The Company of **Biologists**

RESEARCH ARTICLE

An intra-population heterothermy continuum: notable repeatability of body temperature variation in food-deprived yellow-necked mice

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ABSTRACT

Theoretical modelling predicts that the thermoregulatory strategies of endothermic animals range from those represented by thermal generalists to those characteristic for thermal specialists. While the generalists tolerate wide variations in body temperature (T_b), the specialists maintain T_b at a more constant level. The model has gained support from inter-specific comparisons relating to species and population levels. However, little is known about consistent among-individual variation within populations that could be shaped by natural selection. We studied the consistency of individual heterothermic responses to environmental challenges in a single population of yellow-necked mice (*Apodemus flavicollis*), by verifying the hypothesis that T_b variation is a repeatable trait. To induce the heterothermic response, the same individuals were repeatedly food deprived for 24 h. We measured T_b with implanted miniaturised data loggers. Before each fasting experiment, we measured basal metabolic rate (BMR). Thus, we also tested whether individual variation of heterothermy correlates with individual self-maintenance costs, and the potential benefits arising from heterothermic responses that should correlate with body size/mass. We found that some individuals clearly entered torpor while others kept T_b stable, and that there were also individuals that showed intermediate thermoregulatory patterns. Heterothermy was found to correlate negatively with body mass and slightly positively with the BMR achieved 1–2 days before fasting. Nonetheless, heterothermy was shown to be highly repeatable, irrespective of whether we controlled for self-maintenance costs and body size. Our results indicate that specialist and generalist thermoregulatory phenotypes can co-exist in a single population, creating a heterothermy continuum.

KEY WORDS: Torpor, Repeatability, Homeothermy, Endothermy, Mammals, Specialist–generalist

INTRODUCTION

Endothermic homeothermy – the maintenance of a stable and high body temperature (T_b) via internal heat production – requires effective metabolic machinery responsible for the high self-maintenance costs that characterise endothermic animals. The minimal energy requirements of a homeothermic animal can be measured as basal metabolic rate (BMR), i.e. the minimum metabolic rate under thermoneutral conditions, representing self-maintenance costs in endotherms (McNab, 1997; Burton et al., 2011). The high costs of maintaining a high T_b constantly, by way of endogenous heat production, can only be covered where there is a positive energy balance (Angilletta et al., 2010), and this condition may not always be met in natural environments. As many animals do not maintain a constant T_b, endotherms are classified as either homeotherms or heterotherms (McNab, 1983, 2002, 2008; Cooper and Geiser, 2008; Careau, 2013). In the face of an energy or water imbalance, e.g. food limitations and/or a low ambient temperature (T_a) and/or dehydration, heterotherms can reduce metabolism and T_b and enter a state of heterothermy, i.e. torpor (Heldmaier et al., 2004; Geiser, 2004; Vuarin and Henry, 2014). Torpor, defined as a state of inactivity and reduced responsiveness to stimuli, is generally considered to be adaptive in many small mammals and birds. It minimises energy expenditure but may also facilitate the avoidance of predation (Bieber and Ruf, 2009; Turbill et al., 2011; Geiser and Brigham, 2012), and in this way improve survival chances (Lynch et al., 1978; Geiser, 2004; Lebl et al., 2011; Dammhahn et al., 2017).

Heterothermy is variable, and has therefore been divided classically into daily torpor and hibernation (Geiser and Ruf, 1995). Daily torpor, usually lasting less than 24 h, is shorter and shallower, in terms of reduced T_b and metabolism, than hibernation (Geiser and Ruf, 1995; Ruf and Geiser, 2015). However, intermediate forms between hibernation and daily torpor have also been identified (Lovegrove et al., 2001; Dausmann et al., 2012; Geiser and Martin, 2013). Some species can enter torpor bouts lasting less than 24 h, with their metabolism reduced substantially (Lovegrove et al., 2001). Some animals that usually undergo daily torpor may sometimes prolong a torpor bout for a few days (Geiser and Martin, 2013). There are also species that use daily torpor, hibernation and its summer form, aestivation, and all three forms are probably based on the same physiological mechanisms (Wilz and Heldmaier, 2000; Dausmann et al., 2012). As variation in the thermoregulatory patterns of endothermic T_b extends beyond the definitions, the above classical divisions are currently under discussion (Angilletta et al., 2010; Boyles et al., 2013; van Breukelen and Martin, 2015; Levesque et al., 2016; Hetem et al., 2016).

The existence of more than two strategies or even a continuum from homeothermy through to poikilothermy has been suggested (Boyles et al., 2013; van Breukelen and Martin, 2015). Some endothermic species are only able to increase variation of T_b minimally (Chaplin et al., 1984; Yoda et al., 2000; Nieminen et al., 2013), whereas the classical heterotherms include some that can enter shallower or deeper torpor during comparable food-deprivation experiments (Walton and Andrews, 1981; Lovegrove et al., 2001; Nespolo et al., 2010; Chi et al., 2016; Boratyński et al., 2018). Adaptive heterothermy is thus variable, but is probably a

universal phenomenon among endotherms, including those considered classical homeotherms, or animals in general (Angilletta et al., 2006, 2010). This concept allows for a wider look at animal thermoregulation as a whole, with needless simplifications and divisions avoided. The generalising theoretical model accepts that thermoregulatory strategies among animals range from those characterised by wide variation in T_b (among thermal generalists) to those associated with the maintenance of almost constant T_b (in thermal specialists; Gilchrist, 1995; Angilletta et al., 2006, 2010). The model assumes that generalists can operate over a wider range of T_b, but with the consequence of worse performance, and thus fitness, than in specialists at the optimal T_b (Angilletta et al., 2006, 2010). This is considered a fundamental trade-off responsible for the existence of thermal specialists and thermal generalists where thermoregulation is concerned (Angilletta et al., 2010). The variation in T_b observed among mammals seems to support the specialist–generalist model at inter-specific (Boyles et al., 2013) and between-population organismal (Glanville et al., 2012) and biochemical levels (Seebacher and Little, 2017).

While many studies refer to individual variation in heterothermy or torpor use (Kobbe et al., 2011; McKechnie and Mzilikazi, 2011; Vuarin et al., 2013; Przybylska et al., 2017; Eto et al., 2018; Kato et al., 2018), the consistency of among-individual differences in thermoregulatory strategies remains poorly researched. Heterothermy is an extremely plastic trait, and animals may adjust T_b variation in response to the varied availability of energy, energy reserves or environmental conditions (Boyles et al., 2007; Bozinovic et al., 2007; Wojciechowski et al., 2007; Nespolo et al., 2010; Vuarin et al., 2013). Thus, if we are to test for heterothermic 'personality', among-individual variation must be quantified in a statistical model, with reference to within-individual variation. In evolutionary ecology, it is well known that only the repeatable traits within a population, representing consistent among-individual differences, may be subject to natural selection (Lessells and Boag, 1987; Falconer and Mackay, 1997).

