



Body temperature variation in free-living and food-deprived yellow-necked mice sustains an adaptive framework for endothermic thermoregulation

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Abstract

In many mammalian species, variation in body temperature (T_b) exceeds the values suitable for defining homeothermy, making it justifiable and even necessary to resort to the term “heterothermic”. However, T_b data are only available for ca. 1% of extant mammalian species. We investigated variations in T_b in wild free-living and experimentally food-deprived yellow-necked mice *Apodemus flavicollis*, during the temperate-zone autumn-winter period. In line with the adaptive framework for endothermic thermoregulation, we hypothesised that T_b in the mice should be adjustable with the energetic cost-benefit trade-off associated with maintaining homeothermy. In laboratory conditions, mice clearly entered a state of daily torpor when food-deprived. Our study thus makes it clear that *A. flavicollis* is a heterothermic species in which food deprivation results in switching between endothermic and poikilothermic thermoregulation. We also assumed that, in free-living mice, heterothermy increases with elevated environmental challenges, e.g. when the ambient temperature (T_a) decreases. Consistent with this was the inverse correlation noted between variation in T_b in free-living mice and T_a , with most individuals clearly becoming torpid when T_a decreases below 0 °C. It is the increased cost of food hoarding under cold conditions that most likely triggers a state of torpor as a last result. Overall, our study indicates that yellow-necked mice can provide a further example of species sustaining an adaptive framework for endothermic thermoregulation.

Keywords Daily torpor · Yellow-necked mice · *Apodemus flavicollis* · Heterothermy · Body temperature

Introduction

Mammals use endothermic thermoregulation, with the generation of internal heat contributing to a relatively high and stable homeothermic body temperature (T_b). However, many endothermic animals are able to adjust metabolic rate (MR) and T_b in response to environmental challenges, entering a heterothermic state (review in Angilletta et al. 2010).

Classically, adaptive heterothermy was divided into daily torpor (usually lasting less than 24 h) and hibernation (Geiser and Ruf 1995; Geiser 2004; Ruf and Geiser 2015). However, the matter of heterothermy is actually far more complicated, with current knowledge suggesting that daily torpor and hibernation are only points along a continuum of thermoregulatory strategies not fully elucidated as of yet (Boyles et al. 2013). Recent theoretical models accept that animals may be divided into specialists that thermoregulate precisely, and generalists in which a greater variation of T_b can arise (Angilletta et al. 2010). An adaptive framework for endothermic thermoregulation predicts that variation in T_b should increase with a decline in the availability of energy for the maintenance of homeothermy, and/or if the costs of precise thermoregulation increase (Angilletta et al. 2010). Daily torpor allows animals to reduce energy expenditure by ~35% of their basal metabolism (Ruf and Geiser 2015). This is therefore considered the most effective energy-saving strategy (Geiser 2004) animals deploy in response to increased demands for energy (Schubert

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et al. 2010) in the face of decreased food availability or a low ambient temperature (T_a), or a combination of both (Walton and Andrews 1981; Ruf et al. 1993; Lovegrove et al. 2001; Westman and Geiser 2004; Swoap and Gutilla 2009; Nespolo et al. 2010).

Comparative studies indicate that homeothermy is maintained permanently in only some mammalian species studied to date. In the remainder, variable thermoregulation patterns are displayed (Boyles et al. 2013). Thus, there is no support from research for the assumption that most mammals are homeotherms, and that endothermic T_b is not adaptive (Scholander et al. 1950; Angilletta et al. 2010; Boyles et al. 2013; Levesque et al. 2016). Equally, as available information on T_b in mammals extends to a mere 1% of the species, variation in thermoregulatory patterns remains a topic that is not well studied (Boyles et al. 2013). Our limited knowledge of endothermic thermoregulation should thus be seen as one of the most important problems of current environmental physiology (Boyles et al. 2011, 2013; Levesque et al. 2016). Studies investigating T_b variation fill important gaps in our knowledge and are crucial to the modelling of animal energetics (Levesque et al. 2016). They can thus help predict the impact of global climate changes on animal populations (Boyles et al. 2013).

