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Continuous growth through winter correlates with increased resting metabolic rate but does not affect daily energy budgets due to torpor use

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Abstract

Small mammals that are specialists in homeothermic thermoregulation reduce their self-maintenance costs of normothermy to survive the winter. By contrast, heterothermic ones that are considered generalists in thermoregulation can lower energy expenditure by entering torpor. It is well known that different species vary the use of their strategies to cope with harsh winters in temperate zones; however, little is still known about the intraspecific variation within populations and the associated external and internal factors. We hypothesized that yellow-necked mice *Apodemus flavicollis* decrease their resting metabolic rate (RMR) from autumn to winter, and then increase it during spring. However, since the alternative for seasonal reduction of RMR could be the development of heterothermy, we also considered the use of this strategy. We measured body mass (m_b), RMR, and body temperature (T_b) of mice during 2 consecutive years. In the 1st year, mice decreased whole animal RMR in winter, but did not do so in the 2nd year. All mice entered torpor during the 2nd winter, whereas only a few did so during the first one. Mice showed a continuous increase of m_b, which was steepest during the 2nd year. The relationship between RMR and m_b varied among seasons and years most likely due to different mouse development stages. The m_b gain at the individual level was correlated positively with RMR and heterothermy. This indicates that high metabolism in winter supports the growth of smaller animals, which use torpor as a compensatory mechanism. Isotope composition of mice hair suggests that in the 1st year they fed mainly on seeds, while in the 2nd, they likely consumed significant amounts of less digestible herbs. The study suggests that the use of specialist or generalist thermoregulatory strategies can differ with environmental variation and associated differences in developmental processes.

Key words: growth rate, heterothermy, phenotypic flexibility, resting metabolic rate, torpor

As a result of internal generation of heat, endothermic animals are able to maintain homeothermy—a high and relatively stable body temperature (T_b), even when exposed to cold. This allows them to operate at almost constant T_b across a wide range of ambient

temperatures (T_a; Scholander et al. 1950). However, endothermy is associated with high costs of self-maintenance readily measurable in terms of basal metabolic rate (BMR)—the metabolism measured in adult, post-absorptive, normothermic animals in a resting state and experiencing thermoneutral conditions (Riddle et al. 1932; Scholander et al. 1950; McNab 1997). BMR is a summarizing product of all the processes of energy transformation occurring in the metabolically active tissues of individual organisms, and as such is considered the lowest rate of energy expenditure under homeothermy (Burton et al. 2011). BMR can correlate positively with the total daily energy expenditure (DEE) of an animal, in line with the significant role played in its energy budget (Ricklefs et al. 1996; Speakman 2000; Portugal et al. 2016).

Many endothermic animals do not maintain homeothermy permanently and are characterized by a capacity to achieve temporary reductions in both metabolism and T_b through entry into daily or hibernation-related torpor (Ruf and Geiser 2015), or other intermediate forms of heterothermy (Boyles et al. 2013; Boratyński et al. 2019). This is the fastest and most effective energy-saving strategy that small animals use in situations where resources are not readily available (Geiser 2004). Endotherms may thus be classified as specialists or generalists regarding homeothermic thermoregulation, as characterized by narrow or wide variations in T_b (Angilletta et al. 2010). Generalists are able to actively avoid the costs of self-maintenance of their endothermic machinery by increasing T_b variability, and by entering different thermoregulatory states in response to environmental challenges (Geiser 2004; Angilletta et al. 2010). Specialists in homeothermic thermoregulation are able to manipulate their T_b across a narrow range, with corresponding higher energy demands (Angilletta et al. 2010). This physiological specialization enables them to outperform generalists (Angilletta et al. 2010). However, the associated high self-maintenance costs may negatively affect fitness when the availability of energy is limited and/or when climatic conditions are harsh (Burton et al. 2011). This is most likely why many specialists for homeothermic thermoregulation have the capacity to achieve plastic adjustment of energetics (reviews in Swanson et al. 2017; Norin and Metcalfe 2019).

The endothermic energy metabolism is not fixed in any given individual; many species of birds and mammals have the ability to adjust it in response to variable environmental factors (reviews in Lovegrove 2005; McKechnie and Swanson 2010; Swanson et al. 2017; Norin and Metcalfe 2019). In the course of an individual's life, both irreversible and reversible phenotypic changes can occur in response to variable environmental conditions (Piersma and Drent 2003; Pigliucci 2005). For example, BMR can to some extent become determined and fixed in a given individual as a result of plastic responses to environmental conditions at the time of postnatal development (Hammond et al. 2002; Broggi et al. 2005; Verhulst et al. 2006; Careau et al. 2014a, 2014b). However, an adult endothermic animal can also achieve reversible (flexible) adjustments of BMR in response to unpredictable environmental changes, like variations in T_a (McKechnie et al. 2007; van de Ven et al. 2013; Boratyński et al. 2016; 2017a) and/or food availability (Maldonado et al. 2012). Thus, animals evolved a capacity to achieve reversible adjustments of their phenotypes in response to unpredictable intraannual environmental variation.

Many mammals reduce self-maintenance costs to survive winter, given very low T_a and the high costs of obtaining food (Heldmaier 1989; Lovegrove 2005). These adjustments are possible because the consequences of temperate zone winters are highly predictable and efficient physiological mechanisms (seasonal flexibility) have evolved in response. Given their existence in a world characterized by seasonality, mammals and other organisms are capable of achieving suitable adjustments of energy requirements in line with a given season by tracking predictable events, such as changing photoperiod, which are reliable signals compared to other environmental changes that occur seasonally (Bradshaw and Holzapfel 2007; Boratyński et al. 2017b). A photoperiodism refers to the seasonal acclimatization that occurs and is triggered by changes in day length, and is closely controlled by the endocrine system (Steinlechner et al. 1987; Scherbarth and Steinlechner 2010). Survival in harsh winter conditions *inter alia* involves many small non-hibernating mammals experiencing decreases in body size/mass (Iverson and Turner 1974; Wade and Bartness 1984; Heldmaier 1989; Aars and Ims 2002; Lovegrove 2005; Szafrańska et al. 2013; Zub et al. 2014). Such declines may also concern organs that are most active metabolically, including the liver, gastrointestinal tract, muscles, and brain (Pucek 1965; Lynch 1973; Zuercher et al. 1999; Song and Wang 2006; Lázaro et al. 2018; but see also Bozinovic et al. 1990). Reductions in the size of body and organs result in a decrease of whole animal BMR, and thus in energy requirements during winter (Heldmaier 1989; Taylor et al. 2012). However, small mammals can also achieve energy savings through a reduction in body mass (m_b)-adjusted BMR (review in Lovegrove 2005).

Even though Heldmaier's (1989) seasonal acclimatization model looks promising as an explanation of the seasonal variation in energy metabolism occurring in mammals, the data underpinning this are somewhat questionable. Many species have a higher BMR in winter when compared to summer (Lynch 1973; Haim and Fourie 1980; Merritt and Zegers 1991, 2002; Li et al. 2001; Li and Wang 2005b; Zhang and Wang 2007; Li et al. 2010). Nevertheless, most of these studies did not measure the same individual repeatably and thus cannot test the seasonal acclimatization model (discussed in Szafrańska et al. 2013). However, it has been proven, as exemplified by studies on free-living root voles *Microtus oeconomus*, that the responses of individuals from the same population differ substantially across seasons; smaller and younger ones increase in size, whereas bigger and older individuals tend to reduce both m_b and metabolism in winter (Zub et al. 2014). This suggests that processes underlying the growth in wild animals, especially those that were born late in the summer season or experience lower resource availability/quality, can interfere with seasonal acclimatization. Optimal growth is crucial for fitness in wild animals, since it can affect future survival and reproduction (Metcalfe and Monaghan 2001, 2003). Growth in turn is expected to elevate the resting metabolic rate (RMR)—the metabolism under thermoneutral conditions of a normothermic, resting animal that can bear additional energy expenditure, such as the costs of producing new tissues (McNab 1997, 2006).

The work detailed here has thus sought to test if RMR is a seasonally flexible trait in a wild small rodent—the yellow-necked mouse *Apodemus flavicollis* represented by a single population inhabiting the Białowieża Forest (Eastern Poland). The fact that this population lives in a seasonally dynamic environment makes it a good system to study seasonal changes in small mammals. Our main hypothesis was that animals have developed energy-saving phenotypes in winter. According to the seasonal acclimatization model (Heldmaier 1989; Lovegrove 2005), we predicted that the studied animals decrease RMR between autumn and winter, followed by renewed increases in anticipation of spring. However, knowing that individual yellow-necked mice can grow (showing continual m_b gain) during their entire lifetime (Adamczewska 1961; Bergstedt 1965), we did not expect a substantial reduction of m_b in winter.