The time consistency of a trait can be measured when multiple measurements are performed in the same individual, to allow for an estimate of an intra-class correlation coefficient. This describes the fraction ascribable to the among-individual component of phenotypic variance within overall phenotypic variation, i.e. the sum of among- and within-individual variance (Lessells and Boag, 1987; Falconer and Mackay, 1997). As among-individual phenotypic variation includes both genetic and environmental variance, a high level of repeatability may also suggest that a trait is heritable and, as such, potentially responsive to selection (Lynch and Walsh, 1998; Dohm, 2002). For these reasons, the concept of repeatability was for a long time considered important in evolutionary ecology (Lessells and Boag, 1987; Boake, 1989). Surprisingly, only a few studies have focused on the heritability as well as repeatability of heterothermy in wild populations of endotherms (Nespolo et al., 2010; Lane et al., 2011; Dammhahn et al., 2017), so despite many studies being carried out at the species-specific level, our knowledge about variation pertinent to micro-evolutionary processes remains scarce. However, such knowledge is crucial if the processes shaping wild populations in the current circumstances of global warming are to be understood.

We examined individual variation in heterothermy among wild yellow-necked mice, *Apodemus flavicollis* (Melchior 1834) – a species currently known to use torpor when facing energetic challenges, e.g. when food deprived or under harsh environmental conditions (Boratyński et al., 2018). We tested experimentally the hypothesis that T_b variation is a repeatable trait within a single wild

population of endothermic animals. We predicted that T_b variation in circumstances of short-duration (24 h) food deprivation would differ consistently among individuals. Small body size can increase both heat loss and the benefits arising from heterothermy (Angilletta et al., 2010). Moreover, high individual self-maintenance costs may leave animals prone to entering a state of torpor (Cooper and Geiser, 2008). Thus, variation in both body mass (m_b) and BMR may potentially be responsible for variation in heterothermy among individuals. To investigate the consistency of individual-level differences in heterothermy, we included m_b and BMR in the analysis. We predicted that variation in T_b would correlate positively with BMR, but negatively with m_b, and that these covariates would explain most of the among-individual variation in heterothermy.

MATERIALS AND METHODS
Animals and handling
All experimental procedures were approved by the Local Committee for Ethics in Animal Research based in Olsztyn, Poland (decision nos 27/2016 and 62/2017), as well as Poland's Ministry of the Environment (decision no. DOP-WPN.287.7.2016.AN). Mice were trapped in a 0.9 ha plot located in the Strict Reserve of Białowieża National Park, in mixed primeval forest (at 52°43′N, 23°52′E), in the course of two consecutive seasons: 2016/2017 (December–February) and 2017/2018 (December–April). The part of the forest located on the plot was formed mainly of hornbeams (*Carpinus betulus*), pedunculate oak (*Quercus robur*), Norway maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*) and Norway spruce (*Picea abies*). On the plot, 220 wooden traps (baited with oats) were set at 110 trapping points, creating a 10×10 m grid. In total, 93 animals were trapped there, and transferred to the laboratory located at the Mammal Research Institute of the Polish Academy of Sciences, marked with ID passive transponders (RF-IDW-1, CBDZOE, Gryfice, Poland) and kept individually in standard rodent cages (1264, Tecniplast, Buguggiate, Italy), with sawdust and paper tubes at T_a=19±1°C under a natural day–night cycle. Apples, carrots, rodent food (Megan, Kraków, Poland) and water were provided *ad libitum*. Approximately a week after capture, individuals were surgically implanted with miniaturised temperature-sensitive, paraffin wax-coated data loggers (iButton, models DS1923 L and DS1925 L, logger mass=1.8 g, Dallas Semiconductors, TX, USA). The loggers were set to record T_b at 10 min intervals, with a resolution of 0.062°C. Data loggers were calibrated in a water bath against a high-precision (0.1°C) mercury-in-glass thermometer (Jenatherm N, Germany) at five T_a points (17–42°C) after finishing measurements. During surgery, animals were anaesthetised under a 2% mixture of isoflurane (Iso-Vet) and medical oxygen (Air Products, Warszawa, Poland). Mice were injected with antibiotics (Enrobioflox 5%, Biowet Sp. z o.o., Gorzów Wielkopolski, Poland) dissolved in saline (Baxter Manufacturing Sp. z o.o., Warszawa, Poland) to a concentration of 2% for two consecutive days after surgery.

Experimental protocol
Fasting experiments began at least 7 days after surgery, once mice had fully recovered. Initially, we tested 10 mice by inducing heterothermic responses during a 48 h period of food deprivation. However, as three individuals (two females and a male) were unable to pass through this procedure and became hypothermic – unable to rewarm themselves – the experiment was followed by these individuals being placed at T_a=32°C so that they could rewarm passively. Seven individuals (three females and four males) were measured correctly for 48 h (Fig. 1). As there was no difference in

variation of T_b during the first and second days of fasting (see Results), and for ethical reasons, the subsequent 83 animals (29 female and 54 males) were fasted for 24 h only. Experiments began at 15:00 h CET and ended at the same time the next day. We repeated fasting experiments after intervals of at least a week, giving animals time to regain m_b before the next experiment began. All measurements were made during three consecutive experimental sessions conducted between 30 December and 24 April (Fig. S1). Following the first experimental sessions, individuals were measured, and after de-implantation of loggers, either released at the place of capture (2016/2017) or maintained under laboratory conditions (2017/2018). During the 2016/2017 winter season, four females and eight males were recaptured, re-implanted and re-measured after more than a month. Another four females and six males were maintained in laboratory conditions in winter 2017/2018, re-implanted and re-measured again more than a month later. During each year of study, each individual was fasted at least twice (see Fig. S1). In the second year of study, we did not measure the individuals that were measured during the first year.

Respirometry measurements

BMR was measured using indirect calorimetry in an open-flow respirometry system. Animals were placed in 0.85 l respirometry chambers connected to the system. The chambers were placed in three temperature-controlled cabinets (model: KB 53, Binder, Germany), in which T_a was set to thermoneutral conditions (T_a=30°C; Cygan, 1985), during daylight hours for ~4 h. Air was drawn in from outside using an air pump and dried (Drierite Co. Ltd, Xenia, OH, USA), prior to its entering the respirometry system. The air flow was divided into 10 sub-streams and regulated upstream of the chambers (to ~500 ml min^{-1}). The baseline oxygen concentration in air entering the chambers was measured in reference air streams. The airstream was switched between animal chambers and two reference lines using a computer-controlled multiplexer (MUX, Sable Systems International, North Las Vegas, NV, USA). The air from each gas stream was dried (Drierite Co. Ltd) and used for determinations with the aid of two mass-flow meters (ERG-1000, BETA-ERG, Warszawa, Poland), which were calibrated once measurement had ceased using a soap bubble flowmeter (model: Optiflow 570, Humonic Instruments Inc., USA). The fractional concentration of O_2 was measured along two lines simultaneously, using two FC-10a gas analysers (Sable Systems International). Approximately 100 ml of air leaving each respirometry chamber was sampled for 5 min in the case of each chamber, with reference gas sampled at least every 15 min. All of the electronic elements of the respirometry system were connected to a PC via an analog-to-digital interface (U12, Sable Systems International), with data acquisition (ExpeData software, Sable Systems International) at 1 Hz. Using two parallel respirometry systems, we were able to measure 10 individuals simultaneously. As animals were exchanged once during daily measurements, we were able to carry out measurements for a total of 20 individuals daily. We measured BMR 1–2 days before and 1–2 days after each fasting experiment. As measurements before fasting are more precise in describing individual initial self-maintenance costs, only these were used in the statistical analysis. As the equipment was a limiting factor, animals were always selected randomly for measurements; BMR was measured at least twice in 29 females and 49 males (Fig. S2). m_b was measured before each fasting experiment and each BMR measurement to the nearest 0.1 g (ScoutPro 200, Ohaus, Parsippany, NJ, USA).