The work detailed here sought to investigate thermoregulatory patterns in wild yellow-necked mice *Apodemus flavicollis*, a species regarded as homeothermic (Koteja 1995; McNab 2008, 2009). *Apodemus flavicollis* is a relatively common species found across most of Europe, as well as parts of Asia (Michaux et al. 2005). This small, nocturnal (Buchalczyk 1964; Wójcik and Wołk 1985), food-hoarding species inhabiting the temperate-zone establishes autumnal caches of seeds with the intent of surviving the winter (Vander Wall 1990). Thus, the population dynamics of yellow-necked mice in the Primeval Białowieża Forest are found to relate closely to the level of mass-seeding (or masting) achieved by the main deciduous tree species (Pucek et al. 1993; Stenseth et al. 2002). From a physiological perspective, most small mammal species are characterised by a winter survival strategy involving reduced energy expenditure, improved insulation, and an increased capacity for heat production (Lovegrove 2005). However, this does not seem to be the case for yellow-necked mice, among which the above parameters are not modified, with the implication therefore being that different survival strategies are used (Cygan 1985).

It has been suggested that *A. flavicollis* uses heterothermy via daily torpor to reduce the costs of self-maintenance in the face of harsh winter conditions (Cygan 1985; Aeschmann et al. 1998). This is in fact likely, given that torpor has been recorded in three other *Apodemus* species (Walton and Andrews 1981; Masaki et al. 2005; Eto et al. 2014). However, while studies by Cygan (1985) and Aeschmann et al. (1998) found individual yellow-necked mice with low T_b , their respective experimental designs did not permit distinction-drawing between torpor and pathological

hypothermia. Cygan (1985) confined measurement to rectal temperature, and failed to detail the measurement conditions. For their part, Aeschmann et al. (1998) only observed decreased T_b after several hours of exposure to extreme cold, while the accepted assumption would be that most small rodents enter a state of torpor in well-insulated burrows, where T_a is rather close to thermoneutrality (Heldmaier et al. 1990).

In light of the above, the aim of the work presented here was to investigate the thermoregulatory patterns in free-ranging and experimentally tested wild yellow-necked mice. In line with an adaptive framework for endothermic thermoregulation, we hypothesised that yellow-necked mice would be able to go into a state of torpor when exposed to adverse conditions. We predicted that food deprivation for 24 h would be associated with a decline in T_b as mice became torpid, with a spontaneous increase in turn taking place during arousal. We also predicted that heterothermy would grow more prevalent in free-living mice when environmental conditions made the maintenance of homeothermy unprofitable, e.g. when ambient temperature (T_a) decreased substantially.

Materials and methods

Animal trapping

The study was performed during autumn 2017 and winter 2018, and all procedures were approved by the Local Ethical Committee (Decision 62/2017) and the Polish Ministry of the Environment (Decision DOP-WPN.287.7.2016.AN). In total, 84 mice (39 males and 45 females) were captured between 5 and 30 October 2017 on a 1 ha plot (GPS position: 52° 43' N, 23° 52' E) located in the Strict Reserve of the Białowieża National Park (Eastern Poland). The animals were transported to the Laboratory of the Mammal Research Institute of the Polish Academy of Sciences (MRI PAS), located at Białowieża. All mice were kept under laboratory conditions for the time (~1 week) needed to surgically implant T_b data loggers. Then, the animals were released at the place of capture. Between 12 and 17 December 2017, six mice (3 females and 3 males) were successfully recaptured at the study site. Thus, we repeated implantation procedures to recover data and exchange data loggers needed for laboratory measurements in these six individuals only.

