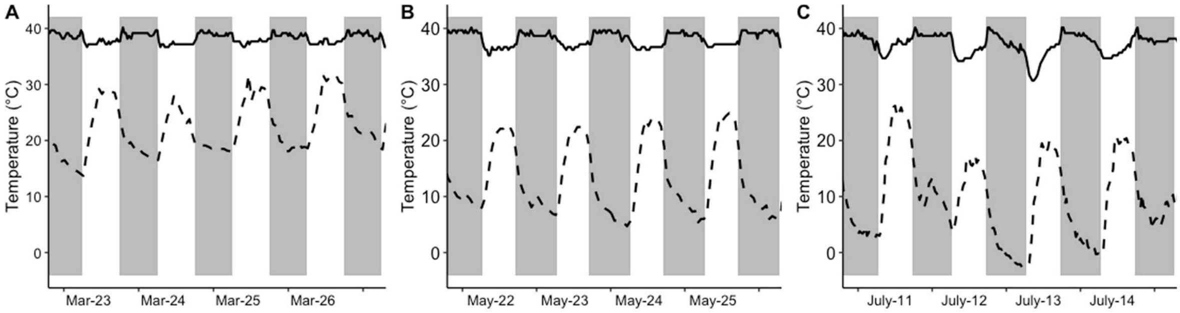

Fig. 3. Increasing daily amplitudes in body temperature over the course of the year (2010). All data stem from the same individual of *Galago moholi* from a population in South Africa. Daily amplitude was lowest in March (A) and increased in late autumn/winter (B). Panel (C) shows shallow torpor on 4 days. Body temperature was ≥2 °C below the modal body temperature of 36.7 °C and bouts clearly differ in visual appearance, i.e. a continuous drop in body temperature versus the plateau in resting body temperature in panel A and B. The *black line* shows body temperature and the *dashed line* ambient temperature; *Grey* and *white* areas indicate photoperiod (*grey:night; white:day*).

recorded in July 2010 (T_a range: 2.7 to 19.9 °C).

Shallow torpor bouts were always entered in the early morning and the timing of torpor entry (T_b below modal T_b) differed significantly from a random distribution (average: 0600 h; test statistic = 0.9706; $p < 0.001$). Minimum T_b was on average reached around 0813 h (test statistic = 0.9794, $p < 0.001$). Duration of bouts ranged from 2.5 to 11.5 h (mean: 6.8 h). Timing of arousal was more variable than entry into torpor and timing of minimum T_b, but the time at which T_b increased above modal resting T_b was still significantly different from a random distribution (mean: 1206 h; test statistic = 0.8422, $p < 0.001$). Body temperatures above 38 °C were usually reached at around 1700 h.

Estimated energy savings of shallow torpor bouts did not only vary with minimum T_b, but also depended on ambient conditions and duration of T_b reductions. The estimated energy saving of the drop in T_b to 30.7 °C (overall torpor bout duration: 5 a.m.- 2:30 p.m.; min T_a: 2.7 °C; max. T_a: 19.9 °C) compared to keeping a T_b of 36.7 °C for the total duration was about 10% over 9.5 h (assuming active rewarming; Fig. S2 in the supplementary material). The smaller bouts of T_b reduction of only about 2 °C below modal resting T_b accounted for estimated energy savings up to 5% (e.g. overall torpor bout duration: 6 a.m.- 3 p.m.; min T_a: 0.5 °C; max. T_a: 20.4 °C).

4. Discussion

We present data on the occurrence of shallow but pronounced reductions in resting T_b ($T_b > 30$ °C) in adult, male African bushbabies that go beyond normal circadian T_b variation and enable noteworthy levels of energy savings. We argue that these represent bouts of shallow torpor.

Interestingly, in addition to daily torpor and hibernation, the bird literature already recognises shallow reductions in T_b of 3–11 °C below active T_b as a distinct energy-saving mechanism (McKechnie and Lovegrove, 2002). These shallow drops in T_b - termed “rest-phase hypothermia” - have been found to enable energy savings of up to 50% (Cooper and Gessaman, 2005) and can thus enhance winter survival of small birds, which are particularly vulnerable to unfavourable temperatures and low food availability (Brodin et al., 2017). Despite their ecological importance, these shallow reductions in T_b are commonly ignored in mammalian studies (but see Canale et al., 2012).