Data preparation

Heterothermy was quantified by reference to the heterothermy index (HI; Boyles et al., 2011a), as calculated on the basis of 24 h T_b recordings during fasting and a normothermic modal T_b obtained during the alpha phase, when food was provided *ad libitum*. Oxygen consumption ($\dot{V}_{O_2}$) was calculated using eqn 11.2 of Lighton (2008), assuming a 0.8 respiratory exchange ratio. BMR was calculated as the lowest stable 2 min $\dot{V}_{O_2}$ recording.

Statistical analysis

All statistics were calculated in R 3.5.1 (https://www.R-project.org/). Linear mixed modelling procedures (LME) with restricted maximum
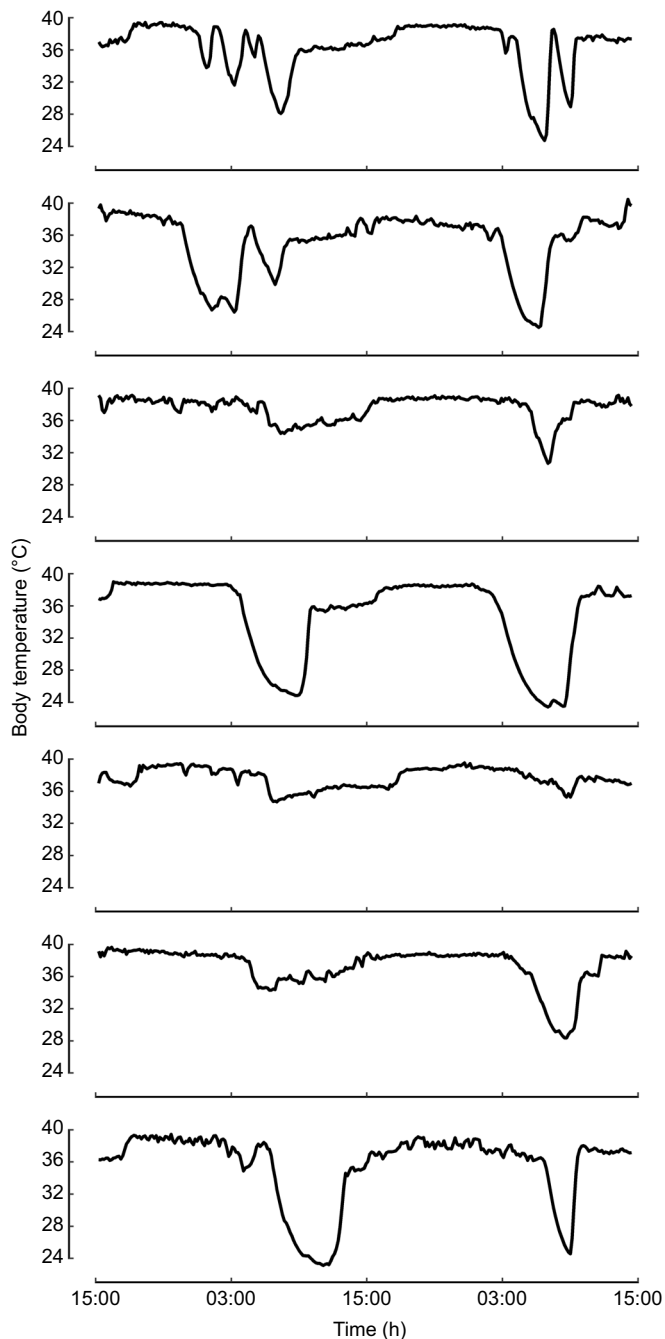

Fig. 1. Body temperature recorded in seven yellow-necked mice deprived of food for 48 h.

likelihood (REML) were used to explain variation in HI and BMR, and to obtain variance components in the lme4 package (https://CRAN.R-project.org/package=lme4). In all the LMEs, animal ID was maintained as the random effect. BMR was compared in LME where m_b was included as a covariate and sex as a factor. In the case of a right-skewed HI distribution resulting in a non-normal distribution and heteroscedasticity of model residuals, the index was always Box–Cox transformed (Box and Cox, 1964). λ values were obtained using the 'boxcoxmix' package (https://cran.r-project.org/web/packages/boxcoxmix/index.html), separately for each tested model prior to final analysis. All covariates were standardised beforehand by subtracting from the mean and dividing by the standard deviation. HI values from the first and second days of the initial 48 h fast were compared using LME, where m_b was a covariate, and the consecutive day of fasting and sex were set as fixed factors. HI of 24 h fasting in the main experiment based on all data were compared in LME where m_b was set as covariate and sex was a factor. We re-ran similar analysis on the basis of available data for BMR measurements, where residual values (rBMR: obtained from linear regression; BMR~m_b; Fig. 2) were included as a covariate. Analysis of deviance based on Type II Sum of Squares from the 'car' package (https://CRAN.R-project.org/package=car) was used to test for differences between factors. Degrees of freedom were estimated using the Kenward–Roger approximation (Luke, 2017).

Repeatability of HI and BMR was estimated as an intra-class correlation coefficient (τ), on the basis of variance components (Lessells and Boag, 1987) obtained from LMEs using the function rptR (Stoffel et al., 2017). Initially, we calculated τ values for whole-animal BMR and HI for LMEs where sex was set as a factor, and then we included the m_b covariate in the model estimation of τ for m_b-adjusted values. We estimated τ for HI on the basis of all measurements (Fig. S1). The τ value for m_b- and BMR-adjusted HI was also calculated using data with which BMR measurements were

associated by additionally including rBMR as covariate (Fig. S2). We also calculated τ values for BMR and HI in both sexes, using separate LMEs under the same procedures (Tables 1 and 2). Long-term τ values for whole-animal and m_b-adjusted HI were calculated using data obtained during the first and last fast in a particular individual collected after an interval of more than a month (mean ~87 days, range 56–105 days; Fig. S1). We also estimated long-term τ values for whole-animal and m_b-adjusted BMR, using data obtained during the first and last fast of a particular individual collected after an interval of more than a month (mean ~78 days, range 56–98 days). Because sexes did not differ in terms of the repeatability of HI and BMR, and given the small sample size in this case, the analysis was conducted in LME where sex was set as a factor.