We expected, however, that mice will reduce m_b gain, which would allow for the reduction of mass-specific metabolism in winter. In order to test the above predictions, we measured m_b, RMR in autumn and the winter-spring period in individuals repeatedly during 2 years of the study. We also measured metabolic rate (MR) and T_b during ~24 h food restriction periods to quantify heterothermy and test whether seasonal flexibility of metabolism affects DEE. Since variation in the diet of wild animals may have a strong impact on BMR or RMR (rewieved by Cruz-Neto and Bozinovic 2004), we analyzed isotope content in mice fur to account for plausible among-year variations in food habitat niches.

Material and Methods

Study site and animals

Animals were captured in the Strict Reserve of the Białowieża National Park (Eastern Poland) (GPS position: 52°43′ N, 23°52′ E). This part of the forest is formed mainly by hornbeam *Carpinus betulus*, pedunculate oak *Quercus robur*, and maple *Acer platanoides*, together with lime *Tilia cordata* and fire-prone spruce *Picea abies*. Seed production of hornbeam and pedunculate oak, that is, tree species that are considered the most important sources of food for yellow-necked mice in Białowieża Forest (Pucek et al. 1993; Stenseth et al. 2002; Selva et al. 2012), was higher during the 1st year of study compared to the 2nd (Table 1; data provided by Białowieża Forest Administration).

The climatic conditions in the study area are predictable from season to season. There are substantial environmental changes between seasons, with average ambient temperatures differing by ~20°C between summer and winter (while absolute temperature extremes in a given year may approach 50°C; data from the Meteorological Station of the Mammal Research Institute of the Polish Academy of Sciences).

Animals were caught using wooden traps (checked every 12 h) and transported to the laboratory of the Mammal Research Institute of Polish Academy of Sciences, located in the Białowieża village, ~3 km away from the place of capture. They were marked individually with radio-frequency identification tags (RF-IDW-1, CBDZOE, Poland) and kept individually in standard rodent cages (model 1264, Tecniplast, Italy) lined with wood shavings, with access to rodent food (Megan, Poland), carrots, apples, and water *ad libitum*. Animal cages were always kept in walk-in climatic chambers at 19 ± 1°C, under a natural photoperiod. In total, 307 mice (185 and 122 in the 1st and 2nd year of the study, respectively) were captured and measured under laboratory conditions. Since we were interested in within-individual variation, only data collected in mice that were measured consecutively along seasons are presented and analyzed (Table 2).

Table 1. Intensity of seed crop for two tree species in autumn 2016 and 2017 in Białowieża Forest

Tree species	Year	Level of seed crop			
		no seeds	low	moderate	high
Pendiculate oak	2016	0	3	5	0
	2017	0	8	0	0
Hornbeam	2016	0	1	5	0
	2017	6	0	0	0

The number of plots arbitrarily categorized as "no seeds," "low," "moderate," or "high" is shown. The same forest sections were inspected during each autumn. Data provided by białowieża Forest Administration.

The yellow-necked mouse is a short-lived species (under 1 year, Adamczewska 1959; maximum lifespan in the wild ~1.3 years; Adamczewska 1961). Mice from Białowieża Forest exhibit high variation in body size (Adamczewska 1959). In the studied population, the body mass of individual mice (sexually mature average female: 10 g, male: 20 g, maximum observed ~68g) varied with the time of year the animal was born, and continuous individual m_b gain was observed (Adamczewska 1961; Kowalski and Ruprecht 1981). This non-hibernating small rodent collects external energy resources as stored caches of seeds in underground burrows (see in Vander Wall 1990). Availability of these resources affects both the reproduction and survival in this species (Pucek et al. 1993). The reproduction investment is strictly related to synchronous seed production of main tree species found in the surrounding habitat (Pucek et al. 1993). As a result, the time of the birth of juveniles, and hence their body size later in life, depends on primary productivity (Adamczewska 1961).

To study changes in m_b and RMR (see section "Seasonal changes in m_b and RMR"), we captured/re-captured mice on a fixed 0.9 ha research plot using 220 wooden traps (baited with oats) at 110 trapping points forming a 10 × 10 m grid. We ran our study over 2 consecutive years from autumn to spring, and in this way had three separate experimental sessions when animals were measured in each year, that is: 1) early autumn (early October), 2) mid-winter (early January), and 3) late-winter/early-spring (end of February to early April). To test phenotypic flexibility, the within-individual changes, we used 72 records from 33 individuals (21 and 12 in the 1st and 2nd year, respectively) that were measured in at least 2 consecutive sessions (6 mice were measured in all 3 sessions; 2 and 4 in the 1st and 2nd year, respectively) within each study year. No mice were captured and then measured in both study years.

To measure the metabolic rate and T_b over a ~24 h period (for details, see section "DEE during fasting"), we used another 30 mice (15 individuals from each year) captured in 20 traps set randomly during both years in mid-winter in the vicinity of the fixed 0.9 ha research plot (at a distance of ~100–300 m). After ~1 week of acclimation to laboratory conditions, those animals were intraperitoneally surgically implanted with miniaturized, paraffin wax-coated T_b data loggers (procedure as described in Boratyński et al. (2018, 2019)). The loggers (logger size = 14 mm × 14 mm, mass = 1.8 g, resolution = 0.0625°C) were set to record T_b every 5 min.

Seasonal changes in m_b and RMR

RMR was measured using indirect calorimetry as the rate of oxygen consumption of an animal at thermoneutral T_a (30°C; Cygan 1985) in the course of a ~4 h period of daylight. Since yellow-necked mice are nocturnal animals (Wójcik and Wołk 1985), they are most likely in a post-absorptive state when measured during the day. Animals were placed in 850 mL respirometry chambers connected to the system. Air was drawn from outside using an air pump and dried (Drierite Co. Ltd, Xenia, OH, USA) prior to entering the respirometry system. Air flow was divided into 10 sub-streams and regulated upstream of the chambers (to ~500 mL min^{-1}). The baseline oxygen concentration in the 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). Air from each gas stream was dried (Drierite Co. Ltd) and used for determinations of the flow rate with the aid of 2 mass-

Table 2. Number of animals that were used to study each of the experimental tasks (for details see the text)

Experimental task	Year of the study	Experimental session	Number of animals	
Seasonal changes in m_b and RMR	1st	Autumn	10[a]	
		Mid-winter		13[a]
		Late-winter/early-spring		
	2nd	Autumn	7[a]	
		Mid-winter		9[a]
		Late-winter/early-spring		
DEE during fasting	1st	Mid-winter	15	
	2nd		15	
Isotopic composition in the fur of mice	1st	Late-autumn	26	
	2nd		15	

[a] The same animals used.

flow meters (ERG-1000, BETA-ERG, Warszawa, Poland), which were calibrated using a soap bubble flowmeter (model: Optiflow 570, Humonic Instruments Inc., USA) once measurement had ceased. The fractional concentration of O_2 was measured along two lines simultaneously, using two FC-10a gas analyzers (Sable Systems International). Approximately 100 mL of air leaving each respirometry chamber was sampled for 5 min, and reference gas was 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 20 individuals daily (each animal was measured for ~4 h). RMR was defined as an average of the lowest stable, continuous 60 s of oxygen consumption observed in a given animal during the whole period of measurements (for details of calculations, see section "Data processing"). The m_b was taken to the nearest 0.1 g before measuring RMR.

During the autumn session of each year, captured animals were kept in the laboratory for 1–2 days (T_a = 19 ± 1°C and natural photoperiod) prior to the measurement of m_b and RMR. In total, during the autumn of the 1st year, animals were kept under laboratory conditions for 3 consecutive days and then released at the place of capture. In turn, during the autumn of the 2nd year, mice were maintained under laboratory conditions for ~1 week following measurement. Once RMR had been recorded (within 1–2 days after capture), 6 of the mice in autumn of the 2nd year were implanted intraperitoneally with miniaturised paraffin wax-coated T_b data-loggers, prior to release at the place of capture (for details, see Boratyński et al. 2018).

During the mid- and late-winter as well as early-spring sessions of both years, mice were acclimated for at least ~2 weeks at 19 ± 1°C under a natural photoperiod, prior to the measurement of m_b and RMR (for details, see section "Study limitations" and Supplementary Material). During this time the aforementioned T_b data loggers were implanted intraperitoneally (for procedural details, see Boratyński et al. 2019), and set to record T_b every 10 min. The response to short-term fasting (no food) was measured for the 1st time ~1 week after recovery from the surgery (after ~2 weeks of acclimation). The procedure, which aimed to induce torpor, was repeated on animals held in home cages at T_a=19 ± 1°C under natural photoperiod and with food deprivation extending to ~24 h, weekly (for details, see Boratyński et al. 2019). Since even short-term fasting could affect animal energetics, our seasonal comparisons related to m_b and RMR measurements were limited to those obtained before the 1st fasting experience during each experimental session was taken (after ~2 weeks of acclimation). During the mid-winter and late-winter/early-spring sessions in the 1st year, animals were maintained under laboratory conditions for a total of ~1 month before being released at the place of capture. During the 2nd year, animals (9 individuals) were maintained in the laboratory between mid-winter and early-spring for technical and ethical reasons (for details, see section "Study limitations" and Supplementary Material).