Our data suggest that a decrease in T_b to 6 °C below modal T_b as seen in bushbabies in this study can lead to energy savings of at least 10% compared to remaining normothermic. The estimated energy savings include the costs of rewarming, and energy savings may be further increased through the use of passive rewarming (Geiser et al., 2004). As individuals entered torpor at the start of the rest phase and aroused around midday, individuals would be able to use the increase in daytime temperatures for passive rewarming as observed in other species (Geiser et al., 2004); the timing of entry and arousal from shallow torpor was similar to the temporal organisation described for deeper torpor bouts in other nocturnal daily heterotherms (Körtner and Geiser, 2000).

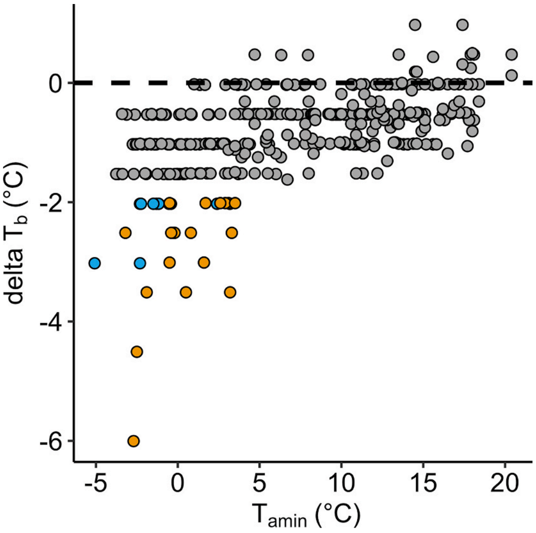

Fig. 4. Temperature dependency of torpor use. The difference between minimum and modal body temperature (delta T_b) during resting in relation to minimum ambient temperature (T_{amin}) for all three individuals of *Galago moholi.* Data were recorded in 2010 and 2011 in South Africa. Delta T_b values $\geq$ -2 °C are colour-coded to represent the two different individuals and are negatively correlated with ambient temperature (see text); delta T_b of the third individual never exceeded -2 °C. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

While *Galago moholi* is able to undergo torpor in response to adverse environmental conditions, individuals only use deep torpor ($T_b < 30$ °C) as a last resort strategy (Nowack et al., 2010, 2013a, 2013b). The lack of regular torpor use in this species has always been surprising, given their comparatively small body size and challenging environment, especially as most other species capable of torpor use do so regularly (Dausmann et al., 2023; Nowack and Turbill, 2022). Behavioural observations suggest that individuals rely on behavioural and ecological adaptations, such as the use of nesting sites with warmer microclimates (tree hollows or nests) and a shift in diet as an alternative to the use of torpor (Nowack et al., 2013b).

The two adult males that used shallow torpor in this study were in good body condition (~180 g) and never used deep torpor with $T_b <$ 30 °C during the time of the study. The use of torpor bouts with a T_b below 30 °C was so far only observed in younger and leaner individuals of the population (Nowack et al., 2013a) and it is not known whether individuals that use deep torpor also enter shallow bouts of torpor, although this seems likely. Shallow torpor seems to be primarily entered in the early morning, whereas entry into deep torpor in *G. moholi* usually already occurs during the active phase at night (Nowack et al., 2013a). This further supports the idea of deep torpor use as a last resort strategy by animals in poor condition and on especially cold nights with low insect availability, when animals terminate foraging activity and instead enter emergency torpor (Nowack et al., 2013a), whereas shallow torpor is used to enhance energy budgeting during the regular rest phases. Nevertheless, shallow torpor was found to be correlated to daily minimum T_a and only observed when temperatures dropped below 5 °C, indicating that even shallow torpor is triggered by increased energy expenditure or lower insect availability during colder nights. Our data are also in line with studies showing that individuals in good body condition or a surplus of food undergo shallower or shorter bouts of torpor (Ruf et al., 1991). Furthermore, edible dormice (*Glis glis*) in good body condition regulate their T_b at a higher level during hibernation and spend more time euthermic (Bieber et al., 2014), male golden hamsters (*Mesocricetus auratus*) undergo shallower bouts when food-supplemented (Siutz et al., 2018) and Djungarian hamsters (*Phodopus sungorus*) avoid the use of deep torpor when food deprived by choosing warmer microclimates (Wojciechowski and Jefimow, 2006). Importantly, although the level of energy saving is not as pronounced as during deeper torpor, shallow reductions of metabolism may allow energy savings without having to deal with the apparent costs associated with deeper torpor bouts and a markedly lowered T_b.