RESULTS

BMR correlated positively with m_b of individuals (β±s.e.=0.11±0.02, t_{109}=4.62, P<0.01; Fig. 2), while m_b-adjusted BMR did not differ between sexes ($F_{1,85}$=0.17, P=0.68). There were no differences between sex- and m_b-adjusted HI obtained during the first (mean±s.d.=2.98±1.26) and second day of fasting (mean±s.d.=3.04±1.26; $F_{1,6}$=0.02, P=0.90); individuals showed similar T_b patterns on the two days (Fig. 1). There was also no difference between sexes ($F_{1,4}$=0.12, P=0.75) and covariate m_b did not affect the HI in this case (β±s.e.=0.00±0.37, t_4=0.01, P=0.99). However, HI obtained during the main experiment clearly correlated negatively with m_b (all data: β±s.e.=−0.11±0.02, t_{260}=4.63, P<0.01; data adjusted for rBMR: β±s.e.=−0.08±0.03, t_{157}=2.54, P=0.01; Fig. 3A). m_b-adjusted HI was also slightly positively correlated with rBMR (β±s.e.=0.03±0.01, t_{194}=2.54, P=0.01; Fig. 3B). There was no difference between sexes in m_b-adjusted HI ($F_{1,111}$=0.13, P=0.72) and m_b- and rBMR-adjusted HI ($F_{1,95}$=0.19, P=0.66).

Both whole-animal and m_b-adjusted BMR proved to be repeatable when all data were included in the analysis, and this
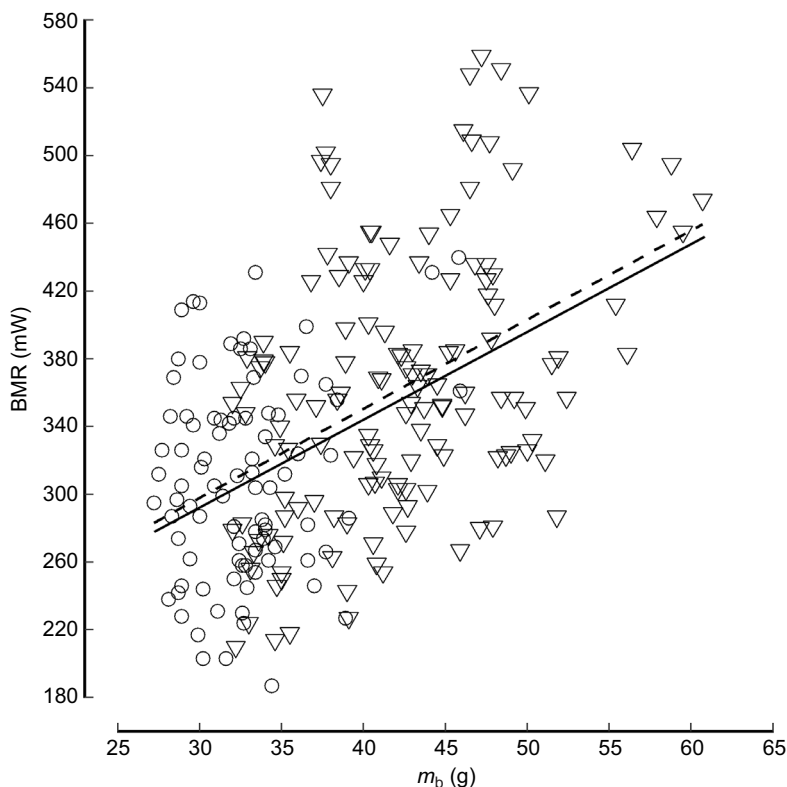

Fig. 2. Relationship between basal metabolic rate (BMR) and body mass (m_b) in male (triangles) and female (circles) yellow-necked mice. The solid line indicates the relationship predicted by the linear mixed effect model. The dashed line indicates the relationship predicted by the linear model that was applied to obtain residual BMR used for further analyses.

Table 1. Repeatability estimates (τ) for basal metabolic rate (BMR) in male, female and all yellow-necked mice based on measurements obtained at intervals of 7–98 days

Model	Males			Females			All		
	τ (95% CI)	n	N	τ (95% CI)	n	N	τ (95% CI)	n	N
~m_b	0.65 (0.49–0.76)	144	49	0.33 (0.10–0.53)	88	29	0.56 (0.43–0.67)	223	78
~1	0.66 (0.48–0.77)	144	49	0.35 (0.07–0.55)	88	29	0.58 (0.45–0.69)	223	78

'All' data were adjusted for sex as a factor. Repeatability was estimated based on models without covariates (~1) or with the covariate body mass (~m_b). CI, confidence interval; n, number of data points; N, number of individuals. In all cases, $P<0.001$.

was true when the two sexes were tested separately (Table 1). However, long-term repeatability of sex-adjusted BMR was not found to be significantly higher than zero when only the most distant measurements (Fig. S2) were analysed [whole-animal BMR: τ=0.00 (95% CI: 0.00–0.54), $P=0.50$; m_b-adjusted BMR: τ=0.00 (95% CI: 0.00–0.55), $P=1.00$]. HI proved repeatable in both sexes, regardless of whether covariates were included or not (Table 2, Fig. 4). Sex- and m_b-adjusted HI was significantly repeatable in a long-term comparison [τ=0.61 (95% CI: 0.30–0.83), $P<0.01$] and the same was true for whole-animal sex-adjusted HI [τ=0.59 (95% CI: 0.24–0.82), $P<0.01$]

DISCUSSION

Food-deprived mice showed varied thermoregulatory responses; some individuals clearly entered torpor, while others maintained homeothermy or showed intermediate T_b variation (Figs 1, 4 and 5). We found that heterothermy did not differ between the first and second day of fasting (Fig. 1). This suggests that extended food deprivation would probably not enhance individual heterothermic responses (but see Solymár et al., 2015; Przybylska et al., 2017). Short-term (24 h) experiments thus suffice to indicate among-individual differences in the capacity to down-regulate T_b, and thus metabolism, under challenging environmental conditions. As predicted, heterothermy correlated negatively with m_b (Fig. 3A), but

only slightly positively with m_b-adjusted BMR (Fig. 3B). Nonetheless, consistency among individual differences was not affected by either of these covariates (Table 2). Our study thus clearly indicates that consistently high individual variation in the capacity for heterothermy may exist within a single population. The frequency of occurrence of individuals representing different thermoregulatory strategies differed in the two consecutive years of the study. There were more animals that might be classified as specialists for homeothermic thermoregulation as opposed to generalists, with these being more numerous during the first study year and fewer in number during the second (Fig. 5). Evidently, the heterothermy continuum within the single population may be shaped by among-year differences in environmental conditions in the animals' natural habitats. This renders inappropriate any assumption regarding heterothermy, as well as the specialist–generalist conceptual model and the classical divisions based on averaged variation at the species-specific level. All models for endothermic thermoregulation should be considered at within-species or rather within-population levels, and/or include among-individual variation.

