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Flexibility in thermal physiology and behaviour allows body mass maintenance in hibernating hazel dormice

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Abstract

Studying animals under natural or semi-natural conditions is essential to better understand the implications of a warming climate on species survival. Here, we provide evidence of the effects of increasing winter ambient temperature (T_a) on the thermal physiology, feeding behaviour and body mass (BM) of a small mammalian hibernator, the hazel dormouse *Muscardinus avellanarius*. We collected skin temperature, metabolic rate (MR) and BM data from captive, hibernating dormice exposed to two winters of differing intensity in outdoor aviaries. Additionally, we obtained skin temperature data from one free-ranging individual during the hibernation period. Statistical modelling showed that T_a and time since the start of hibernation both had significant non-linear effects on the probability of arousal from torpor. During the warmer winter (T_a<0°C on 26 days), foraging resulted in higher BMs for some individuals, despite more frequent arousals, than during the colder winter (T_a<0°C on 86 days). As expected, T_a had a non-linear effect on MR during torpor, with the lowest energy expenditure at intermediate T_a, and normothermic MR was minimal when T_a was warmer. The negative effect of increased arousal frequency on BM was counteracted by the positive effect of foraging on BM. Conforming with the accumulating body of evidence on high flexibility in physiological responses in many small mammals, we found that the thermoregulatory and behavioural responses of dormice during hibernation were more flexible than previously observed for this temperate, fat-storing species. The ability to respond to prevailing environmental conditions might help *M. avellanarius* cope with increasing winter T_a predicted for ongoing global warming.

Introduction

Climate change can severely impact diverse aspects of animal ecology, including physiology, phenology, and distribution (Thomas *et al*., 2004; Boyles & Brack, 2009; Ozgul *et al*., 2010). Species distribution boundaries are often linked to energetic constraints, but the mechanisms driving the effects of changing ambient temperature (T_a) on animal ecophysiology require further investigation to improve their predictive value. This is of concern, since the effects of climate on physiology may be especially important for the survival of small hibernating endothermic animals that are sensitive to changes in T_a during winter.

One of the critical determinants of successful overwintering is the management of energy expenditure and body fat reserves, which is influenced by social behaviour, age, sex, disturbances, hibernaculum temperature and winter length (Humphries, Thomas & Speakman, 2002; Boyles & Brack, 2009; Jonasson & Willis, 2011). In temperate zones, hibernators typically arouse periodically from multiday torpor bouts during hibernation, that is periods usually lasting less than 24 h when body temperature (T_b) and metabolic rate (MR) rise to normothermic levels (French, 1985; Barnes, 1989). These arousals are the most energetically expensive events during hibernation (Wang, 1978). Arousals occur most frequently at the beginning and end of hibernation (e.g. French, 1982), indicating a circannual rhythm and the influence of an external Zeitgeber such as day length or T_a (Körtner & Geiser, 2000). Arousal frequency increases with increasing T_a in the hibernaculum (Geiser & Kenagy, 1988; Geiser & Broome, 1993). During torpor, energy expenditure of thermoconforming animals is greatly reduced but MR during torpor (TMR) increases passively with increasing T_a above a species-specific hypothalamic T_b set point (T_{set}; Geiser, 2004). As T_a below the T_{set} decreases, TMR rapidly increases and animals arouse more often (Geiser & Kenagy, 1988). Additionally, very low sub-zero T_a could induce emergency arousals to avoid injury (Geiser & Kenagy, 1988; Humphries, Thomas & Kramer, 2003). Consequently, energy expenditure during hibernation is strongly influenced by T_a. During winter in temperate zones, increasing average T_a associated with anthropogenic climate change is likely to severely affect the energy budgeting of small mammals hibernating at relatively stable T_a (Humphries, Thomas & Speakman, 2002), which could decrease survival (Turbill & Prior, 2016). Conversely, small mammals like the hazel dormouse *Muscardinus avellanarius*, that experience variable T_a when hibernating in poorly insulated nests beneath leaf litter on the forest floor, might profit from small increases in T_a if this results in decreased energy expenditure (Boyles & McKechnie, 2010). Moreover, animals living at the edge of their distributional ranges may have already reached their physiological limits and will consequently struggle to maintain a positive energy balance.

Detailed high-resolution data describing the effects of naturally fluctuating T_a on hibernation physiology, and how they affect the energy reserves and body mass (BM) of hibernating animals, are scarce. Moreover, the inclusion of ecologically relevant parameters in mechanistic models is essential for improving the accuracy of predictions of the effects of climate change on animal species (Levesque, Nowack & Stawski, 2016; Maino *et al*., 2016), and model outputs need to be validated by empirical data (Hulme, 2005). In an earlier study, we showed that increasing T_a significantly alters skin temperature (T_{skin}) and MR patterns of *M. avellanarius* during hibernation (Pretzlaff & Dausmann, 2012). In the present study we investigate the relationship between natural T_a and parameters of hibernation physiology (MR and arousal probability) and how these physiological responses to changing T_a affect the BM of hibernating dormice, by statistically modelling the aforementioned data. We used T_{skin}, MR and BM of temporarily captive dormice held under naturally fluctuating T_a and photoperiod during two winters of differing intensity at the edge of the species' distribution in northern Germany ('winter 2009/2010' (as used by Pretzlaff and Dausmann (2012)) and 'winter 2011/2012', which was characterized by warmer T_a than the first period). Additionally, we obtained T_{skin} data from one free-ranging individual during hibernation.