We have previously argued that one reason for the rare use of torpor in adult bushbabies could be the priority of reproduction as bushbabies mate in autumn and are pregnant over the winter period (Nowack et al., 2010). Reproduction and torpor use seem to be mutually exclusive in many species (but see McAllan and Geiser, 2014) as foetal development is slowed at lower T_b and spermatogenesis is assumed to halt (Fietz et al., 2004). In addition to reproductive constraints, torpor use is also associated with costs on a cellular level such as telomere attrition caused by high metabolic rate during rewarming (if passive rewarming from low temperatures is not feasible (Hoelzl et al., 2016; Nowack et al., 2019)), reduced immune function (Prendergast et al., 2002), as well as reduced perception and locomotion abilities (Nowack et al., 2016; Rojas et al., 2012), making individuals more susceptible to predation (please see Carey et al. (2003) for a comparative overview of the costs of torpor). However, the relationship between torpor depth and body condition seems to vary between species. Studies on mouse lemurs report that heavier individuals undergo deeper torpor than smaller or leaner individuals (Vuarin et al., 2013), which may help individuals to maintain their body mass during lean periods.

Humphries et al. (2003) have suggested that the trade-off between energetic benefits and ecological and physiological costs of torpor should entail optimisation of torpor use and that the optimal response may be context-depending. Individuals should increase torpor use and depth to maximise energy reserves, i.e. to enhance body condition for reproduction or migration, but should reduce the frequency duration or depth of torpor when the costs exceed the benefits, such as when excess energy reserves are available. Individual differences in torpor use are generally found to be shaped by a variety of factors, such as reproductive stage (Grinevitch et al., 1995), life history (age: e.g. Bieber and Ruf, 2012), roost type (e.g. Reher et al., 2022a), body condition (e.g. Faherty et al., 2017), or consistent differences in behaviour (e.g. Jonasson and Willis, 2012). Furthermore, in addition to energetic benefits, there are a number of other functions of torpor, such as water conservation (Geiser and Brigham, 2012; Nowack et al., 2017; Reher et al., 2022b), which may explain variability in torpor use. Crucially, such phenotypic plasticity will likely be of importance when it comes to survival under variable and changing environmental conditions (Canale and Henry, 2010).

As shown above, small drops in T_b may be physiologically and ecologically important but they are difficult to distinguish from normothermic reductions in T_b – especially when T_a is high - and using a cut-off temperature to differentiate between normothermia and torpor often leads to the omission of shallower bouts of torpor. This is a well-recognised problem (e.g. Barclay et al., 2001; Boyles et al., 2011a; Fjelldal et al., 2023; Lovegrove and Smith, 2003; McKechnie et al., 2007) and although the use of a clear cut-off also has its merits (e.g. Brigham et al., 2011) the limitations of using arbitrary thresholds are severe and may hinder our understanding of heterothermy in endotherms.

Most mammals and birds show a daily amplitude in T_b corresponding to their activity phase, which is associated with a moderate decrease in metabolic rate (Aschoff, 1981). While this amplitude is rarely visible and energy savings are minimal under constant laboratory conditions, free-ranging small mammals can show a marked difference between active and resting T_b during winter (Cooper and Withers, 2004; Dausmann et al., 2023). Tattersall (2012) found that circadian changes in metabolic rate during diurnal resting in pygmy marmosets (*Cebulla pygmae*) are more pronounced than what can be expected from changes in activity alone, highlighting that circadian changes in T_b and metabolic rate can also be important energy saving strategies for small mammals and some authors have suggested the existence of an energy-saving continuum (Boyles et al., 2011b; McKechnie and

Lovegrove, 2002). Data from non-Holarctic species have indeed shown that energy-saving options are more variable than previously thought and that intermediate states are possible (Nowack et al., 2020). Notably, torpor can also be employed when individuals are within or above their thermoneutral zone and characterised by metabolic depression with only a small -or even without - a decrease in T_b (Grimpo et al., 2013; Reher and Dausmann, 2021; Song et al., 1997). This emphasizes the need to carefully evaluate the use of threshold temperatures.