DEE during fasting

After ~1–2 weeks of recovery (~2–3 weeks of acclimation, at the beginning of February), measurements of the metabolic rate and T_b were made during 23.5 h fasting periods (Figure 1). Mice were placed in 2 separate 850 mL chambers constructed of translucent polypropylene (HPL 808, Lock&Lock, Hana Cobi, South Korea), connected to a respirometry system for 23.5 h. The system allowed simultaneous measurement of O_2 consumption in 2 individuals. To avoid animals' dehydration, water in a bottle (model ACBT0152, Tecniplast, Italy) was mounted in each chamber lid. For animal comfort, ~3 g of sawdust from each individual's home cage was placed in the respirometry chambers. The chambers were placed in two temperature-controlled cabinets, in which T_a was set to ~17 ± 1°C (model: KB 53, Binder, Germany). The upstream air flow was regulated to ~400 mL·min^{-1} and measured with 2 mass-flow meters (ERG-1000, Warsaw, Poland) in each chamber. The mass-flow meters were calibrated using a soap bubble flowmeter (model: Optiflow 570, Humonic Instruments Inc., USA) following completion of all measurements. Every 30 min of readings of oxygen consumption, we automatically sampled a 1-min reference reading of baseline air using an automatic, two-line computer-controlled multiplexer (MUX, Sable System Int., USA). The air from each gas stream was dried (Drierite, USA) and ~80 mL min^{-1} of air from each stream subsampled to measure the fractional concentration of O_2 using two gas analyzers (FC-10a, Sable System Int.). All electronic elements of the respirometry system were connected to a PC via an analog-to-digital interface (U12, Sable Systems Int.), with data acquisition using ExpeData software (Sable System Int.) at 1 Hz. After ~1 week of recovery from surgery (~2 weeks of acclimation), we also measured the m_b and RMR of those mice (at the end of January), using the same procedure and equipment as with the mice used to study seasonal phenotypic flexibility of RMR (see section "Seasonal changes in m_b and RMR"). m_b was measured before and

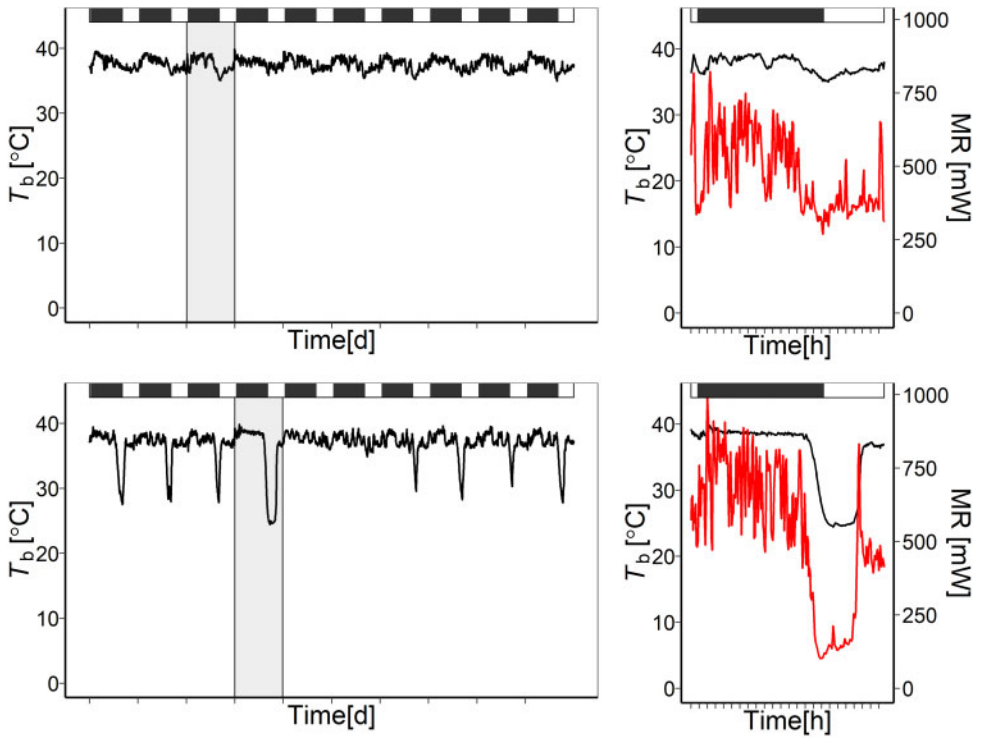

Figure 1. Time course of body temperature (T_b) readings in two representative yellow-necked mice during 10 consecutive days of measurements (plots on left). Nine subsequent days of measurements were conducted at home cages during winter 2017 (upper plots) and 2018 (lower plots). Gray shading indicates 23.5 h period when mice were measured in respirometry chambers without access to food. In addition (plots on right), time course of T_b and metabolic rate (MR) readings (in red) of two mice during daily measurements in respirometry chambers in winter 2017 and 2018. Black-and-white boxes refer to the dark–light cycle.

after each fasting experiment as well as RMR measurement to the nearest 0.1 g.

Isotopic composition in the fur of mice

Since variation in the diet of wild animals may have a strong impact on BMR (reviewed by Cruz-Neto and Bozinovic 2004), we used the stable isotope composition of animal hair as an approach to draw conclusions about mice diet indirectly. To test whether mice in the 2 different years differed in diet and responded to variation in seed production, we studied the carbon (^{13}C) and nitrogen (^{15}N) isotope content in their fur. To do this, we collected fur from 41 randomly-selected mice living in the fixed 0.9 ha research plot, in the late autumn (December) of the 2 subsequent years of study (26 and 15 individuals, respectively). Since we did not measure isotope content in food resources, our interpretation was strengthened by a previous study done on yellow-necked mice from the Białowieża Forest, where authors used stable isotopes in the rodents' hair, as well as plant biomass to measure the importance of seeds in the rodents' diet (Selva et al. 2012, see below). Hair isotopic composition reflects the diet from a period longer than 1–2 months (Miller et al. 2008). Once the keratin structure is established, hair is metabolically inactive (O'Connell and Hedges 1999), so isotopic turnover should follow moulting. The moulting pattern in mammals is complex and not fully understood. We found that fur cut in the late autumn sometimes did not regrow during the following winter (Chibowski P, unpublished data). Trophic discrimination factors for ^{13}C and ^{15}N isotopes are unknown for yellow-necked mice, and data obtained have to be used with caution. Carbon isotopic discrimination factors vary strongly between studies; values observed have been in the range from the 0.3‰ noted in deer mice *Peromyscus maniculatus* (Miller et al. 2008) to the 2.9‰ characterizing white-footed mice *Peromyscus leucopus* (DeMots et al. 2010). For these reasons, we opted not to use the absolute stable isotope values of diet sources from Selva et al. (2012), or those from any other article, but instead focusing on the findings of the former authors that isotopic composition of deciduous tree seeds is characterized by higher values for ^{13}C (~2.3‰) and lower values for ^{15}N (~1.4‰) isotopes when compared to the composition of herbs growing in the same environment.

Sample preparation and stable isotope analysis were both done at the Laboratory of Biogeochemistry and Environmental Conservation, University of Warsaw. Hair samples were treated following the protocol after O'Connell et al. (2001). To remove surface lipids, samples were submerged for 2 h in a 2:1 methanol: chloroform solution, rinsed with the same solution and submerged subsequently in distilled water for another 2 h. Samples were then subjected to repeated rinsing with distilled water, dried at 50°C for 24 h, and—for increased homogeneity—subsequently ground in liquid nitrogen using a pestle and mortar. Each sample then supplied a specified amount (~0.5 mg) that was weighed into a tin capsule, combusted in a Thermo Flash 2000 elemental analyzer (Thermo Fisher Scientific, USA), and measured for stable isotope composition in a Thermo Scientific Delta V Plus continuous-flow isotope ratio mass spectrometer (Thermo Fisher Scientific, USA).