Materials and methods

Study animal and field sites

The hazel dormouse is a predominantly nocturnal, arboreal rodent, which inhabits deciduous and mixed coniferous forests in Europe and northern Asia and hibernates from late October to the end of April. We used five study sites in northwest Germany less than 60 km apart and one approximately 450 km away in eastern Germany (Spitzberg). Three of these were located in deciduous forests: Spitzberg, Linau, Aukrug; and three were located in hedgerows: Bebensee, Thürk, Padenstedt (see supplementary methods for study site coordinates (Appendix S1)). Hourly $T_a \pm 0.5°C$ was measured using temperature data loggers (DS1922L Thermochron iButtons; Maxim Integrated Products, USA) that were attached to trees located at the centre of each study site.

Skin temperature measurements

We recorded hourly $T_{skin} \pm 0.5°C$ of free-ranging and captive individuals using small, 1.1-g temperature data loggers mounted on collars (weetag lite; Alpha Mach, Mont-St-Hilaire, Quebec, Canada). Animals were equipped with collars when torpid. T_{skin} is a reliable indicator of T_b in small mammals that curl into a ball during hibernation (Dausmann, 2005). Measurements in the wild took place in Spitzberg from November 2009 to April 2010 (*n* = 1, male). The T_a data logger on site stopped recording three days earlier than the T_{skin} logger and missing T_a data were taken from a nearby weather station.

Captive animals

We collected 13 hazel dormice in the colder winter of 2009/2010 (8 males, 5 females) and 12 in the warmer winter of 2011/2012 (6 males, 6 females) from nest boxes and nest tubes (Bright, Morris & Mitchell-Jones, 2006) in Aukrug, Linau, Bebensee, Thürk and Padenstedt at the end of September. Therefore, animals were acclimatized to prevailing climatic conditions and experienced their natural preparation period for hibernation. We transferred these animals and their nests to wooden nest boxes that were readily accepted as sleeping and hibernation sites. Each nest box was insulated with 8 cm-thick hemp wadding and placed on the floor of an individual outdoor enclosure (0.75 x 1.0 x 0.5 m). Enclosures were equipped with branches to climb and food (nuts, acorns, berries, mealworms) and water were supplied *ad libitum*. Evidence of food consumption (e.g. bite marks, faecal pellets) was recorded every second day.

T_{skin} was measured continuously from November until May. During one month in the first winter three animals were disturbed by shrews (*Sorex minutus*) and affected data were omitted from analyses. One female died each winter (January 2010; April 2012) from unknown causes. Enclosure $T_a \pm 0.5°C$ and nest temperature inside nest boxes ($T_{nest} \pm 0.5°C$) were measured hourly using iButtons. Animals were released at their sites of capture after emergence from hibernation in early May.

BM ± 0.5 g was determined once per month using a spring balance. Each individual was weighed 8.5 ± 1.5 times.

Torpor patterns

We determined torpor bouts and arousal episodes in both the free-ranging and captured individuals during hibernation. The T_b of resting hazel dormice during arousals is around 36°C and during activity is 38°C (Vogel & Frey, 1995). The T_{skin} of active, normothermic individuals is about 36°C (this study). During the hibernation season, the beginning of a torpor bout was identified when T_{skin} dropped by 10°C or more below its highest T_{skin} during the previous arousal. The arousal was defined when T_{skin} was within 10°C of maximal T_{skin} (Reeder *et al*., 2012). 20% of the captive T_{skin} data loggers failed. In these cases, arousals were identified by comparing T_{nest} to T_a: whenever T_{nest} increased independently of T_a and T_{nest}-T_a increased to over 3°C within an hour, we assumed that the dormouse inside the nest was actively rewarming (Fig. S1; Appendix S1). Collar position was checked monthly during weighing.

Metabolic rate measurement

Oxygen consumption of undisturbed dormice in their individual wooden nest boxes within enclosures was measured continuously to calculate MR using open-flow respirometry (on average for 61 ± 26.5 h per individual). These wooden nest boxes were sealed with modelling clay and served as metabolic chambers (1725 cm^3), with the entrance (Ø30 mm) acting as air inlet. A portable gas analyser with an electrochemical fuel-cell O_2 sensor (Bieler and Lang, Achern, Germany; accuracy <0.02 vol.%) was connected to a nest box using air-tight tubing (Tygon; Saint-Gobain Performance

Plastics, France). Air was pulled through the nest boxes at a flow rate of 50-80 L/h and filtered excurrent air was dried with silica gel before entering the gas analyser. The flow rate and oxygen content of sample air was measured once per minute. To control for oxygen sensor drift, we sampled reference air from outside the nest boxes for five minutes every hour and corrected values using Clampfit v10.3.1.4 (Molecular Devices, Sunnyvale, CA, USA). While hibernation is generally sustained by fat stores, metabolic fuels, and therefore the respiratory quotient (RQ), change at different Ta during hibernation and between torpor and arousal, generally ranging from values of 0.7 to 0.85 (Wang, 1978; Buck & Barnes, 2000), but sometimes >0.85 at different stages of a torpor bout (e.g. Snapp & Heller, 1981). Furthermore, foraging on the food we provided likely increased the proportion of carbohydrate combustion, increasing RQ above levels expected for fat metabolism alone. Therefore, we calculated MR of torpid and normothermic phases, assuming an RQ of 0.85 (combustion of 50% of fat and 50% of carbohydrates), and corrected the values for T_a and barometric pressure, after Withers (2001). Variable, non-steady-state MR data 60 min before and 180 min after an arousal, when animals were rewarming from or cooling into torpor, were omitted from analyses. Oxygen sensors were calibrated prior to measurements using calibration gas made by a gas-mixing pump (type 2KM300/a, H. Wösthoff Messtechnik, Bochum, Germany). MR was averaged hourly for analyses.