Small animals should bear higher costs of maintaining homeothermy and benefit more from heterothermy than larger ones (Angilletta et al., 2010). It has even been suggested or assumed that small body size and/or mass co-evolved with heterothermy (Geiser, 1998; Lovegrove, 2012). A negative correlation between
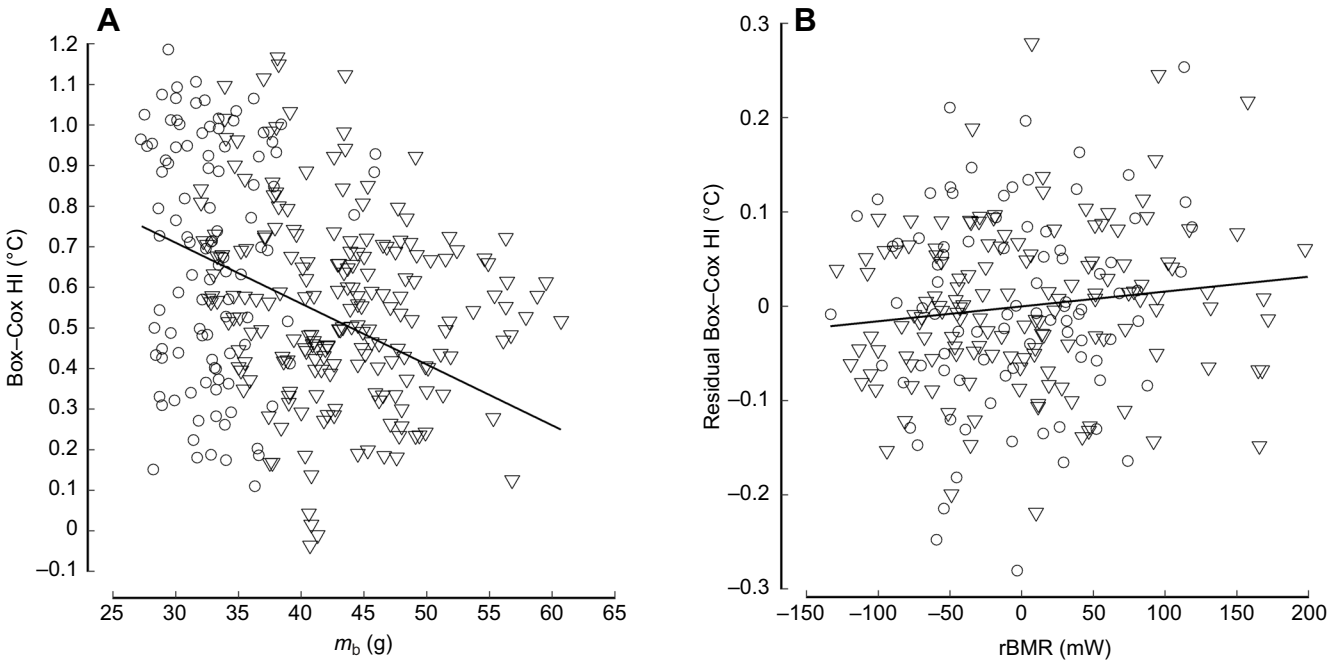

Fig. 3. Correlation between heterothermy indices (HI) and m_b and BMR. (A) Relationship between Box–Cox transformed HI and m_b in male (triangles) and female (circles) yellow-necked mice. (B) Relationship between residual Box–Cox transformed HI and residual BMR (rBMR) in male (triangles) and female (circles) yellow-necked mice. Residual Box–Cox HI were obtained from the linear mixed model: HI~m_b+sex+(1|ID). rBMR was obtained from the linear model: BMR~m_b.

Table 2. Repeatability estimates (τ) for heterothermy indices in male, female and all yellow-necked mice based on measurements obtained at intervals of 7–105 days

Model	Males			Females			All		
	τ (95% CI)	n	N	τ (95% CI)	n	N	τ (95% CI)	n	N
~m_b+rBMR*	0.84 (0.75–0.90)	144	49	0.85 (0.73–0.92)	88	29	0.83 (0.77–0.89)	223	78
~m_b*	0.83 (0.74–0.89)	144	49	0.84 (0.72–0.91)	88	29	0.83 (0.76–0.88)	223	78
~1*	0.82 (0.72–0.88)	144	49	0.83 (0.69–0.91)	88	29	0.83 (0.76–0.88)	223	78
~m_b	0.71 (0.59–0.80)	201	54	0.82 (0.69–0.89)	103	29	0.77 (0.68–0.83)	304	83
~1	0.66 (0.53–0.76)	201	54	0.82 (0.69–0.89)	103	29	0.74 (0.66–0.81)	304	83

'All' data were adjusted for sex as a factor. Repeatability was estimated based on models without (~1) or with covariates [body mass (~m_b) and residual basal metabolic rate (rBMR)]. CI, confidence interval; n, number of data points; N, number of individuals. In all cases, $P<0.001$.
*Values calculated based on data with which BMR measurements were associated.

m_b and heterothermy is apparent among birds and mammals at the species-specific level (Geiser and Ruf, 1995; Boyles et al., 2013; Ruf and Geiser, 2015). In agreement with this, HI and m_b among individual yellow-necked mice proved to correlate negatively (Fig. 3A). The suggestion could therefore be simple, that heterothermy is constrained by body size and/or individual variation in body condition (Christian and Geiser, 2007). The second circumstance is unlikely, however, as the relationship between individual m_b or body condition and heterothermy use has been found to be positive in both fattening and food-hoarding species (Kelm and von Helversen, 2007; Levesque and Tattersall, 2010; Hallam and Mzilikazi, 2011; Kobbe et al., 2011; Vuarin et al., 2013). Alternatively, the relationship between m_b and heterothermy in mice could be explained in terms of a potentially higher rewarming rate due to lower thermal inertia and/or a higher cost of maintaining homeothermy in smaller animals (Geiser and Baudinette, 1990; McKechnie and Lovegrove, 2002; Bradshaw, 2003; Angilletta et al., 2010). However, unlike inter-specific studies (see discussion in Cooper and Geiser, 2008), current work done at the intra-specific level suggests that m_b is not a major factor responsible for individual variation in heterothermy, as in populations of the laboratory mouse *Mus musculus* (Kato et al., 2018) and Japanese field mouse *Apodemus speciosus* (Eto et al., 2018). We can support this statement because, while there was a correlation between m_b and HI, this did not affect the consistency of individual variation in heterothermy (Table 2). The individual variation in fact went beyond the simple relationship between heterothermy and body size (Fig. 3A).

