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Heterothermy use in winter is associated with reduced litter size during following breeding season

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Heterothermy is considered to be the most effective energy-saving strategy improving survival under natural conditions. Interspecific studies suggest that this strategy is also associated with reduced reproductive output. Yet little is known about the reproductive consequences of heterothermy use at the intraspecific level and thus its repercussions for microevolutionary processes. Moreover, as yet no study has aimed to test if litter size and juvenile mass are affected by torpor use in wild captured animals under undemanding laboratory conditions. Here we tested the hypothesis that intraspecific variation in heterothermy use is associated with different reproductive successes, being the result of the evolution of distinct life histories. We predicted that heterothermy use in winter negatively correlates with litter size and juvenile body mass during the subsequent breeding season. To test this prediction, we used yellow-necked mice from a population in which individuals consistently differ in their use of heterothermy in winter. We measured body size (head width) and body mass, basal metabolic rate, as well as metabolism and body temperature during fasting-induced torpor in wild caught mice in winter. Phenotyped mice were bred in the subsequent summer selectively – males and females with similar heterothermy characteristics were paired, the most to the least heterothermic. Dam body size, but not basal metabolism, was positively correlated with litter size (but not juvenile mass). However, when accounting for this relationship, litter size was negatively while juvenile mass was positively correlated with the average heterothermy use of a given couple. Our study indicates that heterothermy use correlates with specific life-history strategies arising from a fundamental evolutionary trade-off between survival and reproduction.

KEYWORDS

heterothermy, daily torpor, reproduction, fitness, body size, metabolic rate, body temperature

Introduction

In natural environments organisms rely on limited resources and must selectively allocate their available energy to a variety of functions, such as growth, reproduction, survival and self-maintenance. The resources that they invest into one function are no longer available to others, leading to a fundamental trade-off and the evolution of distinct life histories (Williams, 1966; Partridge and Harvey, 1988; Stearns, 1992; Roff and Fairbairn, 2007). Animal life-history strategies vary along a slow-fast continuum: species with fast-life histories mature earlier, and have larger reproductive rates and litter sizes, higher mortalities and shorter lifespan than those with slow-life histories (Stearns, 1992; Oli, 2004). It has been argued that in endothermic animals that maintain homeothermy – a high and stable body temperature (T_b) – the slow-fast continuum in the life histories of mammals is associated with the slow-fast continuum in energy metabolism. At the fast end of the life-history continuum, animals have higher metabolic costs of self-maintenance than those at the slow end (Symonds, 1999; Lovegrove, 2003).

Homeothermy enables animals to inhabit a wide range of environments; creates optimal conditions for enzyme function; supports sustained activity and locomotion; increases assimilation capacity; and can improve reproduction (Kemp, 2005). However, the fundamental cost of homeothermy is that the basal metabolic rate (BMR) at the thermoneutral conditions is several times the standard metabolic rate of similarly-sized ectothermic animals (Gillooly et al., 2017), meaning it has substantially higher energy requirements. When energy availability is limited, a high maintenance metabolism can be disadvantageous: the 'compensatory' hypothesis predicts that individuals with a low BMR can allocate more energy to growth, survival, and reproduction (Gadgil and Bossert, 1970; Steyermark, 2002; Larivee et al., 2010). By contrast, when food is not limited, the 'increased intake' hypothesis predicts that animals with a high BMR reflecting more efficient metabolic machinery can better assimilate energy for growth and reproduction, resulting in higher fitness (Bennett and Ruben, 1979; Hayes et al., 1992).