Study limitations

Data for this study were collected as part of a larger study, which aimed mainly to measure heterothermy in yellow-necked mice (see Boratyński et al. 2018, 2019). Thus, there are some methodological

discordances that may raise doubts and require better explanation. For instance, we compared animal traits between autumn, mid-winter, and late-winter/early-spring, but it may be argued that we did not fully test the acclimatization model since we did not measure m_b and RMR of mice in summer. This is because it may affect the main goal of our primary project by influencing individual reproductive success. Moreover, only a few mice that were born during the summer of the 1st year were trapped during the next reproductive season (Boratyński JS, unpublished data); most had likely died (see in Wójcik and Wołk 1985; Pucek et al. 1993), and those that survived were old, 2nd-year animals. We assumed that seasonal changes in energetics ought to be a domain of animals that need to survive the winter. Mammals that respond to photoperiodic changes switch from the summer status to the winter one when day length shortens below a critical photoperiod of ~12 h of light (Hoffmann 1982). In this study, we used autumn measurements of m_b and RMR collected in animals that were measured between 1 and 15 October, when daylight was between ~11:40 h and 11:00 h per day; thus, just after this threshold occurred. The seasonal changes during acclimation to short photoperiod take time, for example, full testis regression takes ~10 weeks in the golden hamster *Mesocricetus auratus* exposed to a short photoperiod (LD 6:18; Vitaterna and Turek 1993). The well-studied Siberian hamster, *Phodopus sungorus*, kept under a natural daylight cycle, starts changing m_b and RMR between September and October, but does not reach its winter status until November (Heldmaier and Steinlechner 1981). Full transformation from summer to winter phenotypes in this species can take even ~20 weeks of acclimation to short days (Heldmaier and Lynch 1986; see also: Li and Wang 2005a). Thus, we assumed that in early autumn we measured animals that were closer to the summer than winter status. Photo-refractoriness—the spontaneous return to summer phenotype—usually happens after ~3 months of winter acclimation (Lynch and Puchalski 1986; Wade et al., 1986). Thus, at the end of February (28th), when we started measurements of animals in the late-winter/early-spring session, individuals were most likely at the end of transition between winter and summer phenotypes. We did not quantify this, but most of the males had fully developed gonads at the beginning of March, but not in January (Boratyński JS, unpublished data; see also: Adamczewska 1961).

Limitations of our study could be recognized in the protocol we used; we acclimated animals to common conditions only during mid-winter and late-winter/early-spring sessions. We decided not to do so during autumn sessions, since our model species is a small food-hoarding rodent, which establishes autumnal caches of seeds crucial for surviving the winter (Vander Wall 1990). We kept some mice longer in the 2nd autumn, but all measurements of RMR were done with the same protocol to allow comparisons with the 1st autumn. To see if different acclimation protocols affect our results, we tested 15 individuals (8 females and 7 males) in mid-winter of 2017 and 2018, captured on the same plot. In these animals, measurements of RMR were repeated 2 times: a few days after capture and after ~2 weeks of acclimation. There were no differences between these measurements in either RMR or m_b (results in Supplementary Material). In the 2nd year of study, we kept animals that were measured in mid-winter until they were measured once again in late-winter/early-spring because there had been extremely harsh winter conditions (–20°C and fresh snowfall), and it was highly probable that in this year the population of mice would decline due to lack of resources. The population dynamics of mice are shaped by masting, that is, the phenomenon of synchronous mass-seeding of main deciduous tree species in certain years (Pucek et al. 1993; Stenseth et al. 2002). Fluctuations in food resources affect over-winter survival rates. These rates are much higher after the occurrence of masting, compared to non-masting years (Pucek et al. 1993). We were unsure whether any mice would be found on plot in the spring since, post-winter in non-masting years, population size can decrease to 1 individual per ha (Pucek et al. 1993; Stenseth et al. 2002). Fortunately, we caught 10 individuals at the plot and its vicinity and tested whether differences in the protocols affected mice energetics. We found no differences in m_b and RMR between mice kept in the laboratory and those captured in late-winter/early-spring (results in Supplementary Material). Thus, we concluded that acclimation to laboratory conditions did not significantly affect our results and conclusions.

Data processing

RMR was calculated by reference to oxygen consumption (VO_2) and excurrent flow rate measurements, using equation 11.2 after Lighton (2008), assuming a respiratory exchange ratio equal to 0.8 (after Koteja 1996). The VO_2 of continuous 23.5 h measurements with incurrent flow-rate measurements was calculated using equation 10.2 after Lighton (2008), again assuming a 0.8 respiratory exchange ratio. DEE was estimated based on energy expenditure (EE) obtained from measurements of MR during a 23.5 h period of food deprivation—calculated as integrated the area below the EE curve. T_b readings of animals measured in home cages and respirometry chambers were used to calculate the heterothermy index (HI) following Boyles et al. (2010):

$$HI = \sqrt{\frac{\sum (\mathrm{T}_{b-\mathrm{mod}} - \mathrm{T}_{b-\mathrm{i}})^2}{\mathrm{n}-1}},$$

where, $T_{b\text{-mod}}$ is the modal T_b of an individual (during alpha phase, food *ad libitum*), $T_{b\text{-}i}$ is the T_b at time i, and n is the number of times T_b is sampled.

Stable isotope ratios were reported as delta (δ), that is, as the deviation in per-mille (‰) from the international PDB (Pee Dee Belemnite) standard for carbon, and atmospheric nitrogen for nitrogen, in line with the equation;

$$\delta_{sample} = \frac{R_{sample}}{(R_{standard} - 1)} \cdot 1000,$$

where, R is the isotopic ratio, that is, $^{13}C/^{12}C$ or $^{15}N/^{14}N$. International standards were measured for calibration and measurement precision, which were <0.1‰ for $\delta^{13}C$ and <0.2‰ for $\delta^{15}N$.

Individual growth rate was estimated as individual change in m_b between consecutive sessions divided by days between measurements. m_b changes may not be related to growth, though they are related to fat deposition, like in hibernating species that store fat as an energy source. However, fat content, which is always relatively low in this species (~15% of dry mass), did not differ among juvenile and adult yellow-necked mice (Sawicka-Kapusta 1968). Thus the individual m_b gain can mainly be considered a component of somatic growth, and its among-individual variation can reflect different development stages. Individual m_b gain calculated based on values obtained before RMR measurements were highly correlated with the gain obtained based on data collected after 24 fasting experiments (Pearson's $r = 0.88$, $P < 0.01$). Since mice lost an average of ~12% of m_b during 24 fasting experiments, this suggests that these animals used almost all fat storage recorded for the species (see in Sawicka-Kapusta 1968). We therefore concluded that m_b changes primarily explained individual growth and not fat gain.

Statistics

General remarks

All statistics were calculated in R 3.5.1 (R Core Team 2018). Continuous variables were always scaled before the analysis using function "scale" of package "base". Analysis of deviance in the "car" package (Fox et al. 2012) was used to test for differences between factors and interactions in all analyses. Degrees of freedom for linear mixed models were estimated using the Kenward–Roger approximation (Luke 2017). To present values for RMR and DEE, we used estimated marginal means and a 95% confidence interval (95% CI), adjusting them for the effects of covariates, factors, and interactions present in the given model. Differences between categorical variables were tested with the Tukey post hoc test. Interquartile range (IQR) is provided when medians are presented.

Seasonal changes in m_b and RMR

In testing for seasonal changes in m_b and RMR, we used data obtained from animals measured in at least 2 consecutive sessions of a studied year. During the 1st year, 10 individuals (5 males and 5 females) were measured repeatedly in autumn and in mid-winter, while 13 (8 males and 5 females) were measured in the mid- and late-winter/early-spring sessions. In turn, during the 2nd year, RMR was measured repeatedly in 7 individuals (4 males and 3 females) in autumn and mid-winter, and in 9 individuals (5 males and 4 females) during the mid-winter and late-winter/early-spring sessions. We measured only 2 and 4 individuals in all 3 experimental seasons in 2016/2017 and 2017/2018, respectively. No mice were measured in 2 consecutive years of study. We compared RMR using Linear Mixed Effects (LME) modeling procedures with restricted maximum likelihood, and with covariate m_b, sex, experimental session, and year included as factors, as well as the interaction between year and session (autumn, mid-winter, late-winter/early-spring) and the random effect of ID in the function "lmer" of the "lme4" package (Bates et al. 2015). However, we initially tested whether the slope between RMR and m_b differs among years or sessions. To do so in the above LME for RMR we also set a 3-level interaction between session, year, and m_b. Then, using function "testInteractions" of package "phia", we compared slopes for different sessions between 2 years, as well as between sessions within year. The 3-level interaction was not significant ($F_{2,41} = 1.56$, $P = 0.222$), however, this was most likely a result of a relatively small sample size. There was clearly no homogeneity in slopes in mid-winters when compared between years (1st year: $\beta \pm SE = 0.41 \pm 0.18$, 2nd year: $\beta \pm SE = 0.73 \pm 0.21$; $F_{1,28} = 4.41$, $P = 0.045$; Figure 3). Moreover, according to Akaike's Information Criterion corrected (AICc) for small sample sizes (Burnham et al. 2011), the model with 3-level interaction explained significantly more variance than the model without it ($\Delta AICc = 12.64$). For these reasons, we decide to maintain globally insignificant interaction and used the post hoc comparison. However, the 3-level interaction was excluded from the final model, when we compared m_b-adjusted RMR (i.e., RMR after controlling for the variation in m_b), assuming no differences in slopes between RMR and m_b.