Heterothermic species are characterised by lower self-maintenance costs than are homeothermic ones (McNab, 1983, 2008; Cooper and Geiser, 2008; Careau, 2013). Moreover, among different species of heterotherms, BMR correlates negatively with the ability to down-regulate metabolism during torpor, suggesting that evolutionary development of endothermic metabolic machinery is a limiting factor for heterothermy (Boratyński and Szafrańska, 2018). However, at the inter-specific level, high BMR – as a significant part of an animal's energy budget (Speakman, 1999; Speakman et al., 2003; Burton et al., 2011) – could also potentially force individuals to deploy an energy-saving strategy. For example, in Siberian hamsters (*Phodopus sungorus*), an increase in BMR during acclimation to cold correlated positively with time spent in torpor (Boratyński et al., 2017). Many studies show that both whole-animal and m_b-adjusted BMR are significantly repeatable (for reviews, see Nespolo and Franco, 2007; Auer et al., 2016; see also Boratyński et al., 2017), and this is also true for the population of yellow-necked mice studied here (Table 1). The suggestion might therefore be that consistent individual differences in self-maintenance costs are potentially responsible for between-individual variation in heterothermy. Indeed, we found that
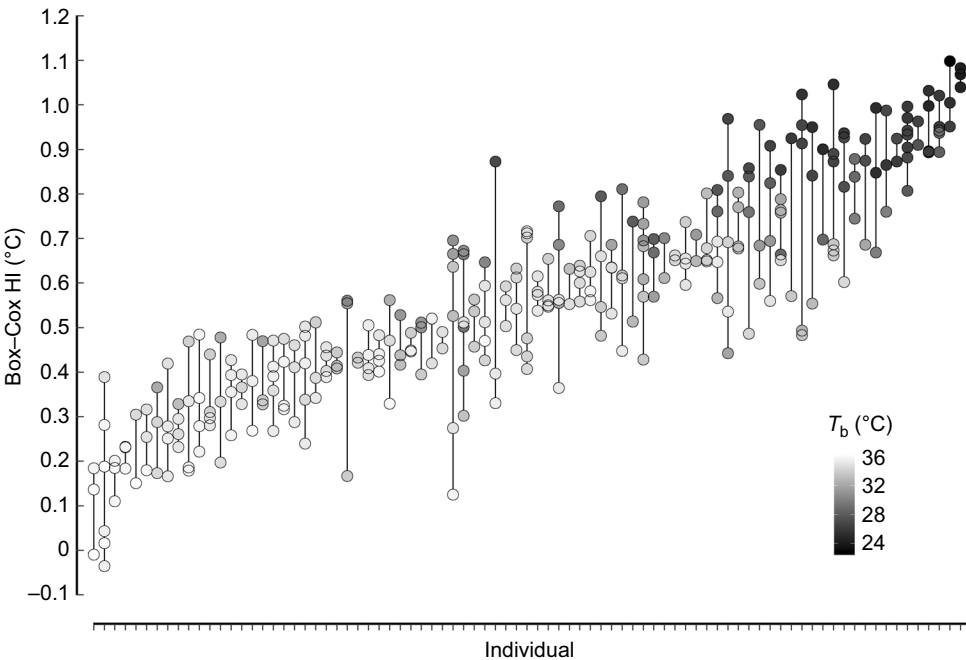

Fig. 4. Individual variation in Box-Cox transformed HI of 83 yellow-necked mice. Individuals on the graph were sorted from the least to the most heterothermic based on individual average. The grey scale indicates individual minimum body temperature (T_b) during fasting. Lines connecting data were obtained for individual mice.
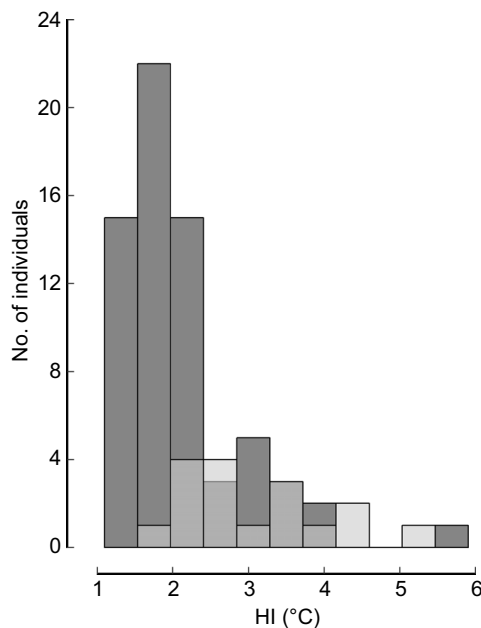
Fig. 5. Distribution of individuals characterised by different HI based on individual average measurements of 83 yellow-necked mice during the first (dark grey) and second (light grey) year of the study. The distribution of HI in a population differed significantly among years (Kolmogorov–Smirnov test: $P<0.01$) and the median (±interquartile range) obtained for animals during the first year was lower (1.82 ± 0.78) than that during the second year (2.77 ± 1.36; Wilcoxon test: $P<0.01$).

heterothermy in food-deprived mice correlated only slightly positively with rBMR obtained a day before fasting, with detectability when high individual variation in HI was accounted for, using random effect residuals (Fig. 3B). However, heterothermy in food-deprived yellow-necked mice in fact proved significantly (non-overlapping confidence intervals) more repeatable than the more labile BMR (Tables 1 and 2). Moreover, in contrast to BMR, HI was also repeatable over a long time scale. Thus, intra-individual changes in BMR can only explain part of the intra-individual variation in HI, but not necessarily the among-individual differences.

Despite individual variation in heterothermy having been discussed by several authors (Kobbe et al., 2011; McKechnie and Mzilikazi, 2011; Vuarin et al., 2013; Przybylska et al., 2017; Eto et al., 2018; Kato et al., 2018), its consistency has only been tested in a few studies (Nespolo et al., 2010; Dammhahn et al., 2017). Heterothermy was recently deemed repeatable in free-living eastern chipmunks (*Tamias striatus*), implying that individual variation results from intrinsic individual differences, or differences in microhabitat conditions experienced (Dammhahn et al., 2017). However, as we investigated individual-level variation under controlled laboratory conditions, the second explanation cannot apply to our study. We cannot fully repudiate the suggestion driven by study of the colocolo opossum (*Dromiciops gliroides*) that some individuals within a population may differ from others in being more or less prone to entering torpor (Nespolo et al., 2010; see also Boyles and Warne, 2013). However, as the repeatability of HI in the yellow-necked mouse proved almost identical, regardless of whether it was adjusted for variation in self-maintenance costs and body size, variation in thermoregulatory strategies is not easy to explain solely by reference to morphological constraints or the energetic propensity to enter torpor.