Animal maintenance and surgical procedures

Under laboratory conditions, mice were individually kept in standard rodent cages (model number 1246; Tecniplast, Italy), with wood shavings and access to rodent food (Megan, Krakow, Poland), carrots, apples, and water ad libitum. The cages were placed in a climatic chamber at 19 ± 1 °C and with a natural photoperiod. The day after capture, mice were

implanted surgically—intraperitoneally—with miniaturised, paraffin wax-coated T_b data loggers (iButton, models; DS1923L and DS1925L, Dallas Semiconductors, TX, USADS1923L, logger mass = 1.8 g) while anaesthetized under a 2% mixture of isoflurane (Iso-Vet, Orzesze, Poland) and medical oxygen (Air Products, Bialystok, Poland). Mice were injected with antibiotics (Enrobioflox 5%, Biowet Sp. z.o.o., Gorzow Wlkp., Poland) dissolved in saline (Baxter Manufacturing Sp. z.o.o., Lublin, Poland) to a concentration of 2% for two consecutive days after surgery.

Temperature measurements

Loggers were set to record T_b in free-ranging animals at 1-h intervals, with a resolution of 0.062 °C. In laboratory experiments, loggers were set to record T_b of mice at 10-min intervals, with a resolution of 0.062 °C. All loggers were calibrated in a water bath against a high-precision (0.1 °C) mercury-in-glass thermometer (Bestell-Nr: 1.07, Germany) at five T_a points between 17 and 42 °C after finishing field and laboratory measurements. Ambient temperature (T_a) was measured at ground level and logged by reference to the meteorological station located at MRI PAS (model pt-100, SKS Sensors, Finland).

Experimental procedures

After 2 weeks of recovery from surgery and acclimation to laboratory conditions ($T_a = 19 \pm 1$ °C and natural photoperiod), animals were made subject to experimentation, being placed in home cages at $T_a = 19 \pm 1$ °C and deprived of food for 24 h (albeit with water provided ad libitum). The experiment started at 15:00 on the first day and concluded at the same time the following day. Three days after the experiment, loggers were removed, followed 1 week later by the release of all individuals at the place of capture.

Data preparation

To quantify deviations of T_b from the optimal temperature, we calculated the heterothermy index (HI), after Boyles et al. (2010), for each day that an individual was at liberty in nature and T_b recorded (HI_f), as was the case during the food deprivation experiment (as HI_e). Since it is not possible to obtain a true optimal temperature for performance in endotherms, we assumed—after Angilletta et al. (2010) and Boyles et al. (2010)—that the relevant temperature was the T_b represented most often by an active animal. We thus calculated the modal T_b for active animals ($T_{b\text{-alpha-mode}}$) on the basis of data collected in the autumn ($T_{b\text{-alpha-mode-1}}$: before release), when mice were free-ranging ($T_{b\text{-alpha-mode-2}}$), after recapture ($T_{b\text{-alpha-mode-3}}$), and during three consecutive days before the fasting experiment ($T_{b\text{-alpha-mode-4}}$). We also calculated $T_{b\text{-mode}}$

in resting animals ($T_{b\text{-rho-mode}}$) for the same time periods, i.e. before an animal was released ($T_{b\text{-rho-mode-1}}$), while it was free-ranging ($T_{b\text{-rho-mode-2}}$), after recapture ($T_{b\text{-rho-mode-3}}$), and prior to the fasting experiment ($T_{b\text{-rho-mode-4}}$). Because $T_{b\text{-mode}}$ differed between field and laboratory measurements, we calculated HI_f assuming different optimal temperatures. One value for HI_f (HI_{f1}) was calculated on the basis of $T_{b\text{-alpha-mode-4}}$, when mice were kept under laboratory conditions with food provided ad libitum. Another HI_f (HI_{f2}) was calculated on the basis of $T_{b\text{-alpha-mode-2}}$ values obtained in free-ranging animals. Minimum T_b values for animals in a state of torpor (i.e. $T_{b\text{-min}}$) were compared between data collected in the field and during the fasting experiment. To conform to the standards accepted in the discipline, we also calculated the “torpor bout duration” (TBD) as the total time an individual mouse spends with T_b below 33.5 °C. The threshold temperature for torpor was calculated based on m_b following Willis (2007).