Statistical analyses

To compare average T_a between the colder winter of 2009/2010 and warmer winter of 2011/2012, we fitted generalized additive models (GAMs) (Zuur *et al.*, 2009) using the package mgcv (Wood, 2006), with 'T_a' as response variable, 'date' and 'time of day' (hours) as smoothed terms and 'Year' as factor. An interaction between 'Year' and 'date' was included to assess whether the change in T_a over time differed between the 2 years. For more details on models see supplementary methods (Appendix S1).

We used generalized linear mixed-effects models (GLMMs) to model arousal probability and MR as a function of T_a, and BM as a function of MR and arousal probability. All GLMMs were fitted with Gaussian error distribution and identity link function, except for the model for arousal probability (binomial error distribution and logit link function). In all GLMMs, 'Year' was included as a fixed effect, that is a factor with two levels; the colder winter of 2009/2010 and the warmer winter of 2011/2012 (see Results). To account for repeated measurements on individuals, these models included 'ID' (individual) as a random intercept. We accounted for temporal autocorrelation by using a first order autoregressive residual model structure. To improve convergence of the GLMMs used to analyse BM (see below), we log-transformed mean MR and the number of arousals per individual during the one month prior to BM measurements.

We used R v3.3.2 (R Development Core Team, 2009) for all statistical analyses except for a *t*-test, U-tests and Spearman-rank correlations, which were conducted using SPSS v23.0 for Windows. Data are presented as mean ± SD unless stated otherwise; n = number of individuals, N = number of measurements where appropriate.

Modelling arousal probability as a function of T_a

We modelled the effects of T_a on arousal probability of captive *M. avellanarius* using as predictor variables 'T_a' (hourly means), 'Time_{hib}' (time since commencement of hibernation, in hours) and 'Year'. We included both linear and quadratic effects of T_a and Time_{hib} on arousal probability because arousals occur less often during mid-hibernation compared to the beginning and end (e.g. Körtner & Geiser, 2000), and arousals are more frequent either when T_a is warmer (e.g. Geiser & Kenagy, 1988) or at very low T_a (Humphries, Thomas & Kramer, 2003). We assigned the starting point of Time_{hib} to the date of the first MR measurement in both years (16 October 2009 and 12 October 2011). Prior to fitting the GLMM we standardized both T_a and Time_{hib} (using standard scores) for better model convergence.

Modelling MR as a function of T_a

MR during torpor

To predict TMR we fitted a GLMM with T_a and Year as predictors. Both linear and quadratic effects were needed to investigate the influence of T_a on TMR because TMR is typically higher both below T_{set} and at higher T_a and it is lower at intermediate T_a (Geiser, 2004). TMR above and below T_{set} differs physiologically: above T_{set} TMR is a curvilinear function of T_b and metabolic inhibition, whereas below T_{set} TMR is a usually linear function of the T_b-T_a differential (Geiser, 2004). For simplicity, we fitted a single curve to all data and did not fit a piecewise regression because we did not know *a priori* where the breakpoints between the separate regressions would be. MR was log-transformed to improve the distribution of model residuals.

MR during arousals

To predict normothermic MR during arousals, we fitted a GLMM with T_a (linear effect) and Year as predictors. Normothermic MR is higher above and below the thermal neutral zone (TNZ) and lowest within the TNZ (Heldmaier & Ruf, 1992). The influence of T_a on normothermic MR was only investigated linearly because measurements in winter were not made within or above the TNZ. MR was log-transformed prior to model fitting.

Modelling BM as a function of MR and the number of arousals

We used a GLMM to predict dormouse BM. Because BM was measured monthly (and other continuous variables were measured at a finer temporal resolution), we aggregated our predictors MR and Number of arousals, monthly. Therefore, as predictors we used mean MR, and the total duration of arousals (‘TotArouse’, hours) during one month before BM measurements, and a categorical predictor ‘Sex’ (levels: female/male). Sex was included because exploratory data analyses indicated that females were on average 3 g lighter than males.

Results

Body mass and torpor use in a free-ranging hazel dormouse

The BM of the free-ranging individual was 20.5 g at capture in November 2009 and decreased by 22% during hibernation to 16.0 g in May 2010. During torpor, median T_{skin} was 1.3°C (range: −1.2–11.2°C) at a median T_a of 1.1°C (−10.5–11.7°C) (Fig. 1). Average torpor bout duration was 9.3 ± 5.4 days (0.6 to 18.3 days) and 98.2% of the hibernation period was spent in torpor (Fig. 1). Arousal frequency increased with increasing daily T_{max}, although the correlation was weak ($r_s = 0.202$, $P = 0.012$, $N = 154$).

Ambient and nest temperature

The hibernation period from October to May 2011/2012 was warmer (median: $T_a = 5.6$°C) than in 2009/2010 (median: $T_a = 3.6$°C). Importantly, the change in Ta over time differed between the two years (Fig. S2; Appendix S1).

Median daily maximum T_a (T_{max}) and median daily minimum T_a (T_{min}) were higher during hibernation period 2011/2012 for most months (Table 1). T_a dropped below 0°C on 81 days in the colder winter (minimum $T_a = -19.5$°C) and only on 26 days in the warmer winter (minimum $T_a = -13.1$°C).

T_{nest} was a good proxy for T_a. The relationship between T_{nest} and T_a was significant in both the colder winter ($r_s = 0.938$, $P < 0.001$, $n = 23$, $N = 4367$; $y = 0.887x + 1.456$) and the warmer winter ($r_s = 0.930$, $P < 0.001$, $n = 23$, $N = 4297$; $y = 0.901x + 1.410$).