Among mammals, heterothermy has been found to be constrained by phylogeny (Boyles et al., 2013). Given also the significant repeatability (Nespolo et al., 2010; Dammhahn et al., 2017; this

study), this suggests that heterothermy is a heritable trait with a strong genetic background. However, heterogeneous nutritional experiences during fetal development may also affect heterothermy among adult mice (Kato et al., 2018). For example, continuous exposure to cold during the development of fat-tailed dunnarts (*Sminthopsis crassicaudata*) was found to increase heterothermy use among adults (Riek and Geiser, 2012). Between-individual variation in heterothermy could thus reflect a plastic phenotype and, thus, the interaction between genotype and environment as well. Last but not least, animal behavioural personality capable of explaining the significant amount of variation in energy metabolism (Careau et al., 2008) could also explain individual variation in terms of the resort to torpor (Menzies, 2010; see also Thompson et al., 2013). But, regardless of whether the heterothermic variation noted reflected individual torpor-use propensity, plasticity, personality or genetic variation as such, continuous among-individual variation in heterothermy supports the specialist–generalist model (Angilletta et al., 2010). Further studies should therefore focus on identifying the variation in animal personality (Menzies, 2010), developmental plasticity (Riek and Geiser, 2012; Kato et al., 2018) or genetic variation that may be responsible for the existence of a specialist–generalist continuum in thermoregulation strategies. For example, in contrast to other physiological traits that may affect fitness, such as BMR and resting or standard metabolic rate (reviewed in Burton et al., 2011; Pettersen et al., 2018), empirical data about the heritability of heterothermy that would indicate the extent to which it is responsive to natural selection are lacking (Angilletta et al., 2010).

Heterothermy is considered the most energy-saving strategy among small animals (Geiser, 2004), and it is often assumed that this trait affects animal fitness by improving survival chances (e.g. Ehrhardt et al., 2005; Geiser and Pavey, 2007; Rojas et al., 2014). In fact, longevity and over-winter survival rates were found to be higher in hibernating than in non-hibernating species (Turbill et al., 2011). Moreover, far fewer heterothermic than homeothermic species have become extinct during the last half century (Geiser and Turbill, 2009). It has even been suggested that, during the mass-extinction event at the Cretaceous–Palaeogene boundary, the capacity for heterothermy proved key to the survival of mammals (Lovegrove, 2012, 2016; Lovegrove et al., 2014). Nonetheless, a single study (Dammhahn et al., 2017) has explored the relationship between individual heterothermy use and both fitness components (survival and reproduction) within a population (see also Maloney et al., 2017). Interestingly, heterothermy in hibernating eastern chipmunks can sometimes correlate negatively with overwinter survival, and this most likely underlines the fluctuating accessibility of selection-modulated resources (Dammhahn et al., 2017). Moreover, heterothermy in hibernating eastern chipmunks and also in the more homeothermic wild rabbits (*Oryctolagus cuniculus*) was found to affect reproduction negatively (Dammhahn et al., 2017; Maloney et al., 2017). This means that the influence of heterothermy on fitness is not obvious, and that many trade-offs, e.g. between reproduction and survival, may be responsible for within-population variation.

Individual yellow-necked mice exposed to environmental challenges can present homeothermic, heterothermic or intermediate forms of endothermic thermoregulation (Figs 1, 4 and 5). Interestingly, the number of animals presenting particular strategies changed from year to year in the studied population (Fig. 5). We have no data to test whether these changes result from natural selection and/or developmental plasticity. However, representing as they do populations of a short-lived mammal, yellow-necked mice undergo substantial year-to-year changes caused by variations in primary

production (Pucek et al., 1993). Following synchronous seed production (masting), mainly of oak trees, the mouse population grows. Equally, during years without seeds, the population crashes as a consequence of a high winter mortality rate caused by a scarcity of resources within the environment (Pucek et al., 1993; Stenseth et al., 2002). During the first year of our study, acorn fall was ∼50% higher than in the second year (T. Podgórski, unpublished). This was accompanied by changes in the number of mice trapped on the plot at the end of the autumn and winter–spring periods; 66 individuals were captured during the first year, as opposed to only 17 during the second. We therefore hypothesised that between-year changes in the frequency of occurrence of thermoregulation specialists and generalists (Fig. 5) relate to resource availability. The specialists showing little T_b variation were dominant phenotypes when food was abundant, but eliminated when resources were limited. This may suggest the existence of a specialist–generalist trade-off (Angilletta et al., 2010), probably having a basis in the differential survival and reproductive success of more- and less-heterothermic animals (Dammhahn et al., 2017; Maloney et al., 2017).

Our study would seem to argue for the specialist–generalist model (Angilletta et al., 2010) at the between-individual level, rather than any classical division of endothermic animals into homeotherms and heterotherms: daily heterotherms and hibernators. Thus, by reference to this individual level, we agree with conclusions to the effect that the terms deployed in thermal physiology should be redefined (Angilletta et al., 2010; Canale et al., 2012; Boyles et al., 2013). Most importantly, we stress that high-consistency individual variation and a wide spectrum of thermoregulatory strategies do exist, not only among species but also within single populations. The range of HI values observed in the mice studied here extends to ∼15% of the range noted among 50 different mammal species (Boyles et al., 2013). Moreover, the relationships that describe among-species variation in heterothermy (Ruf and Geiser 2015; Boratyński and Szafrańska, 2018) may not necessarily gain application within populations. Heterothermy is considered a trait that may account for species extinctions in the face of recent global changes (Canale and Henry, 2010; Boyles et al., 2011b; Levesque et al., 2016). Against that background, our results emphasise that an understanding of within-population thermoregulatory variation and its drivers is likely to be of greater importance in thermal physiology and the prediction of climate-change impacts than are species-specific comparisons (see Levesque et al., 2016). Studies of individual variation at within-population levels can thus be seen to offer important predictions as to what trajectory change at species-specific levels will follow.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.197152.supplemental