Many mammals and birds can display substantial temporal and regional variation in T_b that allows them to avoid 70-95% of the energy loss associated with their BMR (Ruf and Geiser, 2015). Thus, many endotherms reduce self-maintenance costs by abandoning homeothermic thermoregulation. This is most likely why many endothermic species have evolved or maintained the ability to be heterothermic, e.g., by being able to enter torpor (Grigg et al., 2004; Lovegrove, 2017). Torpor in endotherms is a controlled process characterized by greatly reduced metabolic rates (MR) and T_b (Ruf and Geiser, 2015), and thus, it is considered to be the most effective energy-saving response to food shortage (Geiser, 2004). Adaptive heterothermy has traditionally been divided into daily torpor and hibernation (multi-day torpor). Daily torpor is shorter and usually reduces MR and T_b less than steady-state hibernation (Geiser and Ruf, 1995). This ancestral trait in mammals (Grigg et al., 2004) likely allowed animals to survive the short- and long-term environmental devastation that occurred during the K-Pg boundary asteroid impact (Lovegrove, 2017), and nowadays may be slowing the extinction rate (Geiser and Turbill, 2009, Hanna and Cardillo, 2014). Heterothermy has also been suggested to be a strategy for avoiding predators (Hoelzl et al., 2015; Turbill and Stojanovski, 2018; Turbill et al., 2019; but see Humphries et al., 2003). Thus, many studies have assumed that heterothermy improves survival, especially under challenging environmental conditions (Ehrhardt et al., 2005; Geiser and Pavey, 2007; Rojas et al., 2014; Dammhahn et al., 2017).

Despite many benefits, heterothermy also has significant physiological costs (Humphries et al., 2003; Landes et al., 2020). Torpor can lead to memory disorder (Millesi et al., 2001), reduced immunocompetence (Bouma et al., 2010), dehydration and compromised ionic balance (Thomas and Geiser, 1997), oxidative stress (Buzadžić et al., 1990) and sleep debt (Daan et al., 1991; Royo et al., 2019). Moreover, in females torpor can be used to enhance body condition before lactation, however lowering T_b during pregnancy significantly delays juvenile development (Racey and Swift, 1981; Willis et al., 2006; Canale et al., 2012). Heterothermy can also affect negatively reproduction in males as normothermy is required for gonadal growth and maturation (Barnes et al., 1986; McAllan and Geiser, 2014). Thus, during reproduction, endotherms minimize torpor use and enter shallow heterothermy states only under energetically stressful conditions (Levesque and Lovegrove, 2014; McAllan and Geiser, 2014). During reproduction, an organism requires high MR and T_b to process and transfer nutrients to growing offspring (Kenagy et al., 1989), which correlates with high levels of reproductive hormones (Hinds et al., 1996). As torpor is associated with very low levels of reproductive hormones and MR, the physiological states of reproduction and torpor are at least partially incompatible (McAllan and Geiser, 2014).

The evolution of heterothermy may have significant implications for other life-history-related traits. The extreme form of heterothermy – hibernation, is also associated with lower basal metabolism (Cooper and Geiser, 2008; Careau, 2013; Boratyński and Szafrańska, 2018) as well as with a slow-living life history (Turbill et al., 2011; Bieber et al., 2018). Since hibernating species have longer life spans and higher survival but lower reproductive rates than non-hibernating species, studies have suggested these contrasting thermoregulatory strategies are associated with an evolutionary trade-off between survival and reproduction (Turbill et al., 2011; Ruf et al., 2012). Heterothermy use consistently differs among individuals within populations (Nespolo et al., 2010; Dammhahn et al., 2017; Boratyński et al., 2019), and it is likely a heritable trait (Lane et al., 2011; Grabek et al., 2019). However, little is known about the fitness consequences of among-individual variation in heterothermy use at the population level (but see Dammhahn et al., 2017).

Here we tested the hypothesis that intraspecific variation in heterothermy use is associated with variation in reproductive success, as a result of the evolution of distinct life histories within a species. To test this prediction, we measured individual use of winter heterothermy during short-term fasting in wild-caught yellow-necked mice *Apodemus flavicollis*, and then reproduced them selectively. We expected that heterothermy use by individuals in winter would negatively correlate with their litter size and mass during the subsequent reproductive season.