General hibernation patterns

Both the free-ranging and captive hazel dormice showed a torpor-arousal pattern typical of seasonally hibernating mammals, with more frequent arousals occurring at the start and end of the hibernation season and longer torpor bouts in the middle (Fig. 1). T_{skin} regularly decreased below 0°C and appeared to be defended at just under −2°C with a T_{skin} as low as −2.9°C in captive individuals. In the free-ranging individual minimal T_{skin} was −1.2°C (Fig. 1).

Body mass, torpor use and metabolic rate of captive hazel dormice

Mean body mass at capture was 25.3 ± 3.9 g ($n = 13$) before the colder winter and 20.8 ± 3.4 g ($n = 12$) before the warmer winter. Mean BM then increased before the start of hibernation by 7.5 ± 3.8 g in the colder winter and 10.0 ± 3.0 g in the warmer winter to 32.5 ± 3.7 g and 30.7 ± 3.3 g, respectively. Mean BM did not differ between winters ($t_{23} = 0.854$, $P = 0.402$). Most individuals reached minimum BM in May in the colder winter (23.3 ± 4.8 g) and in March or April in the warmer winter (22.1 ± 6.4 g). In the warmer winter, most hazel dormice gained weight again before their release because they emerged earlier from hibernation and foraged during the more frequent arousals. Mean emergence date (when hazel dormice began to arouse every day) was earlier in the warmer winter (11 April 2012 ± 15.0 d) than in the colder winter (23 April 2010 ± 12.1 d; $U = 8.5$, $Z = -3.609$, $P < 0.001$, $n = 23$).

During mid-hibernation (January to March), foraging occurred less frequently in the colder winter (1.8 ± 2.0 times; range: 0–7 times) than in the warmer winter (14.2 ± 10.3 times; range: 3–33 times; U = 5.0, $Z = -3.501$, $P < 0.001$, $n = 21$). Increased foraging activity led to increased body mass during the warmer winter in six individuals, four of which gained mass in January and two in March. Hence, dormice gained weight when foraging more frequently during arousals only during the warmer winter (warmer winter: $r_s = 0.469$,

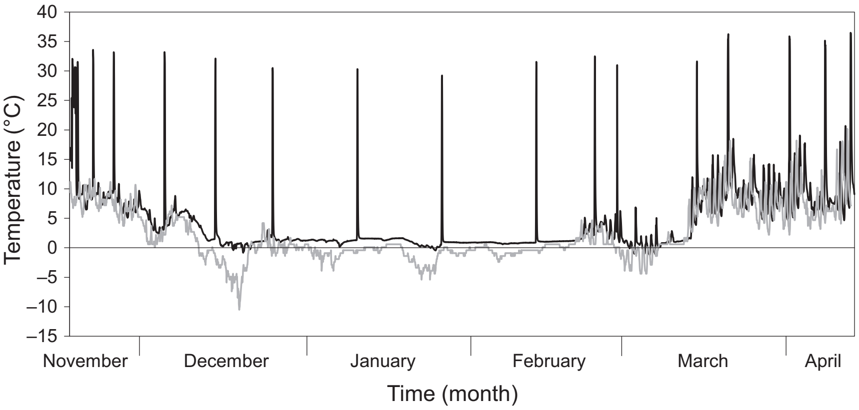

Figure 1 Skin temperature (black) and ambient temperature (grey) of a single free-ranging hazel dormouse during hibernation in the colder winter from November 2009 to April 2010. The horizontal line indicates 0°C.

Table 1 Median daily minimum, mean and maximum ambient temperature (°C) and (range) for each month of the study periods in the colder winter of 2009/2010 and the warmer winter of 2011/2012; an asterisk indicates a significant difference between years: U-Tests for every month

	October	November	December	January	February	March	April	May
Median daily T_{min}								
2009/2010	4.4 (0.1–10.7)	6.1 (0.6–9.7)	−1.4 (−10.0–4.6)	−4.4 (−18.5–0.1)	−3.2 (−13.5–2.6)	1.6 (−19.5–8.7)	4.1 (0.6–9.7)	7.5 (1.5–11.6)
2011/2012	7.1 (0.1–12.7)	5.4 (0.6–11.7)	2.6 (0.6–9.2)	2.1 (−8.0–6.6)	−0.4 (−13.1–5.1)	4.6 (0.6–7.1)	5.6 (−0.9–11.1)	9.1 (1.0–14.1)
Significance	n.s.	n.s.	***	***	n.s.	***	n.s.	n.s.
Median daily T_{mean}								
2009/2010	6.5 (3.4–11.4)	8.2 (4.2–10.8)	0.1 (−7.6–6.5)	−2.4 (−13.5–0.5)	−0.8 (−5.0–3.7)	3.6 (−7.0–11.2)	6.7 (4.0–14.0)	9.3 (3.0–14.5)
2011/2012	8.6 (4.1–13.9)	7.2 (2.3–12.4)	4.7 (1.7–10.0)	3.4 (−6.2–8.2)	0.6 (−10.9–6.7)	7.0 (2.5–8.9)	7.4 (2.6–12.4)	12.1 (6.2–17.5)
Significance	*	n.s.	***	***	**	**	n.s.	***
Median daily T_{max}								
2009/2010	8.7 (5.6–13.2)	9.0 (5.6–12.2)	2.1 (−5.9–9.7)	−0.9 (−7.4–2.6)	0.6 (−3.4–5.6)	7.7 (0.6–13.7)	9.7 (5.1–20.7)	17.9 (6.6–25.9)
2011/2012	10.7 (8.1–15.2)	8.4 (3.6–12.7)	6.6 (2.6–10.7)	5.1 (−4.5–11.7)	2.6 (−8.0–8.1)	9.1 (5.6–14.7)	9.9 (4.1–16.1)	17.9 (8.4–25.9)
Significance	**	n.s.	***	***	*	*	n.s.	n.s.