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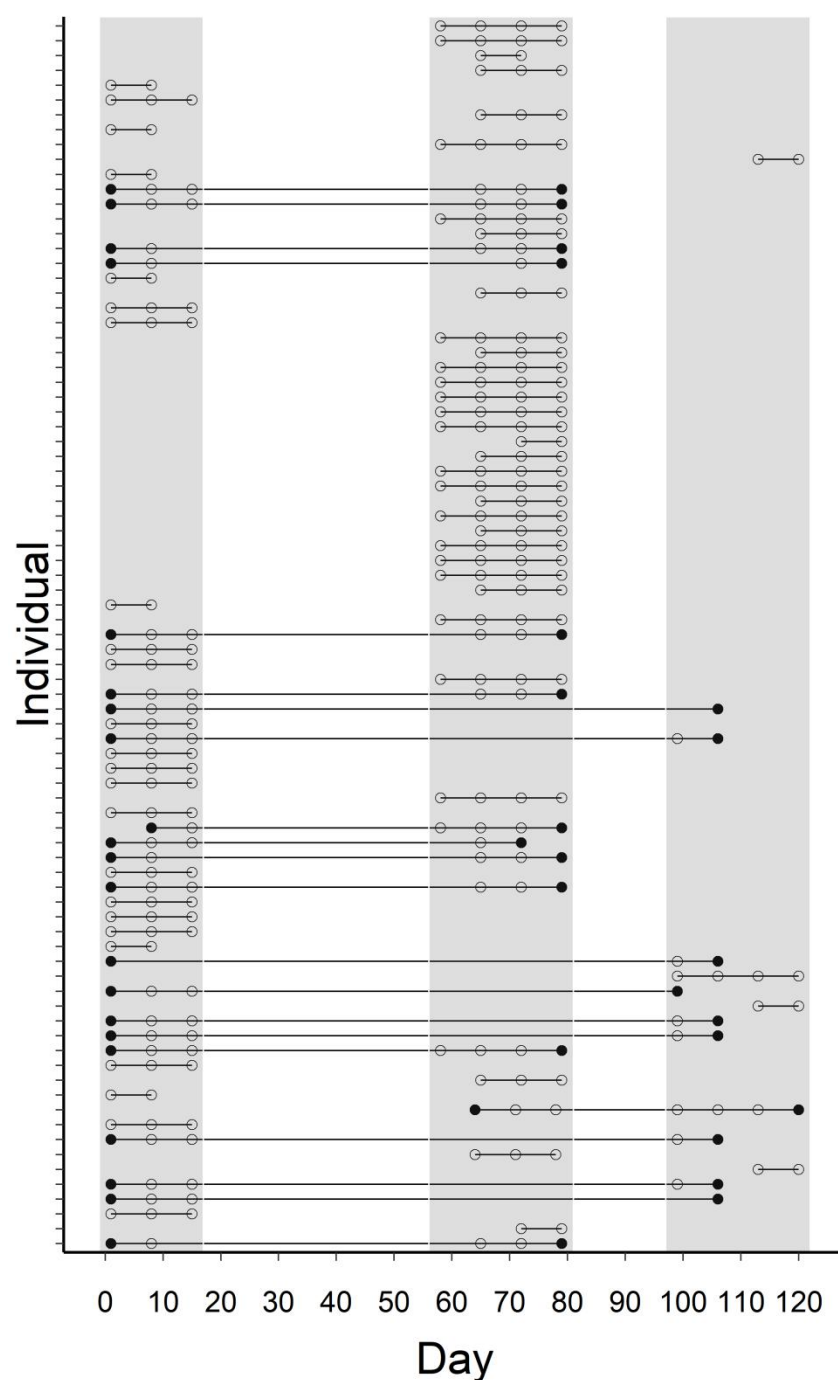
Supplementary Information

Figure S1. Measurements used to estimate repeatability of heterothermy. Points indicate individual measurement of body temperature during 24h fasting. Individuals are connected by lines. Filled points indicate the most distant measurements (>month) that were used to estimate the long-term repeatability. The shaded area refers to the experimental session. Day „0" indicates the 30th of December.
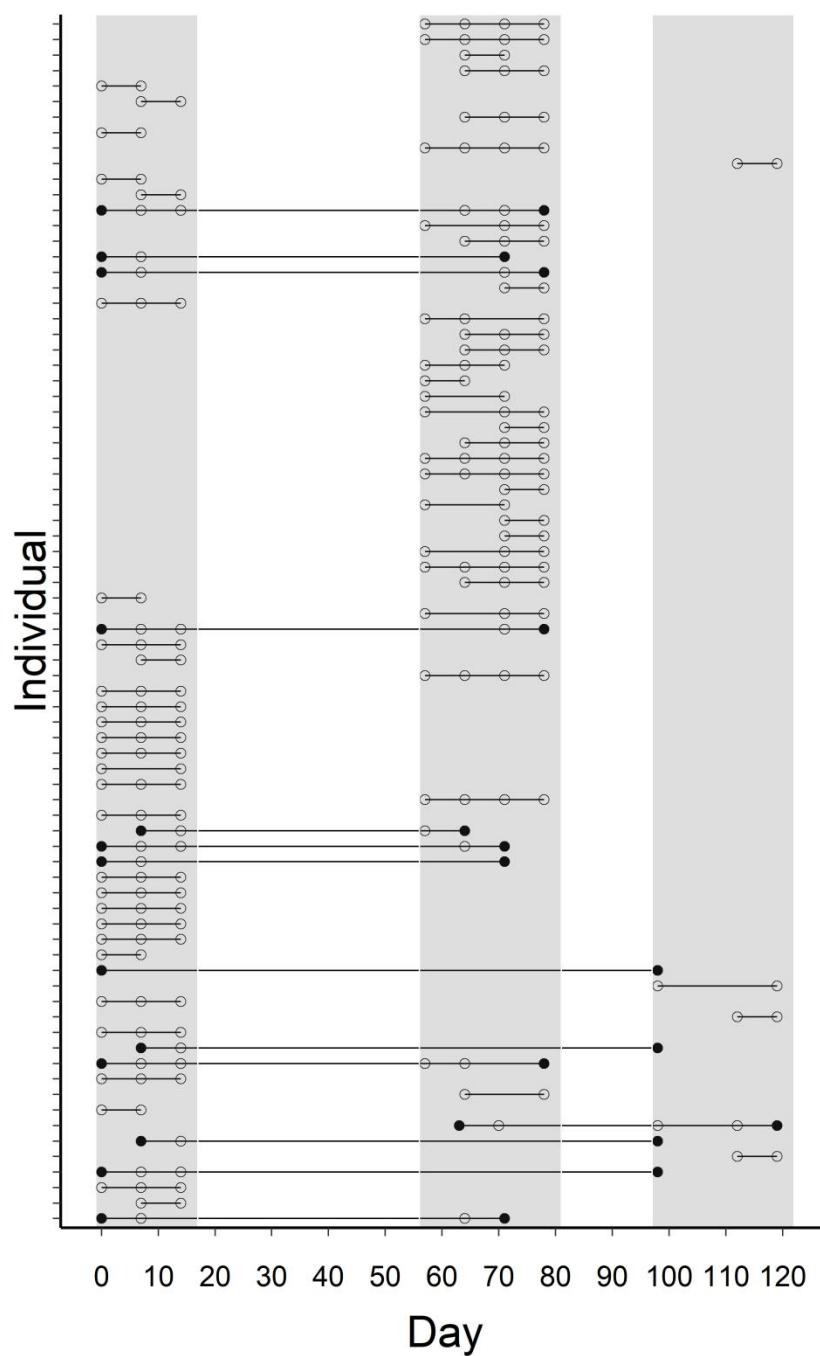
Figure S2. Measurements used to estimate repeatability of basal metabolic rate.
Points indicate measurements of basal metabolic rate the day before fasting.
Individuals are connected by lines. Filled points indicate the most distant
measurements (>month) that were used to estimate the long-term repeatability. The
shaded area refers to the experimental session. Day „0" indicates the 30yh of
December.