5. Conclusion

We report the use of shallow torpor to cope with low food availability and cold environmental conditions during the austral winter by male, adult bushbabies in good body condition. Importantly, the use of shallow torpor with $T_b > 30$ °C allows notable energy savings. Our study further emphasizes that torpor threshold temperatures need to be used with care if we aim to fully understand the level of physiological plasticity displayed by heterothermic species.

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Author contributions

JN, KD and NM designed the study, JN collected and analysed the data and wrote the manuscript, and all authors commented on the draft and have seen and approved the final version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data required to reproduce the above findings are available to download from: 10.6084/m9.figshare.22707850.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103572.

References

Agostinelli, C., Lund, U., 2017. R Package 'circular': Circular Statistics (Version 0.4-93).

Aschoff, J., 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. Comp. Biochem. Physiol. Physiol. 69, 611–619.

Barclay, R.M., Lausen, C.L., Hollis, L., 2001. What's hot and what's not: defining torpor in free-ranging birds and mammals. Can. J. Zool. 79, 1885–1890.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1, pp. 1–7.

Bieber, C., Lebl, K., Stalder, G., Geiser, F., Ruf, T., 2014. Body mass dependent use of hibernation: why not prolong the active season, if they can? Funct. Ecol. 28, 167–177.

Bieber, C., Ruf, T., 2012. Does age matter? Effects of age on hibernation patterns in edible dormice (glis glis). In: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 133–142.

Boyles, J.G., Bennett, N.C., Mohammed, O.B., Alagaili, A.N., 2017. Torpor patterns in desert hedgehogs (*Paraechinus aethiopicus*) represent another new point along a thermoregulatory continuum. Physiol. Biochem. Zool. 90, 445–452.

Boyles, J.G., Smit, B., McKechnie, A.E., 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, J.G., Smit, B., McKechnie, A.E., 2011b. A new comparative metric for estimating heterothermy in endotherms. Physiol. Biochem. Zool. 84, 115–123.

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

Brigham, R.M., Willis, C.K.R., 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.

Brodin, A., Nilsson, J.-Å., Nord, A., 2017. Adaptive temperature regulation in the little bird in winter: predictions from a stochastic dynamic programming model. Oecologia 185, 43–54.

Canale, C.I., Henry, P.Y., 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Clim. Res. 43, 135–147.

Canale, C.I., Levesque, D.L., Lovegrove, B.G., 2012. Tropical heterothermy: does the exception prove the rule or force a Re-definition? In: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 29–40.

Carey, H.V., Andrews, M.T., Martin, S.L., 2003. Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. Physiol. Rev. 83, 1153–1181.

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

Cooper, C.E., Withers, P.C., 2004. Patterns of body temperature variation and torpor in the numbat, *Myrmecobius fasciatus* (Marsupialia: myrmecobiidae). J. Therm. Biol. 29, 277–284.

Cooper, S.J., Gessaman, J.A., 2005. Nocturnal hypothermia in seasonally acclimatized mountain chickadees and juniper titmice. Condor 107, 151–155.

Dausmann, K.H., Körtner, G., Aharon-Rotman, Y., Currie, S.E., Geiser, F., 2023. Flexible employment of torpor in squirrel gliders (*Petaurus norfolcensis*): an adaptation to unpredictable climate? Physiol. Biochem. Zool. 96, 62–74.

Dausmann, K.H., Levesque, D.L., Wein, J., Nowack, J., 2020. Ambient temperature cycles affect daily torpor and hibernation patterns in malagasy tenrecs. Front. Physiol. 11, 522.