$^{*}P \leq 0.05$.

$^{**}P \leq 0.01$.

$^{***}P \leq 0.001$, n.s.=non-significant.

$P = 0.004$, $n = 12$, $N = 36$; colder winter: $r_s = 0.007$, $P = 0.979$, $n = 9$, $N = 17$).

In the colder winter, median T_{skin} during torpor (averaged over a wide T_a range) was 3.0°C, median $T_{nest} = 2.0$°C and median $T_a = 1.9$°C ($n = 13$). In the warmer winter, median T_{skin} during torpor was 4.2°C, median $T_{nest} = 4.1$°C and median $T_a = 3.0$°C ($n = 12$). Average torpor bout duration was 4.7 ± 6.2 days in the colder winter (range: 0.1–25.9 days) and 2.5 ± 3.3 days in the warmer winter (range: 0.1–27.7 days). The average proportion of time spent in torpor from mid-November to mid-April was $90.9 \pm 4.3\%$ in the colder winter and $77.1 \pm 12.3\%$ in the warmer winter.

In the colder winter ($n = 13$) mean TMR (not steady state minima) was 4.50 ± 3.64 mL O_2 h^{-1} (0.17 ± 0.15 mL O_2 g^{-1} h^{-1}) and mean normothermic MR during arousals was 87.32 ± 32.57 mL O_2 h^{-1} (3.13 ± 1.33 mL O_2 g^{-1} h^{-1}). In the warmer winter ($n = 12$) mean TMR was 3.65 ± 2.79 mL O_2 h^{-1} (0.14 ± 0.10 mL O_2 g^{-1} h^{-1}) and mean normothermic MR during arousals was 92.81 ± 28.67 mL O_2 h^{-1} (3.29 ± 1.04 mL O_2 g^{-1} h^{-1}).

Modelling arousal probability as a function of T_a

Arousal probability was significantly affected by all included variables (Table 2) and changed non-linearly with T_a and $Time_{hib}$ (Fig. 2, Table 3). On average, arousal probability was higher in the warmer winter compared to the colder winter. For example, at a T_a of 10°C in mid-March (after 167 days in hibernation), arousal probability was 0.219 in the warmer winter and 0.086 in the colder winter (Fig. 2). The confidence interval was large, reflecting within- and between-individual variation. The effect of $Time_{hib}$ was larger than the effect of T_a (Table 3). We found strong temporal autocorrelation in the probability of arousal between two consecutive time steps (Table 4).

Modelling MR as a function of T_a

MR during torpor

We found significant linear ($\chi^2 = 600.5$, d.f. = 1, $P < 0.0001$) and quadratic ($\chi^2 = 867.0$, d.f. = 1, $P < 0.0001$) effects of T_a on TMR but the effect of Year was non-significant ($\chi^2 = 2.5$, d.f. = 1, $P = 0.115$). As expected, TMR was higher at lower and at higher T_a, and lowest at intermediate T_a (Table 3, Fig. 3a). The lowest 5% of TMR values correspond to the T_a range between approximately −2°C and 11°C. We found an indication of strong temporal autocorrelation in MR.

Normothermic MR during arousals

As expected, normothermic MR decreased with increasing T_a below the TNZ ($\chi^2 = 21.724$, d.f. = 1, $P < 0.0001$; Fig. 3b, Table 3) and did not differ between years ($\chi^2 = 2.31$, d.f. = 1, $P = 0.129$).

Table 2 Likelihood ratio tests of the significance of variables affecting (1) probability of arousal and (2) body mass of hibernating hazel dormice. In the model predicting body mass, logMR is log-transformed mean metabolic rate during the month prior to body mass measurements, and logTotArouse is the log-transformed total number of individual arousals the month before

Response	Predictor	χ^2	d.f.	*P* value
Probability of arousal	Year	7.20	1	0.0073
	Linear effect of Time$_{\text{hib}}$	59.80	1	<0.0001
	Quadratic effect of Time$_{\text{hib}}$	468.97	1	<0.0001
	Linear effect of temperature	222.14	1	<0.0001
	Quadratic effect of temperature	41.69	1	<0.0001
Body mass	Year	0.01	1	0.9255
	Effect of logMR	17.70	1	<0.0001
	Effect of logTotArouse	9.59	1	0.0020
	Sex	3.14	1	0.0762