Since it did not meet assumptions for linear modeling (right-skewed, and non-normal distribution of model residuals), m_b was compared in Generalized Linear Mixed Effects (GLMER) modeling procedures with inverse Gaussian distribution using function "glmer" of "lme4" package. In GLMER for m_b, we included sex, experimental session, and year as factors, as well as interaction between year and session (autumn, mid-winter, late-winter/early-spring) and the random effect of ID.

Among year differences in DEE, heterothermy, and isotope content

The RMRs of mice used to estimate DEE during fasting were compared using a Linear Model (LM), with m_b included as a covariate and sex and year as factors. We used the same modeling procedure, and the same explanatory variables included in the modeling procedure, to compare DEE during fasting.

This study complements our previous work revealing that heterothermy is a repeatable (individually consistent) trait and differs between studied years (Boratyński et al. 2019). This study generated a smaller dataset of 32 mice (T_b was not measured in one mouse), for which seasonal changes in RMR were then estimated. Due to right-skewed distribution, non-normal distribution or model residuals, and heteroskedasticity we compared HI in GLMER with inverse Gaussian distribution (log-link) using function "glmer" of "lme4." We compared HI between the 2 years of the study to test the current and previous results for compatibility, using GLMER modeling procedures with average HI obtained for an individual within an experimental session as the dependent variable, while m_b was a covariate, sex, experimental session and year were factors while animal ID was a random effect. We also set the interaction between experimental session and year. Then, we ran a similar GLMER but without covariate m_b to analyze whole animal HI. The HI of mice used to measure DEE during fasting was compared in the LM, with m_b included as covariate, and sex and year as factors.

Isotopic composition of $\delta^{13}C$ and $\delta^{15}N$ in fur was compared between years separately using LMs where year was included as a factor. We used the "SIBER" package (Jackson et al. 2011) to compare the sizes of isotopic niches in the 2 study years. We calculated the Standard Ellipse Area (SEA) by reference to maximum likelihood estimates for means and covariance matrices relating to individuals in the 2 years.

Body mass gain

Since yellow-necked mice grow continuously throughout winter (see section "Results"; see also Adamczewska 1961; Bergstedt 1965), we aimed to test whether this is associated with individual variation in m_b, RMR and HI. We used LME to check whether different growth rates observed in both years are associated with initial m_b, RMR, and HI. In the initial LME we included factors such as year and the intersession when growth rate was estimated (between autumn and mid-winter or between mid-winter and late-winter/early-spring), as well as covariates such as residual RMR (rRMR: obtained from the linear relationship between RMR~m_b) in preceding and following sessions, m_b in a preceding session, and HI in a given session. Because m_b was correlated with HI (Pearsons $r = 0.34$, $P = 0.03$), to avoid collinearity at the 1st step, we checked the model without HI. Nevertheless, as m_b did not significantly explain the growth rate ($\beta \pm SE = -0.30 \pm 0.21$; $t_{29} = -1.45$, $P = 0.18$), we decided to omit this covariate in the final model. Although rRMR in the following session was not correlated with that of the preceding session, rRMR in the following session was also excluded from the modeling procedure due to its insignificant impact on growth ($\beta \pm SE = 0.17 \pm 0.13$; $t_{29} = 1.30$, $P = 0.23$). Final LME contained the following factors: year, sex, and intersession; and covariates: rRMR obtained in preceding session and HI in a given session. Animal ID was always maintained as a random effect.

Ethical approval

All experimental procedures were approved by the Local Committee for Ethics in Animal Research in Białystok, Poland (Decisions no.

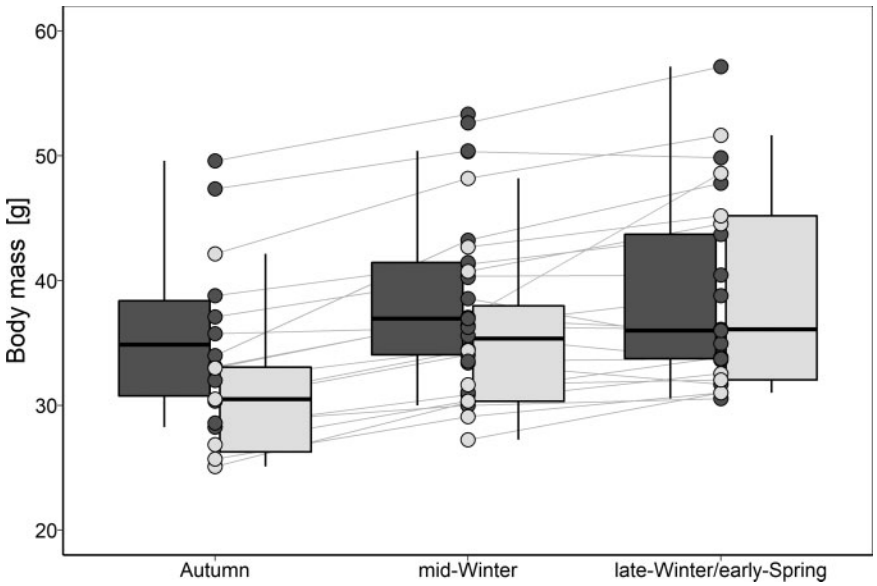

Figure 2. Changes of body mass in yellow-necked mice during 2 study years (dark gray: 2016/2017, light gray: 2017/2018). Consecutive measurements of the same individuals (dots) are connected with lines. Each boxplot shows the median (line inside), 25–75 percentile ranges (box edges), and non-outlier ranges (whiskers).

27/2016 and 62/2017) and the Polish Ministry of Environment (Decision no. DOP-WPN.287.7.2016.AN).

Results

Seasonal changes in m_b and RMR

Female mice (median ± IQR: 31.1 ± 3.9 g) were lighter than males (40.8 ± 11.7 g; $\chi^2 = 29.42$, $P < 0.001$). Year and experimental session proved significant predictors of m_b (year: $\chi^2 = 13.42$, $P < 0.001$; session: $\chi^2 = 27.04$, $P < 0.001$); however, there was also a significant interaction between these 2 factors ($\chi^2 = 16.58$, $P < 0.001$), given a higher gain of m_b in mice during the 2nd study year than noted in the 1st year (Figure 2). In both years mice increased m_b from autumn (1st year: median ± IQR: 34.9 ± 11.0 g, 2nd year: 30.5 ± 7.4 g) to mid-winter (1st year: 37.0 ± 8.6 g, 2nd year: 35.4 ± 9.6 g; $P < 0.001$). During the 1st year mice did not increase m_b between mid-winter and late-winter/early-spring (median ± IQR: 36.0 ± 12.1 g; $P = 0.71$). Only mice measured during the 2nd year increased m_b between mid-winter and late-winter/early-spring (median ± IQR: 36.1 ± 15.4 g; post hoc: $P = 0.001$). Mice in the early autumn of the 2nd year had lower m_b than in the 1st year around the same time (post hoc: $P < 0.01$). The m_b of mice captured in the 2nd and 1st year did not differ significantly in mid-winter (post hoc: $P = 0.18$), nor in late-winter/early-spring (post hoc: $P = 0.84$; Figure 2).

RMR correlated positively with m_b in animals (β ± SE = 0.58 ± 0.14; $t_{38} = 4.26$, $P < 0.001$). The slope for this relationship between RMR and m_b did not differ between autumn (β ± SE = 0.82 ± 0.14) and mid-winter (β ± SE = 0.44 ± 0.13; $\chi^2 = 3.20$, $P = 0.07$), autumn and late-winter/early-spring (β ± SE = 0.62 ± 0.13; $\chi^2 = 0.76$, $P = 0.39$), nor between mid-winter and late-winter/early-spring ($\chi^2 = 0.96$, $P = 0.33$) during the 1st year of study (Figure 3). There were also no significant differences in slope between autumn (β ± SE = 0.71 ± 0.17) and mid-winter (β ± SE = 0.74 ± 0.15; $\chi^2 = 0.13$, $P = 0.72$), autumn and late-winter/early-spring (β ± SE = 0.48 ± 0.13; $\chi^2 = 0.45$, $P = 0.50$), nor between mid-winter and late-winter/early-spring ($\chi^2 = 1.71$, $P = 0.19$) during the 2nd year of study (Figure 3). The relationship between RMR and m_b did not differ between the 1st and 2nd year of study during autumn ($\chi^2 = 0.01$, $P = 0.93$) and late-winter/early-spring ($\chi^2 = 0.03$, $P = 0.86$). However, the slope for the relationship between RMR and m_b differed marginally between years in mid-winter sessions ($\chi^2 = 3.91$, $P = 0.048$; Figure 3).