Faherty, S.L., Campbell, C.R., Hilbig, S.A., Yoder, A.D., 2017. The effect of body mass and diet composition on torpor patterns in a Malagasy primate (*Microcebus murinus*). J. Comp. Physiol. B 187, 677–688.

Fietz, J., Schlund, W., Dausmann, K.H., Regelmann, M., Heldmaier, G., 2004. Energetic constraints on sexual activity in the male edible dormouse (*Glis glis*). Oecologia 138, 202–209.

Fjelldal, M.A., Stawski, C., Sørås, R., Wright, J., 2023. Determining the different phases of torpor from skin- or body temperature data in heterotherms. J. Therm. Biol. 111, 103396.

Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu. Rev. Physiol. 66, 239–274.

Geiser, F., Brigham, R.M., 2012. The other functions of torpor. In: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World. Springer, Berlin, Heidelberg, Germany, pp. 109–121.

Geiser, F., Drury, R.L., Körtner, G., Turbill, C., Pavey, C.R., Brigham, R.M., 2004. Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes, B.M., Carey, H.V. (Eds.), *Life in the Cold: 12th International Hibernation Symposium*. University of Alaska, Fairbanks, pp. 51–62.

Grimpo, K., Legler, K., Heldmaier, G., Exner, C., 2013. That's hot: golden spiny mice display torpor even at high ambient temperatures. J. Comp. Physiol. B 183, 567–581.

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

Heldmaier, G., Ortmann, S., Elvert, R., 2004. Natural hypometabolism during hibernation and daily torpor in mammals. Respir. Physiol. Neurobiol. 141, 317–329.

Hoelzl, F., Cornils, J.S., Smith, S., Moodley, Y., Ruf, T., 2016. Telomere dynamics in free-living edible dormice (*Glis glis*): the impact of hibernation and food supply. J. Exp. Biol. 219, 2469–2474.

Humphries, Murray M., Kramer, Donald L., Thomas, Donald W., 2003. The role of energy availability in mammalian hibernation: an experimental test in free-ranging eastern chipmunks. Physiol. Biochem. Zool. 76, 180–186.

Jonasson, K.A., Willis, C.K.R., 2012. Hibernation energetics of free-ranging little brown bats. J. Exp. Biol. 215, 2141–2149.

Knox, C., Wright, P., 1989. Thermoregulation and energy metabolism in the lesser bushbaby, *Galago senegalensis moholi*. S. Afr. J. Zool. 24, 89–94.

Kobbe, S., Ganzhorn, J., Dausmann, K.H., 2011. Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 181, 165–173.

Körtner, G., Geiser, F., 2000. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. Chronobiol. Int. 17, 103–128.

Levesque, D.L., Nowack, J., Stawski, C., 2016. Modelling mammalian energetics: the heterothermy problem. Climate Change Responses 3, 7.

Lovegrove, B.G., 2012. The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. Biol. Rev. 87, 128–162.

Lovegrove, B.G., Smith, G.A., 2003. Is 'nocturnal hypothermia' a valid physiological concept in small birds? A study on Bronze Mannikins *Spermestes cucullatus*. Ibis 145, 547–557.

McAllan, B.M., Geiser, F., 2014. Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. Integr. Comp. Biol. 54, 516–532.

McKechnie, A.E., Ashdown, R.A.M., Christian, M.B., Brigham, R.M., 2007. Torpor in an African caprimulgid, the freckled nightjar *Caprimulgus tristigma*. J. Avian Biol. 38, 261–266.

McKechnie, A.E., Lovegrove, B.G., 2002. Avian facultative hypothermic responses: a review. Condor 104, 705–724.

Nowack, J., Delesalle, M., Stawski, C., Geiser, F., 2016. Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. Sci. Nat. 103, 73.

Nowack, J., Levesque, D.L., Reher, S., Dausmann, K.H., 2020. Variable climates lead to varying phenotypes: "weird" mammalian torpor and lessons from non-holarctic species. Frontiers in Ecology and Evolution 8, 60.

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

Nowack, J., Mzilikazi, N., Dausmann, K.H., 2013a. Torpor as an emergency solution in *Galago moholi*: heterothermy is triggered by different constraints. J. Comp. Physiol. B 183, 547–556.