Material and methods

Animals and protocol

We studied mice from a single population in Białowieża Forest (Eastern Poland) in primaeval stands composed mainly of pedunculate oak *Quercus robur* and hornbeam *Carpinus betulus* trees. The wild mice (N=133) were captured at 39 locations at least ~400 m apart using wooden live traps and transferred to a laboratory in the Mammal Research Institute in Białowieża Village (~15km away from sampling sites). Before carrying out laboratory measurements, mice were kept in standard individual rodent cages at 16°C, under natural photoperiod and with access to water and food *ad libitum*. Before midday on trapping day, each animal was tagged individually with thermosensitive programmable identification transponders (model: IPTT-300, Biomedic Data Systems Inc., Seaford, US). Transponders were pre-calibrated in a water bath at five temperatures (range=18-42°C) against a precise (0.1°C) mercury-in-glass thermometer (Jenatherm N, Germany). Transponders were implanted subcutaneously under a 2% mixture of isoflurane (Iso-Vet) and oxygen anesthetic in the abdomen. While mice were still under anesthesia we measured their head width (HW) as a body size indicator with a caliper, to the nearest 0.1mm (Measy DG, Ecotone, Gdańsk, Poland) and weighed them to the nearest 0.1g (ScoutPro 200, Ohaus, Parsippany, NJ, USA). After a ~week of habituation, BMR (and corresponding body mass) was measured in each mouse. After a second ~week, we measured MR and T_b during 23h fasting experiments aimed at inducing torpor. All phenotypic measurements were done between end of January and the 21st of March in the winters of 2022 or 2023. After measurements, animals that used torpor (defined as entering an evident state of torpor with T_b<32°C) characterized by varied use of heterothermy were selected for breeding (40 individuals from 21 locations: 20 females and 20 males). In mice selected for breeding, we repeated measurements of HW. Between May and September, selected pairs were placed in big breeding cages equipped with branches allowing them to climb, and lined with leaves, wooden shavings, coco fibers and nest-box. The breeding cages were housed in walk-in climatic chambers at T_a=23°C with a natural photoperiod. Paired heterothermic mice were selected based on the degree of heterothermy they used (the most heterothermic male was paired with the most heterothermic female). After three weeks males were separated from females and released at their place of capture. We checked for the presence of juveniles twice a week. In total 17 pairs (each individual was allowed to breed once) with contrasting heterothermy use were successfully bred. One-month-old juveniles were separated from their mothers (and housed in laboratory till natural death), counted, and weighed to the nearest 0.1g. Females were then released at their place of capture.

Measurements

The metabolic rate of mice was measured as oxygen consumption using indirect calorimetry with an open-flow respirometry a ~week after capture. The air used for measurements was pulled from outside, dried (silica gel 2-5mm, Chempur, Piekary Śląskie, Poland) and purified with activated coconut carbon (0.6-2.36mm, Acrivsorb 109, Browin S.zoo, Łódź, Poland). For BMR measurements animals were held in 300mL custom-made glass chambers placed at a thermoneutral zone (~30°C; Cygan 1985) in temperature-controlled cabinets (model: KB 53, Binder GmbH, Tuttlingen, Germany), and the flow through each chamber was set to ~250mL·min^{-1} and measured incurrently (FlowBar-8, Sable Systems International, Las Vegas USA; henceforth: SSI). The chambers were connected to a two-line multiplexer (MUX, SSI), which allowed us to extract air from two chambers at once and measure six individuals by sampling air automatically. During BMR measurements animals were held in chambers for ~4h, meaning we measured 12 individuals in an 8h work day. The dry air (silica gel 2-5mm, Chempur, Piekary Śląskie, Poland) leaving chamber was sampled at a rate of ~100mL·min^{-1} to pass through one of two gas analyzers (FC-10a, SSI) connected to one of two lines. The electronic elements of the respirometry system were connected to the computer via an analogue-digital interface (UI-2, SSI), and data were acquired at 1Hz using the software (ExpeData, SSI). During metabolic rate measurements, the air from each chamber was sampled for 140s, every 10min (initial and final baselines were sampled for 10s and 170s, respectively).

To induce torpor we deprived animals of food for ~23h in moderately cold conditions (~16°C). A similar protocol was used successfully by us previously (see: Boratyński et al., 2018; Boratyński et al., 2019; Boratyński et al., 2021). Heterothermy use measurements were conducted after BMR measurements (up to two weeks after capture). Continuous automatic T_b measurements (sampled every few seconds) carried out during short-term fasting were obtained from the transponders with dedicated readers (FSP-7005; Bio Medic Data Systems, Inc., Seaford, USA; henceforth: BMDS) connected to PCs via data acquisition stations (DAS-8010; BMDS). Due to equipment limitations, we measured T_b in five individuals daily. Animals were placed in 850mL chambers constructed of polypropylene containers (model: HPL 808, LocknLock Co., Seoul, Republic of Korea) lined with 4g of shavings. Chambers were connected to a respirometry system (see above), and the air was set to flow through at a rate of ~350mL·min^{-1}. The air leaving each chamber was subsampled at a rate of ~200mL·min^{-1}. This allowed us to measure both T_b and MR over ~23h starting at ~2 pm of the first day and finishing at ~1 pm of the next. One hour was needed to switch animals between measurements. We used the same sampling protocol and respirometry system, as for BMR, to obtain metabolic measurements during fasting.