Statistical analysis

We ran the linear mixed modelling (LME) procedure using the “lme4” package, in order to compare data including gender and animal ID as random effects in the whole analysis. However, as the distribution obtained for HI was highly right-skewed, we used the Box-Cox transformation prior to carrying out the analysis. Most likely because they were still growing, mice increased in body mass (m_b) from autumn to winter by ca. 4% (autumn 31.47 ± 6.51 g, winter 32.68 ± 7.18 g; $\chi^2 = 7.59$, $p < 0.01$). While m_b was initially included in all models as a covariate, its lack of effect on any tested variables ensured its exclusion from the final models. $T_{b\text{-mode}}$ values were compared between data collected in early autumn under laboratory conditions, in the field, under laboratory conditions following recapture, and prior to the fasting experiment. From this analysis, we excluded data for $T_{b\text{-alpha-mode-3}}$ and $T_{b\text{-rho-mode-3}}$ for two individuals, given the non-representative nature of the data (Fig. 1). We compared HI_e with the maximum daily HI_{f1} or HI_{f2} , $T_{b\text{-min}}$ observed during fasting with $T_{b\text{-min}}$ obtained in the field, and TBD observed during fasting with the maximum TBD observed in the field. Daily HI_{f1} and HI_{f2} were tested in LMEs in which the minimum daily ambient temperature (T_a) was included as a covariate. Type II Wald chi-square tests were used to estimate the significance of factors and covariates in all models. The Tukey test was applied in post hoc comparisons. All analyses were performed in R (R Core Team 2013), ver. 3.4.3.

Results

There was no significant correlation between m_b and any of the tested variables ($T_{b\text{-alpha-mode}}$'s: $\chi^2 = 0.18$, $p = 0.67$; $T_{b\text{-rho-mode}}$'s: $\chi^2 = 0.08$, $p = 0.78$; $T_{b\text{-min}}$: $\chi^2 = 0.68$, $p = 0.411$; TBD:

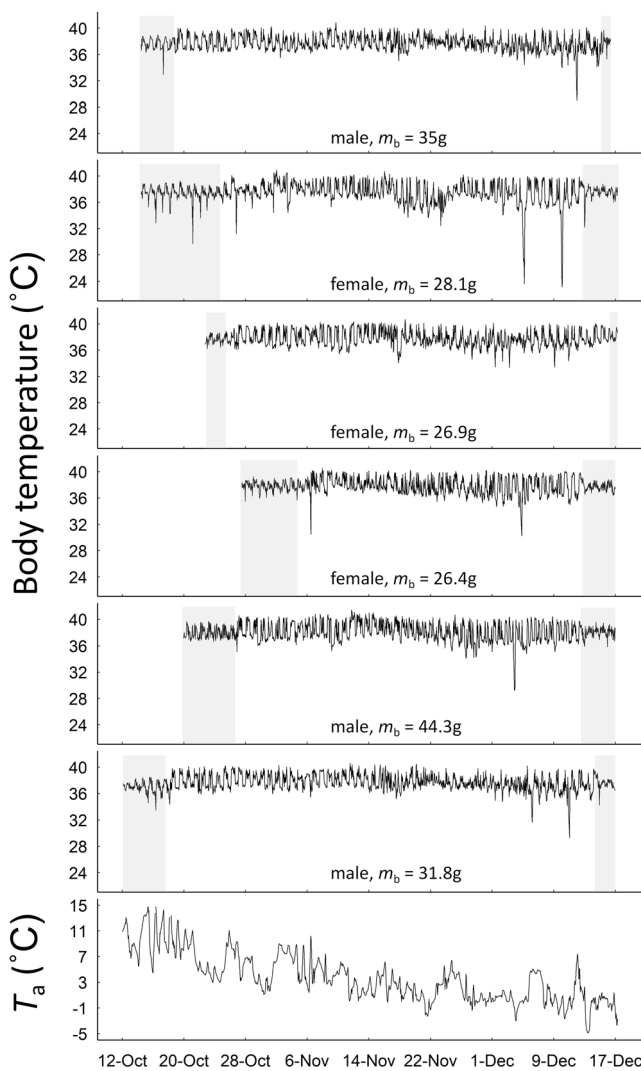


Fig. 1 Body temperature (T_b) recorded in six free-ranging *A. flavicollis* individuals during autumn 2017 in Białowieża Forest. Shaded boxes indicate T_b recorded before release or after recapture, when animals were kept under laboratory conditions (food ad libitum, ambient temperature = 19 °C, and with natural photoperiod). The lower panel represents changes in the minimum daily ambient temperature (T_a) during the study period

$\chi^2 = 0.20$, $p = 0.65$; HI_e and/or maximum HI_{f1} : $\chi^2 = 0.42$, $p = 0.51$; HI_e and/or maximum HI_{f1} : $\chi^2 = 0.90$, $p = 0.34$; daily HI_{f1} : $\chi^2 = 0.08$, $p = 0.78$; daily HI_{f2} : $\chi^2 = 0.20$, $p = 0.66$). Mice clearly become torpid under both field and laboratory conditions (Figs. 1 and 2). Daily torpor was found to last for only several hours, while TBD did not differ in measurements made in the laboratory (4.11 ± 1.35 h) or the field (3.5 ± 1.98 h; $\chi^2 = 0.50$, $p = 0.48$; Fig. 2). Furthermore, T_{b-min} during torpor was not shown to differ significantly in comparisons made between animals in the laboratory (26.34 ± 1.72 °C) and those experiencing free-ranging conditions (29.06 ± 3.32 °C; $\chi^2 = 3.17$, $p = 0.075$). $T_{b-alpha-mode}$ showed significant differences between laboratory and field measurements ($\chi^2 = 30.65$, $p < 0.001$) and was higher among free-ranging animals

($T_{b-alpha-mode-2} = 39.55 \pm 0.32$ °C), as opposed to those kept in laboratory conditions ($T_{b-alpha-mode-1} = 37.73 \pm 0.55$ °C, $T_{b-alpha-mode-3} = 37.95 \pm 0.35$ °C and $T_{b-alpha-mode-4} = 38.33 \pm 0.77$ °C). Each of the $T_{b-alpha}$ values obtained under laboratory conditions differed significantly from those observed in free-ranging animals ($p < 0.05$). $T_{b-rho-mode}$ did not differ between compared periods ($T_{b-rho-mode-1} = 37.21 \pm 0.14$ °C, $T_{b-rho-mode-2} = 37.00 \pm 0.22$ °C, $T_{b-rho-mode-3} = 37.33 \pm 0.15$ °C, and $T_{b-rho-mode-4} = 37.20 \pm 0.48$ °C; $\chi^2 = 3.67$, $p = 0.30$). Finally, no significant differences were recorded between HI_e (4.21 ± 1.24 °C) and maximum daily HI_{f1} (3.73 ± 1.37 °C; $\chi^2 = 1.05$, $p = 0.31$), or else between HI_e and HI_{f2} (4.38 ± 1.47 °C, $\chi^2 = 0.11$, $p = 0.74$). Heterothermy in free-ranging mice in turn correlated negatively with the minimum daily T_a (HI_{f1} : $\beta \pm SE = -0.02 \pm 0.01$, $\chi^2 = 11.42$, $p < 0.001$; Fig. 3a, HI_{f2} : $\beta \pm SE = -0.03 \pm 0.01$, $\chi^2 = 29.15$, $p < 0.001$; Fig. 3b).