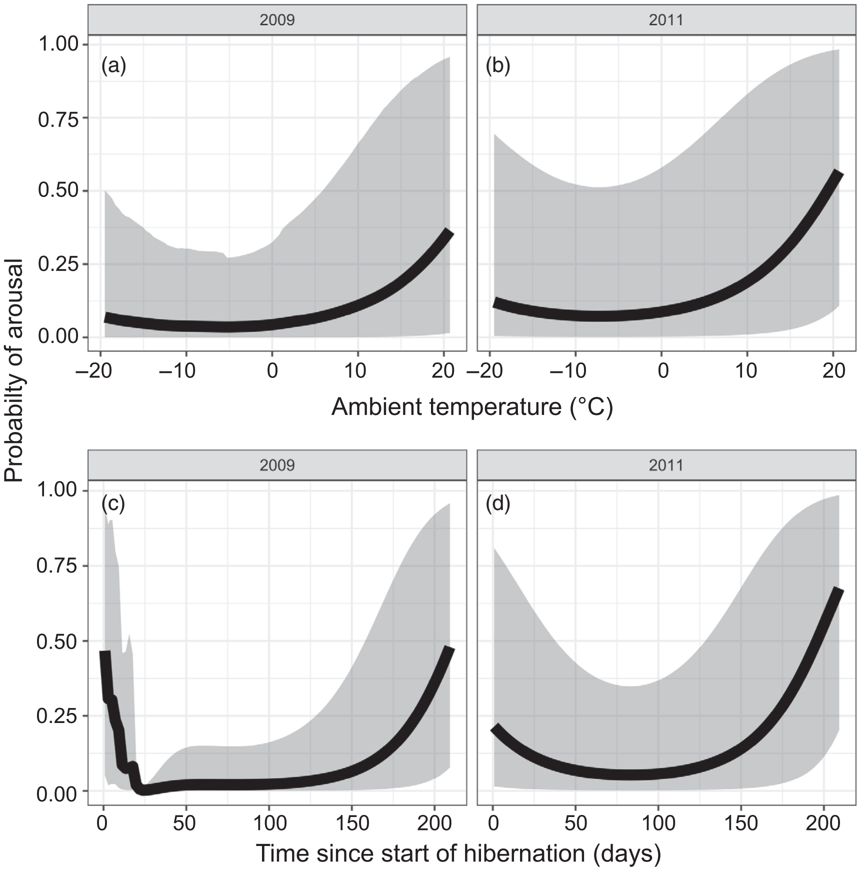

Figure 2 The effect of ambient temperature (a, b) and time since start of hibernation (c, d) on the probability of arousal for captive hazel dormice during the colder winter of 2009/2010 (a, c) and the warmer winter of 2011/2012 (b, d), estimated using generalized linear mixed-effects models.

Modelling body mass

Body mass decreased significantly with the total number of arousals in the month before BM measurement ($\chi^2 = 9.59$, d.f. = 1, $P = 0.002$; Fig. 4a) and increased with increasing average MR the month before BM measurement (χ^2=17.70, d.f. = 1, $P < 0.0001$; Fig. 4b), but was not affected by Year or Sex (Table 2).

Discussion

We found that increasing winter T_a, an aspect of global climate change, affected the hibernation physiology and BM of a small hibernating rodent, the hazel dormouse *M. avellanarius*. The probability of arousal from torpor and TMR were both non-linearly related to T_a, whereas normothermic MR declined with increasing T_a below the TNZ. These thermoregulatory

Table 3 Coefficient estimates ± SE obtained with the four models fitted to assess the effect of ambient temperature on hazel dormouse hibernation physiology

Response	Predictor	Level	Estimate	SE
Probability of arousal	Intercept		−5.140	1.827
	Year	2011	1.095	0.345
	Linear effect of Time_{hib}		0.908	0.092
	Quadratic effect of Time_{hib}		0.874	0.042
	Linear effect of temperature		0.575	0.039
	Quadratic effect of temperature		0.143	0.020
Metabolic rate during torpor	Intercept		1.084	0.097
	Year	2011	−0.109	0.069
	Linear effect of temperature		−0.039	0.001
	Quadratic effect of temperature		0.004	0.000
Metabolic rate during arousal	Intercept		4.369	0.075
	Year	2011	0.097	0.064
	Linear effect of temperature		0.009	0.002
Body mass	Intercept		26.091	1.731
	Year	2011	0.163	1.906
	Effect of logMR		2.108	0.491
	Effect of logTotArouse		1.129	0.361
	Effect of Sex	Female	3.290	1.918

For factor variables, the intercepts are ‘2009’ for Year and ‘male’ for Sex. Column ‘Level’ shows the estimated difference between the intercept and the other factor. In the model predicting body mass, ‘logMR’ is log-transformed mean metabolic rate during the month prior to body mass measurements, and ‘logTotArouse’ is the log-transformed total number of individual arousals the month before.

Table 4 Random structure of the four models fitted to understand the effect of ambient temperature on hazel dormouse hibernation physiology

Response	Variance explained by ID	Variance explained by temporal autocorrelation	phi
Probability of arousal	0.718	6.6310	0.9982
Metabolic rate during torpor	0.029	0.0588	0.9878
Metabolic rate during arousal	0.023	0.0229	0.9883
Body mass	20.19	NA	NA

Variance is explained by random factors ‘ID’ and ‘temporal autocorrelation’ and the autocorrelation parameter ‘phi’ is shown. A phi value close to 1 indicates strong positive temporal autocorrelation.

responses, combined with adjustments to foraging behaviour, allowed the dormouse to buffer the effects of environmental conditions on BM to potentially increase its chance of survival during the winter.

Arousal pattern data during hibernation under natural conditions are important for better understanding the thermal energetics of free-ranging animals inhabiting temperate or arctic regions (e.g. Landry-Cuerrier *et al*., 2008; Hoelzl *et al*., 2015). Our study provides the first continuous T_{skin} data during hibernation of a free-ranging hazel dormouse, which closely matched the patterns of individuals that hibernated in captivity. Torpor bout duration ranged from 0.6 to 18.3 days in the free-ranging individual and from 0.1 to 27.7 days for the captive individuals, similar to other free-ranging, temperate hibernators (Young, 1990; Lee, Barnes & Buck, 2009).