Data analysis

Calculations

Oxygen consumption ($\dot{V}O2$) was calculated following equation 10.2 in Lighton (2008) assuming a 0.8 respiratory exchange ratio. For each individual, in total, we obtained at least 20 and 140 samples of V̇O2 while measuring BMR and torpor use, respectively. We selected only the last 20s (120s were needed to full flush of air in the oxygen analyzers) of each 140s sample as individual metabolic rate measurements. We considered BMR and torpor metabolic rate (TMR) as the lowest values obtained for a given mouse.

Many distinct methods exist to describe thermoregulatory patterns in endotherms (Boyles, 2019). However, most of them are based on just one component (mostly T_b). Here we used principal component analysis (PCA) to obtain a single variable describing an individual's heterothermy use as a consequence of torpor bout duration (TBD: time spent with T_b<32°C), minimum T_b ($T_{b\text{-min}}$) during torpor, and corresponding metabolic suppression (for details of physiological parameters see Supplementary Table S1). Since m_b-adjusted MR during torpor correlates positively with m_b-adjusted BMR (Boratyński and Szafrańska, 2018), we calculated metabolic suppression as maintenance minus torpor metabolism. The relative reduction of metabolism during torpor (RRMT) was calculated as the difference between residual BMR and residual TMR (residuals were calculated based on linear relationships between $\log_{10}$-transformed BMR and $\log_{10}$-transformed m_b, and between $\log_{10}$-transformed TMR and $\log_{10}$-transformed m_b, respectively).

We calculated relative litter size as the number of juveniles in a given litter divided by the maximum number of juveniles ever recorded in a litter in the local population (eight individuals, Adamczewska, 1961). We calculated best linear unbiased predictions (BLUP) as conditional modes of the random effects from the linear mixed model (juvenile m_b was the dependent variable, sex was a factor and couple was a random effect) to estimate the average m_b for a litter.

Statistics

All statistics were done in R v.4.3.1 (https://www.R-project.org/).

To account for all three parameters of heterothermy (TBD, $T_{b\text{-min}}$, and RRMT) in the future analysis we used PCA to estimate their common vector as the first principal component (PC1). PC1 correlated positively with $\log_{10}$-transformed TBD and RRMT but negatively with $\log_{10}$-transformed $T_{b\text{-min}}$ (see Results).

Since variance in heterothermy use differed between males and females, we compared PC1-heterothermy using a generalized least squares model (GLS) using the R function gls. We used the constant variance function (varIdent) to allow unequal variations in heterothermy use for male and female mice. In the GLS for PC1-heterothermy, we included as covariates residual head width (obtained from the linear model: HW~sex) and body condition (obtained as residuals from the linear model: $\log_{10}$-transformed m_b~$\log_{10}$-transformed HW) and sex (a centered continuous predictor) as a factor. In this model, we also included interactions between sex and body condition, and sex and residual HW.

Since relative litter size and BLUP-juvenile m_b were correlated (Pearson r=-0.55, *P*=0.022), we compared them in a bivariate linear model (LM). This model included as covariates dam body size (female head width), dam residual basal metabolic rate (obtained from the linear relationship between BMR and m_b), and average PC1-heterothermy for dam and sire.

Function visreg of R was use for visualization of regression models. All continuous variables were scaled using R function scale prior to analysis.

Results

PC1 explained ~83% of the variance in the three studied parameters of heterothermy and was positively correlated with TBD (r=0.93) and RRMT (r=0.86) but negatively with $T_{b\text{-min}}$ (r=-0.94). Body size and body condition and its interactions with sex did not explain PC1 (heterothermy use), which was only higher in females (PC1: mean ± SE = 0.58 ± 0.94) than males (PC1: mean ± SE = -0.58 ± 1.88; Table 1).