No significant differences in m_b-adjusted RMR were noted between males and females ($F_{1,34} = 0.06$, $P = 0.82$). This parameter was found to be significantly affected by experimental session ($F_{2,48} = 28.82$, $P < 0.001$), but not by year ($F_{1,64} = 2.95$, $P = 0.09$). However, there was a significant interaction between these two factors ($F_{1,45} = 24.28$, $P < 0.001$), indicating that variation in RMR differed from year to year. The m_b-adjusted RMR of mice during the 1st year decreased from autumn (424 mW [95% CI: 393–455 mW]) to mid-winter (292 mW [95% CI: 271–314 mW]; post hoc: $P < 0.001$), and then increased in late-winter/early-spring (360mW [95% CI: 333–387 mW]; post hoc: $P < 0.01$). In the 2nd year, mice did not change m_b-adjusted RMR between autumn (381 mW [95% CI: 340–422 mW]) and mid-winter (396 mW [95% CI: 367–425 mW]; post hoc: $P = 0.99$), but did experience a decrease in late-winter/early-spring (304mW [95% CI: 272–336 mW]; post hoc: $P = 0.001$). Finally, during the 1st year, mice showed significantly lower m_b-adjusted RMR in mid-winter as compared to counterparts in the 2nd year (post hoc: $P < 0.001$; Figure 3). This was also true in animals for which we estimated DEE during fasting, where the m_b-adjusted RMR was lower in the 1st year (at 292 mW [95% CI: 265–319 mW]) than in the 2nd (at 391 mW [95% CI: 360–422 mW]; $F_{1,26} = 30.21$, $P < 0.001$).

Among year differences in DEE, heterothermy, and isotope content

DEE during 23.5 h of fasting in respirometry chambers did not correlate with m_b (β ± $SE = 0.01 \pm 0.28$, $t_{26} = 0.03$, $P = 0.98$), and did not differ either between sexes ($F_{1,26} = 1.00$, $P = 0.33$) or between

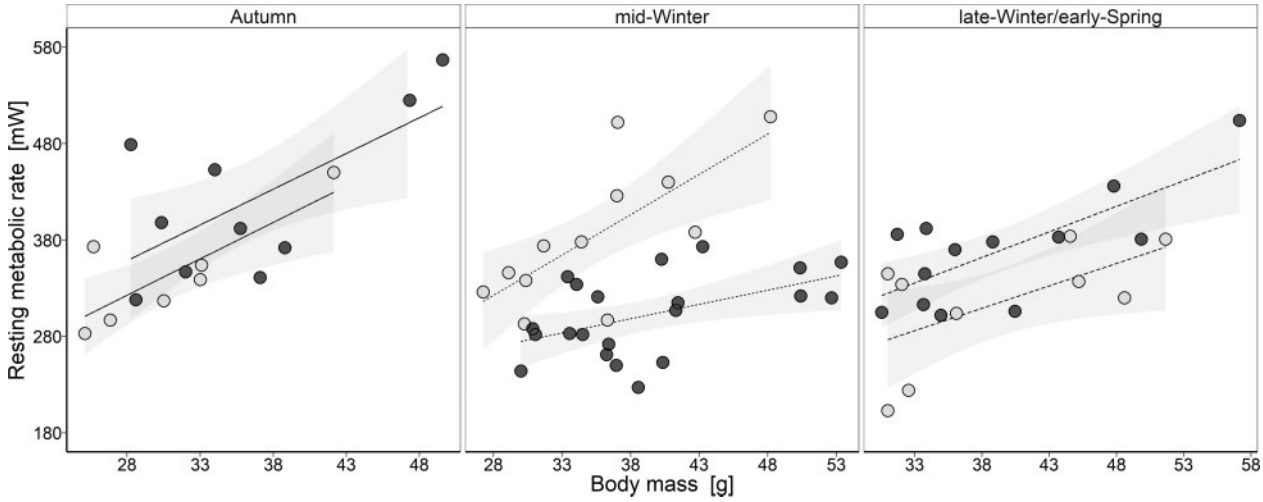

Figure 3. Relationship between resting metabolic rate and body mass in yellow-necked mice during 2 years (dark gray: 2016/2017, light gray: 2017/2018) in 3 experimental sessions.

years of study (year 1: 44.30 kJ [95% CI: 39.46–49.09 kJ] and year 2: 40.60 kJ [95% CI: 35.15–46.05 kJ]; $F_{1,26} = 1.30$, $P = 0.27$).

HI tended to correlate negatively with m_b ($\beta \pm SE = -0.21 \pm 0.11$; $t = 1.83$, $P = 0.07$). m_b-adjusted as well as whole animals' HI did not differ between the sexes (m_b-adjusted; $\chi^2 = 0.19$, $P = 0.66$, whole animal; $\chi^2 = 1.33$, $P = 0.25$). There were also no differences between experimental sessions for whole animal HI ($\chi^2 = 1.77$, $P = 0.18$). Experimental session was significant for m_b-adjusted HI ($\chi^2 = 4.70$, $P = 0.03$). The year affected both m_b-adjusted as well as whole animal HI (m_b-adjusted HI; $\chi^2 = 8.64$, $P = 0.003$, whole animal HI; $\chi^2 = 18.50$, $P < 0.001$). The interaction between experimental session and year was not statistically significant for m_b-adjusted HI ($\chi^2 = 3.56$, $P = 0.06$); however, a significant interaction between experimental session and year was found for whole animal HI ($\chi^2 = 9.91$, $P < 0.001$; Figure 4). Whole animal HI decreased between mid-winter and late-winter/early-spring in the 2nd year (mid-winter: median ± IQR: 3.76 ± 1.6°C, late-winter/early-spring: 2.36 ± 1.6°C; $P < 0.05$) but did not change between sessions in the 1st year, when mice showed generally lower values (mid-winter: median ± IQR: 1.73 ± 1.0°C, late-winter/early-spring: 1.90 ± 0.9°C; $P = 0.54$). For the mice for which DEE during fasting was estimated, HI was lower in the 1st year when compared to the 2nd (respectively median ± IQR: 1.62 ± 1.7°C vs. 5.80 ± 1.0°C; $F_{1,26} = 47.77$, $P < 0.001$). Moreover, mice measured during the 2nd year used torpor both when fed and when fasted (Figures 1 and 5).

Both $\delta^{13}C$ and $\delta^{15}N$ content in the fur of mice differed between years ($\delta^{13}C$: $F_{1,39} = 25.30$, $P < 0.001$; $\delta^{15}N$: $F_{1,39} = 4.30$, $P < 0.05$). Values for $\delta^{13}C$ were lower in the 2nd year than the 1st. The opposite relationship was observed for $\delta^{15}N$ values (Figure 6). SEAs for $\delta^{13}C$ and $\delta^{15}N$ isotopic composition were 1.82 ‰^{2} in 2016 and 3.52 ‰^{2} in 2017.

Body mass gain

On average, males (1.39 g·mo^{-1} [95% CI: 1.03–1.74 g·mo^{-1}]) gain m_b faster than females (0.51 g·mo^{-1} [95% CI: 0.06–0.95 g·mo^{-1}]; $F_{1,24} = 1.00$, $P = 0.01$). The intersessional period and year were not significant factors for growth rate (intersession: $F_{1,24} = 0.68$, $P = 0.42$, year: $F_{1,23} = 0.07$, P = 0.80). Gain of m_b was found to be positively correlated with the variation in residual RMR obtained in the preceding session ($\beta \pm SE = 0.44 \pm 0.14$; $t_{32} = 3.10$, $P = 0.01$; Figure 7) and HI ($\beta \pm SE = 0.41 \pm 0.16$; $t_{29} = 2.63$, $P < 0.05$; Figure 8).

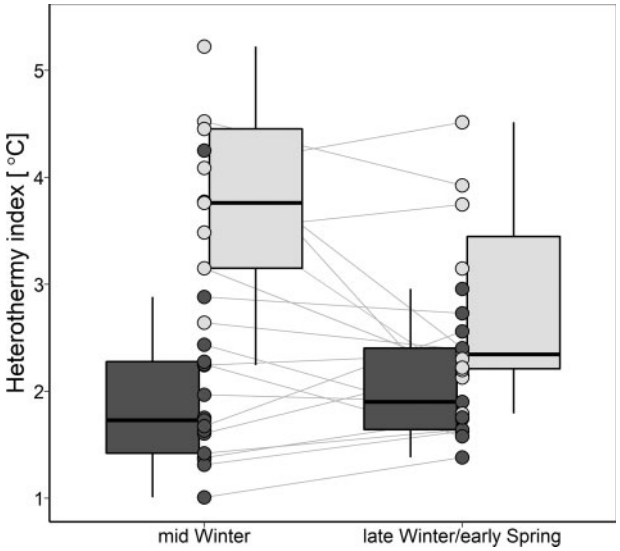

Figure 4. Heterothermy indices in yellow-necked mice during 2 years (dark gray: 2016/2017, light gray: 2017/2018) in 2 experimental sessions. Consecutive measurements of the same individuals (dots) are connected with lines. Each boxplot shows the median (line inside), 25–75 percentile ranges (box edges), and non-outlier ranges (whiskers).