Arousal probability of captive dormice was affected by T_a and Time_{hib}. The timing of hibernation is influenced by internal time-keeping mechanisms that are synchronized by external Zeitgebers such as day length and T_a (Helm *et al*., 2013). The natural hibernaculum of hazel dormice is typically beneath leaf litter, not below the ground like many other small hibernating mammals. Therefore, T_a and day length may have a greater influence on hibernation patterns for this species, especially in the north of its range where snow cover is usually sparse and as a consequence hibernaculum T_a is less buffered. As seen in other small mammals in the wild, arousal probability was higher at the beginning and end of hibernation (e.g. Young, 1990; Park, Jones & Ransome, 2000). Moreover, in accordance with previous studies, arousal probability was higher at warmer and colder T_a and lowest at intermediate T_a (Fig. 2a,b) (e.g. Speakman & Thomas, 2003). Arousal probability was less frequent than expected at T_a below the T_{set} (e.g. Geiser & Kenagy, 1988). This is possibly the result of modelling arousal probability using T_a instead of T_{nest}, which is influenced by a dormouse rewarming inside. Although T_a is a good proxy for T_{nest} (see Results), it is often lower at freezing temperatures due to nest insulation (e.g. Arnold *et al*., 1991; this study) or snow cover. Arousal probability was higher, and emergence from hibernation earlier, in the shorter, warmer winter of 2011/2012 than in 2009/2010. Hibernating ground squirrels (*Urocitellus beldingi* and *Callospermophilus lateralis*) are normothermic more often and for longer during a warmer

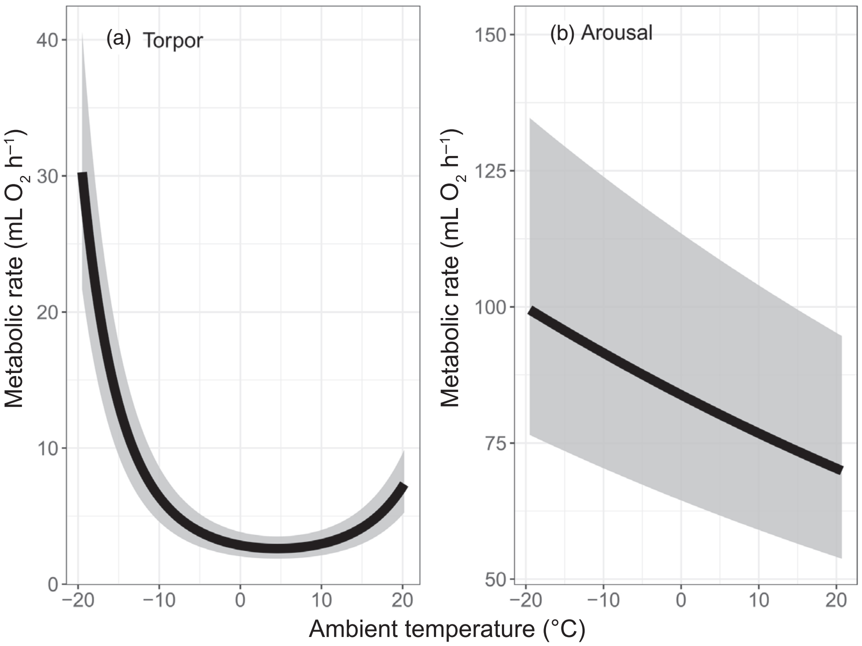

Figure 3 The effect of ambient temperature on the metabolic rate of hazel dormice in (a) torpor and (b) arousal (normothermia), estimated using generalized linear mixed-effects models.

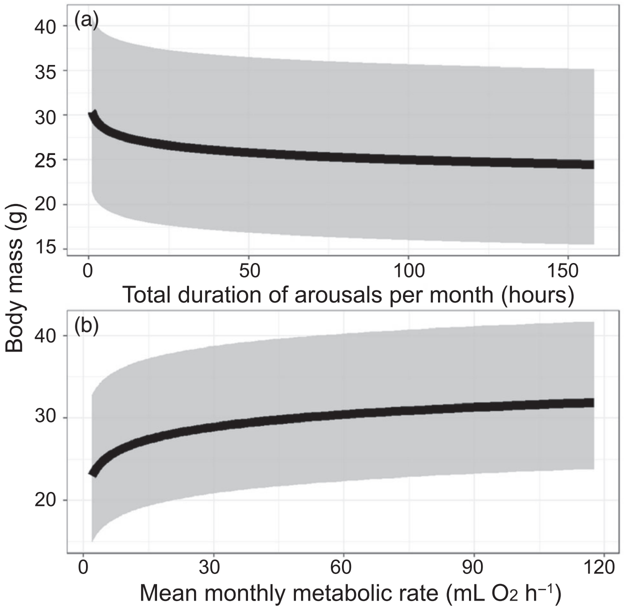

Figure 4 Hazel dormouse body mass predicted by (a) the total duration of arousals per month (h) and (b) mean monthly metabolic rate (mL O_2 h^{-1}), estimated using generalized linear mixed-effects models. The x-axes ranges from the minimum to maximum values of the variables observed in the data.

midwinter (French, 1982), and we assume that the unusually mild and short winter of 2011/2012, with only 26 days dipping below freezing, was the reason driving the higher arousal probability of dormice. Earlier emergence from hibernation could have a positive effect on individuals if it extends the feeding period and advances reproduction, as found in yellow-bellied marmots (*Marmota flaviventris*; Ozgul *et al*., 2010). Conversely, late emergence owing to delayed snowmelt negatively affects the fitness of Columbian ground squirrels *Urocitellus columbianus* (Lane *et al*., 2012). Clearly, climate change would only be non-detrimental if all ecological factors relevant to a species' success shift together, including primary food production and intraspecific mating behaviour, to avoid temporal mismatching. While the results of our study are clear, we concede that investigating the relationships between weather variables and hibernation patterns over additional seasons could reveal the extent of the direct effect of T_a on torpor use in small hibernators in the context of climate change.