As a result of selective breeding, PC1-heterothermy in dam was highly correlated with PC1-heterothermy in sire (Pearson r=0.64, *P*=0.006).

Dam residual BMR was not a significant predictor of relative litter size or BLUP-juvenile m_b in bivariate the LM (Table 2). Litter size and BLUP-juvenile m_b were, however, predicted by dam body size and the heterothermy of males and females that bred together (Table 2). The univariate model for relative litter size indicated it was positively correlated with dam body size (Figure 1A) and negatively with the average of PC1 heterothermy use of dam and

TABLE 1 Results of the generalized least squares model explaining variation in heterothermy use in male and female yellow-necked mice.

Explanatory variable	β ± SE	df	χ^2	*P*
Residual body size	0.29 ± 0.18	1	2.52	0.113
Body condition	0.16 ± 0.16	1	1.00	0.317
Sex (males)	**-0.79 ± 0.33**	**1**	**5.77**	**0.016**
Residual body size:Sex	-0.17 ± 0.37	1	0.21	0.644
Body condition:Sex	-0.18 ± 0.32	1	0.34	0.560
Residual		28		

Heterothermy use was quantified as the first principal component, which correlated with torpor bout duration (0.93), minimum body temperature (-0.94), and relative reduction in body mass-independent metabolism (0.86) during torpor. Body size was quantified as the linear model residual head width that was not explained by sex. Body condition was defined as the residuals from linear regression between $\log_{10}$-transformed body mass and $\log_{10}$-transformed head width. Sex was included as a centered continuous predictor. Bold indicates significance.

sire (Figure 1B, Table 2). The univariate model for BLUP-juvenile m_b indicated only a positive correlation with PC1-heterothermy use of dam and sire (Figure 1C, Table 2).

Discussion

We tested the hypothesis that heterothermy use in winter has long-lasting consequences in the breeding season, under laboratory conditions with unlimited resource availability and non-demanding thermal conditions. We predicted that if heterothermy is associated with long life histories, then more heterothermic animals would have lower reproductive success than less heterothermic ones. We used the yellow-necked mouse as a model for testing these predictions as within a single population of this species we previously found consistent and large variation in thermoregulatory strategies among individuals (Boratyński et al., 2019). We found that the relative litter size was positively correlated with the body size of females, which is consistent with many previous studies (review in: Weller et al., 2023). However, when accounting for this, the relative litter size of a given couple was negatively correlated with the average heterothermy use (a result of torpor depth and length, and corresponding metabolic suppression under heterothermy) of the dam and sire in a couple. This strongly supports previous findings that overall reproductive success (result of litter size and offspring survival) is reduced in most heterothermic individuals within a population (Dammhahn et al., 2017). Thus, our results support the idea that this survival strategy is associated with evolutionary trade-offs and the evolution of distinct life histories.

The 'assimilation capacity' hypothesis predicts that higher maternal maintenance metabolism correlates positively with parental investments and as such can improve reproductive success (Koteja, 2000, 2004). Several studies indicate that BMR and the related sustained MR during reproduction can positively affects parental investments, resulting in improved juvenile growth (Glazier, 1985, Derting, 1989; Kam et al., 2003; Speakman et al., 2004; Sadowska et al., 2013). We measured BMR only in the winter season however, several studies indicate that maintenance metabolism is a repeatable trait (Nespolo and Franco, 2007; White et al., 2013; Auer et al., 2016; for yellow-necked mice see: Boratyński et al., 2019; Strijker et al., 2023) indicating that among-individual variation should be consistent over-time. Thus if maintenance metabolism has significant evolutionary consequences, female maintenance metabolism should positively correlate with litter size and/or juvenile mass. In our study however, mouse BMR was not a significant predictor of relative litter size nor of juvenile average body mass (Table 1), meaning these results did not support the 'assimilation capacity' hypothesis. Although a link between litter size and m_b independent variation in BMR has been found at the interspecific level (Kalcounis-Rueppell, 2007), intraspecific studies have not found support for this relationship (Hayes et al., 1992; Johnson et al., 2001; Johnston et al., 2007; review in: Pettersen et al., 2018; but see also: Boratyński et al., 2013). However, overall reproductive success has been found to correlate positively with BMR in free-ranging bank voles (Boratyński and Koteja, 2010). This suggests that maternal maintenance metabolism affects an interaction between mating, parental investment and offspring survival rather than only litter size.