Discussion

Although we expected consistency in seasonal changes in RMR, the intraindividual variation of energy metabolism substantially differed between years. In the 1st year, individuals decreased RMR between early autumn and mid-winter, and then increased it in late-winter/early-spring (Figure 3). In the 2nd year, however, higher RMR during mid-winter was noted (Figure 3). Our analysis of the relationship between m_b and RMR in different seasons also indicates that the slope varied between years in mid-winter. This suggests that the observed variation in RMR is related to different processes rather

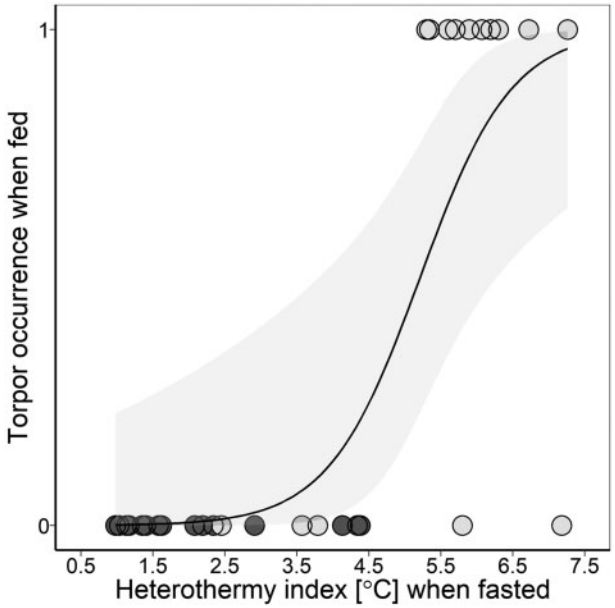

Figure 5. Relationship between torpor occurrence when yellow-necked mice were kept in home cages with access to food *ad libilitum* and heteothermy indices when they were fasted daily at respirometry chambers in winter 2017 (dark gray) and 2018 (light gray). Torpor occurrence was defined as episodes when body temperature decreased below 32°C. Logistic regression curve indicates that HI in fasted mice was a significant predictor for torpor occurrence when mice were kept in home cages with non-limited access to food ($z = 2.53$, $P = 0.011$). Shaded area refers to 95% CIs.

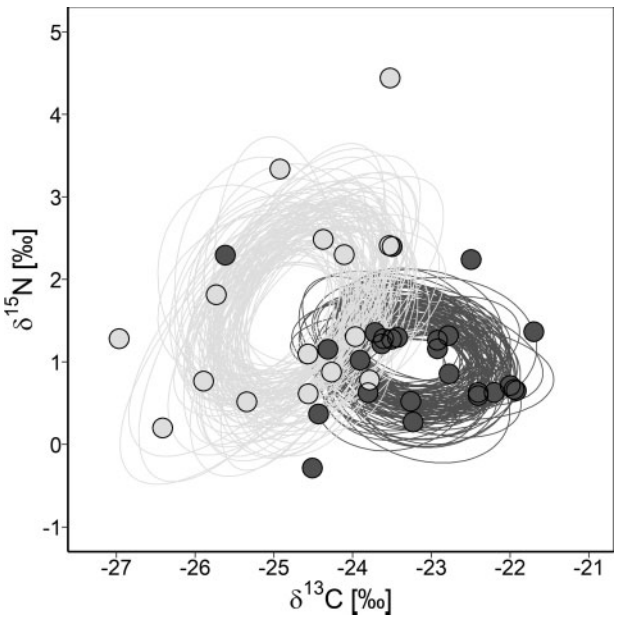

Figure 6. Stable carbon ($\delta^{13}C$) and nitrogen (($\delta^{15}N$)) isotope values of the rodent hair (circles) collected at the study site during autumn of 2016 (dark gray) and 2017 (light gray), with 100 ellipses (lines) sampled based on posterior distributions of data from both years.

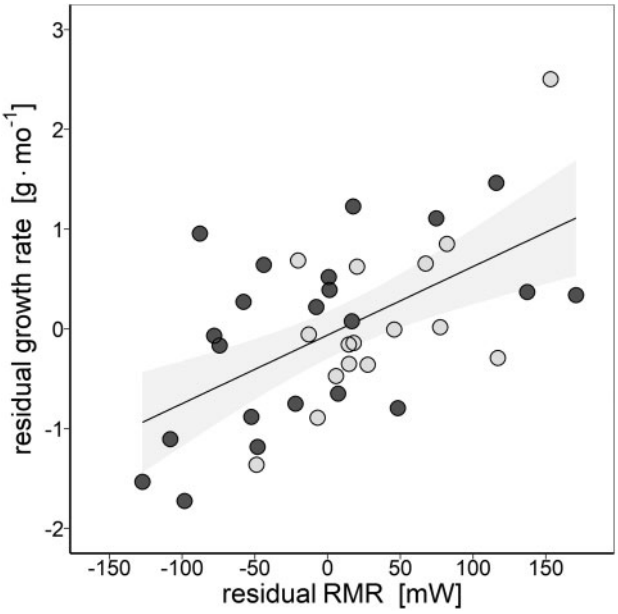

Figure 7. Relationship between residual resting metabolic rate (RMR) and residual growth rate in yellow-necked mice during 2 years (dark gray: 2016/2017, light gray: 2017/2018). RMR was obtained from linear relationship: RMRmb, residual growth rate was obtained from mixed effects model adjusted for variation related to sex and heterothermy use (see "Material and Methods" section for details).

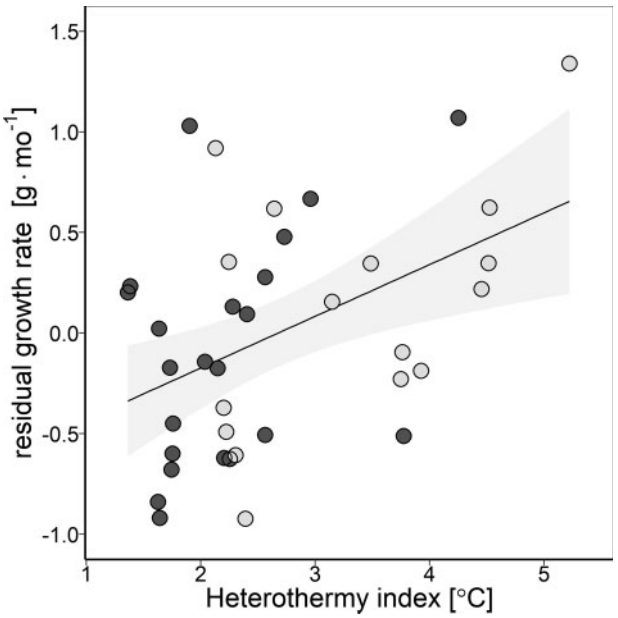

Figure 8. Relationship between heterothermy and residual growth rate in yellow-necked mice during 2 years (dark gray: 2016/2017, light gray: 2017/2018). Residual growth rate was obtained from mixed effects model adjusted for variation related to sex and residual resting metabolic rate (see "Material and Methods" section for details).

than to seasonal acclimatization. The isotope analysis of mouse fur indicated that individuals respond to between-year variations of resources (Table 1) and differentiate their trophic niches (Figure 6). Isotopic data suggested that seeds were the main source of nourishment for studied animals during the 1st year, while during the 2nd, non-masting year, the source consisted of a mix of seeds and green plants (Figure 6; see also Selva et al. 2012). As a result of this resource variation, mice varied in m_b gain within a year

(Figure 2). Individuals from the 1st year grew from autumn to winter and then reached a plateau that lasted until spring. In the 2nd year, growth continued throughout the whole winter season. This variation in growth rate was positively correlated with RMR at the individual level (Figure 7). Altogether, our results suggest that seasonal variation in RMR, and its between-year differences are related to fluctuations in resources that most likely affected the timing of births in a population and/or individual mice development status. All studied animals during the 2nd year used energy-saving torpor as a mechanism for what we assume is compensation for the high self-maintenance costs of being homeothermic (Figures 1 and 5). In contrast, mice in the 1st winter proved to be less heterothermic (see also in Boratyński et al. 2019). By way of a combination of decreases in self-maintenance costs (when homeothermy is being defended) or increases in heterothermy use, mice reached equal DEE. This seems to be in agreement with the seasonal acclimatization model after Heldmaier (1989), which predicts a reduction in energy requirements among small mammals through a combination of a winter decrease in self-maintenance costs when homeothermy is being defended, or else an increase in heterothermy use.