Nowack, J., Rojas, A.D., Körtner, G., Geiser, F., 2015. Snoozing through the storm: torpor use during a natural disaster. Sci. Rep. 5, 11243.

Nowack, J., Stawski, C., Geiser, F., 2017. More functions of torpor and their roles in a changing world. J. Comp. Physiol. B 187, 889–897.

Nowack, J., Tarmann, I., Hoelzl, F., Smith, S., Giroud, S., Ruf, T., 2019. Always a price to pay: hibernation at low temperatures comes with a trade-off between energy savings and telomere damage. Biol. Lett. 15, 20190466.

Nowack, J., Turbill, C., 2022. Survivable hypothermia or torpor in a wild-living rat: rare insights broaden our understanding of endothermic physiology. J. Comp. Physiol. B 192, 183–192.

Nowack, J., Wippich, M., Mzilikazi, N., Dausmann, K.H., 2013b. Surviving the cold, dry period in Africa: behavioral adjustments as an alternative to heterothermy in *Galago moholi*. Int. J. Primatol. 34, 49–64.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. Nlme: Linear and Nonlinear Mixed Effects Models.

Prendergast, B.J., Freeman, D.A., Zucker, I., Nelson, R.J.N., 2002. Periodic arousal from hibernation is necessary for initiation of immune responses in ground squirrels. Am. J. Physiol. Regul. Integr. Comp. Physiol. 282, R1054–R1062.

Reher, S., Dausmann, K.H., 2021. Tropical bats counter heat by combining torpor with adaptive hyperthermia. Proc. Biol. Sci. 288, 20202059.

Reher, S., Ehlers, J., Rabarison, H., Dausmann, K.H., 2018. Short and hyperthermic torpor responses in the Malagasy bat *Macronycteris commersoni* reveal a broader hypometabolic scope in heterotherms. J. Comp. Physiol. B 188 (6), 1015–1027.

Reher, S., Rabarison, H., Montero, B.K., Turner, J.M., Dausmann, K.H., 2022a. Disparate roost sites drive intraspecific physiological variation in a Malagasy bat. Oecologia 198, 35–52.

Reher, S., Rabarison, H., Nowack, J., Dausmann, K.H., 2022b. Limited physiological compensation in response to an acute microclimate change in a Malagasy bat. Frontiers in Ecology and Evolution 10, 779381.

Rojas, A.D., Körtner, G., Geiser, F., 2012. Cool running: locomotor performance at low body temperature in mammals. Biol. Lett. 8, 868–870.

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

Ruf, T., Klingenspor, M., Preis, H., Heldmaier, G., 1991. Daily torpor in the Djungarian hamster (*Phodopus sungorus*): interactions with food intake, activity, and social behaviour. J. Comp. Physiol. B 160, 609–615.

Siutz, C., Ammann, V., Millesi, E., 2018. Shallow torpor expression in free-ranging common hamsters with and without food supplements. Frontiers in Ecology and Evolution 6, 190.

Song, X., Körtner, G., Geiser, F., 1997. Thermal relations of metabolic rate reduction in a hibernating marsupial. Am. J. Physiol. Regul. Integr. Comp. Physiol. 273, R2097–R2104.

Stawski, C., Körtner, G., Nowack, J., Geiser, F., 2015. The importance of mammalian torpor for survival in a post-fire landscape. Biol. Lett. 11, 20150134.

Tattersall, G., 2012. Diurnal changes in metabolic rate in pygmy marmosets: implications for sleep, torpor, and basal metabolism in primates. In: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World. Springer Verlag, Berlin Heidelberg, pp. 471–480.

Team, R.C., 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Vuarin, P., Dammhahn, M., Henry, P.-Y., 2013. Individual flexibility in energy saving: body size and condition constrain torpor use. Funct. Ecol. 27, 793–799.

Wojciechowski, M.S., Jefimow, M., 2006. Is torpor only an advantage? Effect of thermal environment on torpor use in the Siberian hamsters (*Phodopus sungorus*). J. Physiol. Pharmacol. 57 (Suppl. 8), 83–92.