Several hypotheses have been proposed to explain variation in reproductive fitness parameters (e.g. litter size) and/or maternal investment (e.g. offspring mass) in wild living populations – which is likely shaped by a complex interplay between competition, offspring and parent survival, dam body condition, reproductive plasticity and environmental variability (Lack, 1966; Mountford, 1968; Perrins and

TABLE 2 Results of the bivariate linear model explaining variation in relative litter size and litter mass (BLUP-juvenile mass: best linear unbiased predictions for the random effect litter) in 17 breeding mouse couples that had contrasting thermoregulatory strategies.

Explanatory variable	Pillai trace	df	F	*P*
Dam body size	**0.56**	**2,12**	**7.42**	**0.008**
Dam rBMR	0.04	2,12	0.24	0.787
Couple heterothermy	**0.47**	**2,12**	**5.35**	**0.022**
Relative litter size				
Explanatory variable	β ± SE		t	*P*
Dam body size	**0.88 ± 0.22**		**4.01**	**0.002**
Dam rBMR	-0.08 ± 0.18		0.43	0.677
Couple heterothermy	**-0.65 ± 0.22**		**2.97**	**0.011**
BULP – juvenile body mass				
Explanatory variable	β ± SE		t	*P*
Dam body size	-0.43 ± 0.26		1.62	0.130
Dam rBMR	0.16 ± 0.22		0.71	0.491
Couple heterothermy	**0.71 ± 0.26**		**2.67**	**0.019**

Dam body size was quantified as head width. Dam residual basal metabolic rate (BMR) was quantified as residuals from the linear relationship between BMR and body mass. Heterothermy was included as the average values obtained for couples. Bold indicates significance.

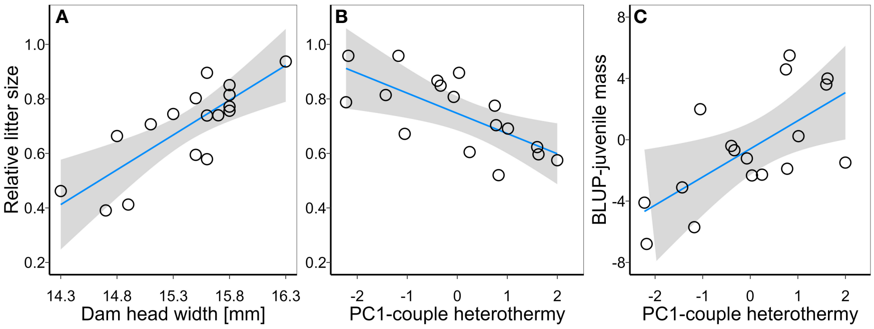

FIGURE 1
Relationships between relative litter size and **(A)** dam body size (Dam head width) and **(B)** heterothermy use of breeding couples (PC1-couple heterothermy); and the relationship between best linear unbiased predictions (BLUP) for juvenile body mass **(C)** and heterothermy use by breeding couple.

Moss, 1975; Reznick, 1985; Boyce and Perrins, 1987; Risch et al., 1995; Morris, 1998; Risch et al., 2007). It is apparent, however, that maternal body size/weight is a key trait associated with litter size and/or litter mass. Body size/mass of adults tends to correlate negatively with litter size across a variety of different-size species (Tuomi, 1980), but both traits are correlated positively at the intraspecific level (Schai-Braun et al., 2021; Weller et al., 2023). The positive correlation between female body size and litter size (Figure 1A) observed in our study is following this general pattern. Body size/mass and litter size/mass can be heritable (Réale et al., 1999; Thomas et al., 2002; Coltman, 2005; Hare and Leighton, 2006), and artificial studies have indicated that selecting for one of these quantitative traits can result in a correlated increase of the other (Bünger et al., 2005). According to the 'resource availability hypothesis' the body mass/size is positively correlated with resource availability (Blackburn and Hawkins, 2004; Alhajeri et al., 2020). Since we collected animals from different locations that likely varied in resource availability, the correlation between maternal size and litter size may reflect natural selection constraining allometry limiting female reproductive capacity (e.g. uterine capacity). Alternatively for the natural selection, a similar might be the result of permanent environmental effect, shaping parental phenotype during development.