Discussion

As we predicted, yellow-necked mice entered a state of torpor when food-deprived under laboratory conditions, or when, as free-living animals, they encountered harsh environmental conditions (Figs. 1, 2 and 3). Mice fasted in the laboratory became torpid at the end of the alpha phase (Fig. 2a). While the same was generally true among free-ranging mice, and while most mice achieved a state of torpor at the same time as in the laboratory experiment, some torpor episodes also occurred in the middle of the alpha phase (Fig. 2b). We thus present the first incontestable results in support of the hypothesis that *A. flavicollis* is a heterothermic species, making use of daily torpor (cf. Cygan 1985; Aeschmann et al. 1998). Torpor has also in fact been observed in closely related species like the wood mouse *A. sylvaticus* (Walton & Andrews 1981), the Korean field mouse *A. peninsulae* (Masaki et al. 2005), and the large Japanese field mouse *A. speciosus* (Eto et al. 2014). Since adaptive heterothermy, including different torpor patterns, is considered a plesiomorphic trait (Lovegrove 2012) which displays a strong phylogenetic signal (Boyles et al. 2013), it is likely that this energy-saving strategy is a phenomenon common to all *Apodemus* species.

The comparative study suggested that work pursued under laboratory conditions may underestimate the use of torpor, with different species—mainly hibernators—found to enter deeper and longer torpor bouts under field conditions, as opposed to in laboratory experiments (for review, see Geiser et al. 2000). However, there are exceptions to this assumption, and the use of torpor by white-footed mice *Peromyscus leucopus* was demonstrably similar under laboratory conditions (Vogt and Lynch 1982) and among free-ranging individuals (Vogt et al. 1983). Moreover, some other species like the Cape rock elephant shrew *Elephantulus edwardii*, African

Fig. 2 Daily course of body temperature (T_b) in six individuals of *A. flavicollis*. **a** Recordings of T_b during 24-h food deprivation experiment under laboratory conditions. The box below refers to the light-dark cycle. **b** Changes of T_b that exceed the 33.5 °C threshold in six free-ranging mice during autumn 2017 in Białowieża Forest. Different symbols indicate different individuals