Our model showed that the energy expenditure of thermoconforming hazel dormice was lowest during torpor between T_a of approximately −2°C and 11°C. Similarly, Buck & Barnes (2000) found that arctic ground squirrel TMR (*Urocitellus parryii)* was stable at T_a between 0 and 12°C. In torpid alpine marmots (*Marmota marmota*), TMR increased below 5°C in the laboratory and at 0°C TMR was already four times the minimal values at 5°C (Arnold *et al*., 1991). Arctic ground squirrels (minimum hibernaculum temperature = −18.0°C; Barnes, 1989) and hazel dormice (minimum hibernaculum temperature = −16.1°C; this study) have a diet higher in polyunsaturated fatty acids than alpine marmots (minimum hibernaculum temperature = 1.8°C; Arnold *et al*., 1991, 2011), which might permit minimal energy expenditure at a wide range of low T_a in these species. Moreover, a diet rich in polyunsaturated fatty acids may enhance survival at extremely low T_a by lowering the melting points of cell membrane lipids (Frank, 1992). Membrane lipid fluidity maintains functional integrity at very low T_a when polyunsaturated fatty acids are present (Frank, 1992), which could maximize energy conservation during torpor by contributing to the lowering of the T_{set}, thereby enabling longer and deeper torpor bouts (Geiser & Kenagy, 1987; Munro & Thomas, 2004).

Interestingly, the effects on BM of the total number of arousals and average MR one month prior to BM measurement seemed to cancel each other out. BM loss during hibernation was slightly lower in the lighter free-ranging animal than in captive individuals (about 22 versus 30%, respectively), but similar to previously reported values for hazel dormice (15–36% including juveniles born in May/June; Juškaitis, 2014). This is expected because larger individuals lose more body fat during hibernation as maximizing energy savings is less essential for them compared to smaller individuals (Boyles *et al*., 2020). A European beech (*Fagus sylvatica,* L.) seed crop occurred in the study sites during both autumns, but was more intense in 2009 (Paar *et al*., 2014), which might explain higher body masses at capture that year. As hypothesized, BM was lower when individuals aroused more frequently, consistent with findings that arousals are energetically expensive (Wang, 1978). Contrary to our expectations, BM was higher when individuals used more energy during the month before BM measurements. However, individuals with higher energy expenditures remained normothermic for longer during arousals and used this time to leave the nest and eat the food available in the enclosures, thereby gaining mass.

We show that hibernation is more flexible than previously observed for the temperate, fat-storing hazel dormouse, both within and between years, indicating the high potential for this species to adapt during times of changing environmental conditions. Small hibernators are able to adjust their hibernation patterns to prevailing external and internal conditions including food and habitat availability, weather, body condition, predation risk or illness (Boyles *et al*., 2020; Geiser, 2020). For example, large within- and between-individual variation in hibernation patterns have been reported in small temperate (Landry-Cuerrier *et al*., 2008; Jonasson & Willis, 2012; Turner *et al*., 2012a,b) and tropical (Dausmann *et al*., 2004; Kobbe, Ganzhorn & Dausmann, 2011) species. Such variation could be a prerequisite for microevolution or indicate phenotypic plasticity, allowing small hibernating mammals to respond to environmental changes in a broader way (Jonasson & Willis, 2012; Boutin & Lane, 2014).

Animals must also balance the depth and duration of torpor bouts to minimize the costs and maximize benefits of its use (Boyles *et al*., 2020). Minimizing the duration and depth of torpor when food or body fat reserves are available might help to avoid negative physiological effects of torpor including a reduced immune-competence, sleep deprivation and increased oxidative stress (Humphries, Thomas & Kramer, 2003; Bieber *et al*., 2014). Conversely, when body condition is poor, foraging during warmer hibernation periods could be an important short-term response to climate change (Boutin & Lane, 2014). We observed that some dormice foraged frequently, whereas others seldom did, even though they hibernated in outdoor enclosures under identical ambient conditions within a season. Similarly, garden dormice (*Eliomys quercinus*) forage during arousals throughout hibernation in South France (Ambid *et al*., 1990) and some bat species forage during hibernation during mild winters (Park, Jones & Ransome, 2000; Hope *et al*., 2014). Moreover, free-ranging food-hoarding eastern chipmunks (*Tamias striatus*) displayed a high flexibility in torpor use during winter in response to food availability and T_a (Landry-Cuerrier *et al*., 2008). The behavioural and physiological flexibility of hazel dormice that we observed, combined with their ability to broaden their diet during times of food scarcity (Juškaitis, 2007; Bertolino *et al*., 2016), will likely help them adapt to and survive changing environmental conditions.

Our study contributes to the growing body of literature describing intraspecific flexibility in physiological responses. We show that the hazel dormouse is able to adjust its torpor patterns and energy expenditure during the hibernation season in response to prevailing environmental conditions, thereby maintaining a sufficiently high BM. In light of anthropogenic global warming, our models indicate that increasing winter T_a may have diverse effects on small hibernating endotherms and favour those with physiological and behavioural flexibility. Importantly, food availability during warmer winters, when arousal frequency increases, will be vital for replenishing depleted fat reserves and ensuring survival in hibernators that do not store food. Many species have been shown or are predicted to shift their distribution poleward with increasing T_a (Humphries, Thomas & Speakman, 2002; Hickling *et al*., 2006). Hazel dormice in northern Germany, particularly those at the edge of their current distribution, may reconnect with populations in Denmark, whose distribution ranges have been separated due to habitat loss and fragmentation. Therefore, it will be increasingly important to establish and maintain habitat corridors where animals are able to travel to regions with more suitable climates.

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Author contributions

KHD and IP conceived and designed the study; IP conducted the fieldwork and collected the data; VR and IP conducted statistical analyses; IP took the lead in writing the manuscript;

all authors discussed the results and contributed to the final manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Information.