When accounting for the relationship between dam body size and litter size, parents' heterothermy explained the variation in number of juveniles. Heterothermy use in winter among individuals from a single population has previously been found to correlate negatively with overall reproductive success in summer in free-ranging eastern chipmunks *Tamias striatus* (Dammhahn et al., 2017). This suggests the existence of a trade-off between this energy-saving strategy for increasing survival and reproductive investments. However, overall reproductive success is the result of mating intensity, litter size and offspring survival; thus, it is unclear from that study which of these traits (if any alone) negatively correlates with heterothermy. As we bred mice under laboratory conditions with access to unlimited food resources and at undemanding thermal conditions, the reproductive success we observed can be considered their reproductive potential (likely close to maximal). Thus, our study suggests that the reduced reproductive success observed in free-ranging animals using heterothermy does not necessarily result from losing mating opportunities or from other traits (as suggested by Dammhahn et al., 2017), but could be the direct result of highly heterothermic animals having reduced reproductive capacity. We also observed that bred couples' heterothermy use was positively correlated with the body mass of one-month-old juveniles. Since higher juvenile body mass can improve survival (Ringsby et al., 1998; Brown et al., 2022), this result suggests that heterothermic animals invest more into offspring quality than quantity. However, there was also a negative correlation between average juvenile mass and juvenile number. Thus, lower juvenile mass in less heterothermic animals does not necessarily have to be correlated with parents' physiologies but could be constrained by higher litter size itself.

The modern theoretical model for adaptive thermoregulation suggests the existence of a continuum of thermoregulatory strategies (Angilletta et al., 2006; 2010). Since the overall area under the theoretical performance curve is expected to be maximized (but also finite), thermoregulatory specialists (e.g. strictly homeothermic animals) operating at a narrow T_b range should perform better at optimal temperatures than thermoregulatory generalists – heterothermic animals characterized by a wide T_b range (Angilletta et al., 2006, 2010). This varying thermosensitivity can underlie/cause (Boyles and Warne, 2013; Seebacher and Little, 2017) intraindividual variation in the performance of skeletal muscles (Choi et al., 1998; Rojas et al., 2012; James et al., 2015), immune function (Butler et al., 2013), and generally complex molecular networks (Schwartz and Bronikowski, 2013). Finally, the specialist-generalist model predicts that, as a result of the cost-benefit trade-off, different thermoregulatory strategies should promote distinct (reproduction or survival) fitness components (Angilletta et al., 2010). If heterothermy improves survival (Turbill et al., 2011; Dammhahn et al., 2017; Geiser and Ruf, 2023) but simultaneously impairs reproduction (Dammhahn et al., 2017; this study), then both these strategies can coexist among individuals within a single population as a result of the fundamental evolutionary trade-off.

The evolutionary consequences of the different thermoregulatory strategies could have important implications for mouse population dynamics, which is strongly affected by food availability (Pucek et al., 1993; Bogdziewicz et al., 2016). Typically, the mouse population increases in the spring and summer following masting (synchronized seed production of forest trees) and crashes two years later (Pucek et al., 1993; Zwolak et al., 2016). While the post-mast increase in rodent abundance is most likely driven by an extended breeding season, winter breeding and high overwinter survival (Pucek et al., 1993; Zwolak et al., 2016), the factors affecting the post-outbreak crash are less well-known but probably involve density-dependent inhibition of maturation and breeding (Elias et al., 2006), predation (Pucek et al., 1993), disease, and parasites (Pedersen and Greives, 2008). The results of our experiment provide another explanation for the observed steep decline in mouse abundances after the post-masting peak. The proportion of individuals using heterothermy in winter increases when food resources become scarce (Dammhahn et al., 2017; Boratyński et al., 2021), which likely contributes to the much lower reproduction rates in the following breeding season.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Local Committee for Ethics in Animal Research in Olsztyn (decision no. 67/2020). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JB: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review and editing. KI: Investigation, Writing – review and editing. KZ: Conceptualization, Funding acquisition, Investigation, Supervision, Writing – review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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