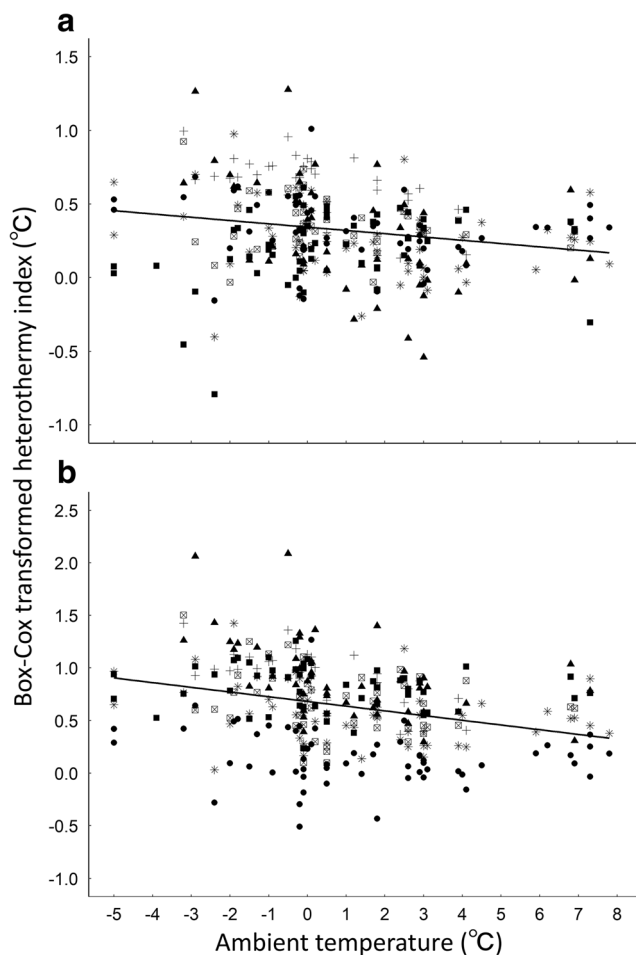
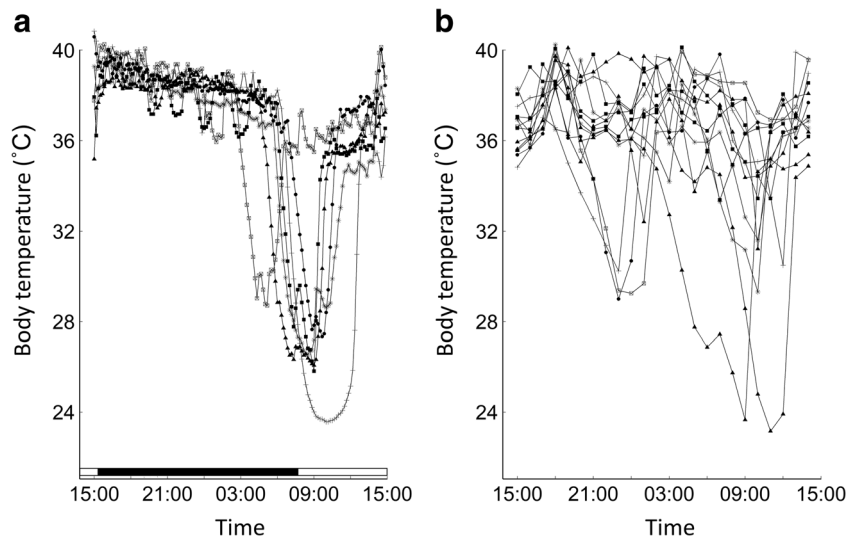


Fig. 3 Relationship between Box-Cox transformed heterothermy indices of free-living mice (HIF) and minimum daily ambient temperature. **a** Value for HIF calculated on the basis of modal body temperature during alpha phase under laboratory conditions. **b** HIF value based on modal body temperature during alpha phase obtained in free-ranging animals. Note a different scales for Box-Cox transformed HIF on each plot. Different symbols indicate different individuals

hedgehog *Atelerix frontalis* were, or African lesser bushbaby *Galago moholi* were even found to use torpor more frequently in laboratory experiments than in the field (Nowack et al. 2010; Geiser and Mzilikazi 2011; Hallam and Mzilikazi 2011; Boyles et al. 2012a). This is most likely because the natural conditions animals are exposed to are not always harsh enough to enforce the resort to torpor. We found no significant differences between the length and depth of torpor engaged in by free-ranging and laboratory food-deprived mice. That said, minimum T_b during torpor did tend to be lower during food-deprivation experiments in a laboratory, as compared to episodes of torpor in natural conditions. Moreover, free-ranging mice only increased heterothermy and entered torpid states when T_a decreased significantly (Figs. 1 and 3). Thus, despite field measurement being crucial to our understanding of the ecological factors affecting the use of torpor in nature (Boyles et al. 2013; Levesque et al. 2016), laboratory studies performed under standardised conditions are also essential in investigating potential individual differences in the capacity for, and resort to, heterothermy. Our study makes it clear that food-deprivation experiments are effective in the study of heterothermy in yellow-necked mice, and may, for example, gain use in the study of individual differences, and hence the genetic background to heterothermy.

Only modal T_b during the alpha phase (not the resting phase) was found to differ significantly when laboratory and field measurements were compared (Fig. 1). This indicates that diurnal oscillations in T_b were more marked under free-ranging conditions than in the laboratory. Diurnal oscillations in T_b are synchronised with the period of activity, with nocturnal animals including *A. flavicollis* presenting a higher T_b at night, even when this is measured under laboratory conditions (Refinetti 1994, 1999a, b). Differences between laboratory and field values for modal T_b , indicating higher diurnal oscillations in free-ranging animals, might thus be plausibly

ascribed to greater motor activity. The yellow-necked mouse is a food-hoarding species in which individuals establish autumnal caches of seeds to help them survive the winter (Vander Wall 1990). This should be accompanied by an increased level of activity and the generation of heat in muscle tissue. However, increased T_b during the alpha phase was not a mere by-product of motor activity (Bolles et al. 1968; Honma and Hiroshige 1978; Refinetti 1994, 1999a,b), as it actually tended to precede the increase in activity (Refinetti and Menaker 1992). Additionally, diurnal oscillations of T_b in *A. flavicollis* are associated more with diurnal variations in non-shivering thermogenesis (NST) than with locomotor activity (Gębczyński and Taylor 2004). NST increases rapidly at times of exposure to the cold (Heldmaier et al. 1990), with the attendant increase in heat production correlating positively with increased T_b (Hislop and Buffenstein 1994; Woodley and Buffenstein 2002). Since free-ranging mice are more inclined to operate at lower T_a than those kept in the laboratory, their higher alpha $T_{b\text{-mode}}$ may reflect higher obligatory and facultative heat production. Skeletal muscles work better when hotter, and this may ultimately improve performance in hoarding mice. In fact, vertebrate skeletal muscles achieve their highest level of performance at the highest tested temperature—close to 40 °C in the case of laboratory mice (James 2013; James et al. 2015).

A theoretical cost-benefit model for adaptive thermoregulation predicts that variation in T_b in endothermic animals should increase where it becomes unprofitable to maintain a high, homeothermic T_b , i.e. when environmental requirements increase and/or energy supply is limited (Angilletta et al. 2010). In support of this are the food-limitation or deprivation experiments, indicating that many endothermic species go into a state of torpor when energy supply is reduced (subject as reviewed by Vuarin and Henry 2014). All the mice studied became unambiguously torpid when facing experimental food deprivation (Fig. 2a). Thus, the yellow-necked mouse resembles many small animals in its abandonment of homeothermy and facultative use of heterothermy to survive periods of sudden energy limitation; the species should therefore be considered a thermoregulation generalist (sensu Angilletta et al. 2010). Studies by Schubert et al. (2008, 2010) show that an increase in the costs of obtaining food results in the abandonment of homeothermy in laboratory mice, which thus enter a state of torpor. When exposed to cold, endothermic animals must experience an increase in metabolic rate if the heat needed to maintain the state of homeothermy, and thus a supply of energy, is to be generated (Scholander et al. 1950). This means that in endothermic homeothermic animals, the consequence of exposure to substantially decreased T_a may be an energy imbalance. To survive such conditions, many small endothermic species generate heterothermic responses (Ruf et al. 1993; Masaki et al. 2005; Nespolo et al. 2010; Boyles et al. 2012a,b; Przybylska et al. 2017). Consequently, heterothermy in free-living *A. flavicollis* correlates negatively with T_a (Fig. 3),

and clearly defined episodes of torpor appear at the beginning of winter, when T_a decreases below 0 °C (Fig. 1). Since all mice were able to go into torpor under moderate T_a , and since a single food-deprivation event forced them to do so, we conclude that free-ranging mice managed to acquire sufficient resources, presumably due to their hoarding behaviour, to off-set the need for heterothermy throughout the majority of the study and only relied on torpor during the coldest periods. Our study suggests that, during autumn, individuals of *A. flavicollis* maintain hot bodies for so long as food hoarding remains beneficial, and hence until the first signs of winter. Winter decreases in T_a and the likely increased costs of foraging then trigger a mixture of endothermic and poikilothermic thermoregulation methods via a form of adaptive thermoregulation that supports the cost-benefit model (Angilletta et al. 2010).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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