Since the metabolic rate is a measure of all the chemical syntheses in the organism, its decrease must be associated with a reduced rate of synthesis of new cells, resulting in a direct decrease of growth. Studied mice showed a constant increase in m_b, which could be understood as the continuous growth of individuals. The phenomenon of uninterrupted growth in winter, which likely lasts until the following reproductive season in our study organism, was suggested by Bergstedt (1965). The reproduction of yellow-necked mice in the study area is highly influenced by food abundance and environmental conditions, and the breeding period is not fixed and could last from April till December (Adamczewska 1961). Thus, m_b differences in the autumn of both years, which differed in food abundance, could be a result of different birth periods, which also result in differences in developmental processes of individual mice. This suggests that smaller mice were late-born individuals in a population, or experienced nutritional deficiencies that limited their growth early in the season. The late-born animals, depending on environmental conditions, are expected to accelerate the growth rate in compensation or prolong development to a given stage (Metcalfe and Monaghan 2001, 2003). For example, late-born garden dormice *Eliomys quercinus* can reach the size of older individuals in weeks, due to a higher growth rate. However, this is possible only by doubling energy intake (Mahlert et al. 2018). It seems that in yellow-necked mice, development was not highly accelerated;. However, at the end of the study, mice from both years did not differ in m_b as a result of prolonged winter growth of animals in the 2nd year (Figure 3). It is well known that the growth rate is influenced, or even set, by the interaction of m_b and metabolic rate (McNab 2006; Lovegrove 2009; but see also: Derting and McClure 1989; Larivée et al. 2010; Burton et al. 2011). Growing animals also have higher RMR than non-growing ones (Jorgensen 1988; Chappell and Bachman 1995) and the speed of growth is positively correlated with RMR during the plateau phase (Careau et al. 2012). Because fast growers need greater assimilation of energy, the positive relationship between growth rate and RMR can be predicted by the "increased intake" hypothesis (Olson 1992; Biro and Stamps 2010). Indeed, among-individual variation in mice, RMR collected during the previous session in autumn correlated positively with the latter's individual gain of m_b between autumn and mid-winter. The same was true for the other sessions, and RMR collected during mid-winter correlated positively with growth rate between mid-winter and late-winter/early-spring (Figure 7). Thus the different developmental status of individuals is the most likely explanation for variation in RMR observed in our study.

Different phenotypic variation in RMR in a studied population could be also linked to between-year variation in food availability by processes other than growth. In the 1st year there was a crop of oak and hornbeam seeds, whereas during the 2nd year food availability was likely reduced (Table 1). Stradiotto et al. (2009) noted that during non-masting years home ranges of yellow-necked mice increased substantially, which can be explained not only by mating needs at reduced population density, but also by the need to obtain enough food to maintain a positive energy balance when resources are limited. In turn, maintaining large home ranges leads to increased activity levels, and likely requires optimal body composition (e.g., musculature), and thus the high metabolic rate that can improve performance (Albuquerque et al. 2015) but also elevate self-maintenance costs. However, animals living in stochastic environments with unpredictable food resources can also be plastic in regards to food selection. We found significantly different isotope ratios in the fur of mice originating from 2 study years, which indicates substantial differences in the diet during the animals' development. Lower $\delta^{13}C$ and higher $\delta^{15}N$ content observed in mouse fur from the 2nd year compared to the 1st year (Figure 6) suggested that mice in a non-masting year consumed a significant mixture of seeds and green plants (see section "Material and Methods"; see also: Dróżdż 1966; Zemanek 1972; Selva et al. 2012). Knowing that, we can safely assume that differences in isotopic composition, especially of carbon isotopes, are driven by differences in the consumption of these resources (for isotopes content in food sources, see Selva et al. (2012)). When encountered with a lack of seeds, their preferred food source (Dróżdż 1966; Zemanek 1972; Selva et al. 2012), mice in the 2nd year of study had to search for secondary food, creating a greater dietary niche, which is reflected by a larger area of the isotopic ellipse (Figure 6).

In line with the "food-habits hypothesis", animals that deal with unpredictable food resources and/or utilize food of low quality with a high content of secondary compounds should evolve lower BMR (McNab 1986, 2002; Bozinovic and Sabat 2010) or a high plasticity/flexibility (Maldonado et al. 2012; Rimbach et al. 2017, 2018). However, studies on this topic are often inconsistent, as they observe both increases and decreases in BMR in response to diet quality/availability, or sometimes no effect at all (e.g., Woodall 1989; Degen et al. 1998; Speakman 2000; Cruz-Neto et al. 2001; Genoud 2002; Rezende et al. 2004; Cruz-Neto and Jones 2006; Bozinovic et al. 2007; Perissinotti et al. 2009). This discrepancy could come from a complexity of mechanisms. On the evolutionary scale, animals should always be selected for having the lowest BMR possible (Cruz-Neto and Bozinovic 2004; Swanson et al. 2017). On the ecological scale, on the other hand, when animals show high phenotypic plasticity/flexibility of metabolic machinery responsible for dealing with chronic exposure to a low-quality diet, changes in BMR may depend on the trade-off between energy allocation to food processing organs and other metabolically active tissues (Geluso and Hayes 1999; Cruz-Neto and Bozinovic 2004). The lack of a compensatory mechanism for BMR can be present if an animal experiences reduced food quality/availability and, in consequence, increases investment into the metabolic machinery needed for obtaining and processing energy, as suggested by Careau et al. (2013). If this is the case in our study, animals having extensively developed metabolic machinery are not able to rapidly reduce it (see in Barceló et al. 2009) and must therefore use energy-saving torpor. The importance

of such compensatory mechanisms can also explain why the relationship between RMR and fitness does not always need to be obvious (in the context of the "context-dependence" hypothesis, Burton et al. 2011). Diet quality/availability during early development may have long-lasting effects on animal energetics (Kato et al. 2018), including BMR (Criscuolo et al. 2008; Careau et al. 2014a, 2014b). Thus, high winter RMR during non-masting years might be a result of a developmental plasticity needed for coping with low-resource availability/quality, and no detectable compensatory mechanism present at self-maintenance costs in homeothermic animals.

Despite the fact that BMR is considered a major component of animals energy budgets (Ricklefs et al. 1996; Speakman 2000; Portugal et al. 2016), we found that high RMR did not elevate mice DEE. This was most probably the result of both differences in self-maintenance costs of homeothermy and differences in the use of heterothermy in study years. As a result, the net effect did not differ and the energy expenditure of mice during ~24 h of food deprivation was similar in the 1st and 2nd years. The high self-maintenance costs of being homeothermic may logically force an animal to enter torpor, especially under challenging environmental conditions. Interestingly, mice in the 2nd winter (but not in the 1st) used torpor ($T_b < 32°C$) even when fed *ad libitum* (Figure 1 and 5). RMR did not explain the among-individual variation in heterothermy, and we found that RMR was in fact less repeatable than heterothermy in studied population (Boratyński et al. 2019). It is then less likely that variation in RMR itself directly affected torpor use in studied animals. Our results suggest that heterothermy is a significant compensatory mechanism for increased self-maintenance costs of homeothermic animals and must be taken into consideration when the "food-habits hypothesis" is tested (as suggested by Cruz-Neto and Bozinovic 2004). This should also be considered when testing the "compensation hypothesis" that expects a trade-off between energy allocation for different processes such as growth and maintenance (Olson 1992; Konarzewski et al. 2000). The growth rate of individual mice was not only associated with high self-maintenance costs of homeothermy, but also correlated positively with the use of torpor (Figure 8). The association between growth and torpor use is not well understood (Geiser and Brigham 2012). However, it is known that younger animals use torpor more frequently than adults (Geiser et al. 2006; Geiser 2008). Although reduced metabolism under torpor obviously slows growth temporarily, few studies suggest that the use of torpor as an energy-saving strategy can allow animals to divert saved energy to processes related not only to fattening but also to growth (Giroud et al. 2012, 2014; but see also Mahlert et al. 2018). Thus, increased torpor use can be understood as a compensatory strategy in mice characterized by higher RMR and lower m_b. This finally allows energy allocation for growth even when environmental resources are limited and energy expenditure is elevated.

Increase in torpor use by adults can be related to environmental conditions (low T_a and low nutriment) experienced early in life (Riek and Geiser 2012; Kato et al. 2018). This suggests that plasticity in heterothermy use and the self-maintained costs of homeothermy can be fixed by the environment during development. Alternatively, low energy availability in the environment together with increased self-maintenance costs can lead to high selective pressure on thermoregulation, and result in selection for more thermoregulatory generalist phenotypes (*sensu* Angilletta et al. 2010). Our study suggests that when plastic responses leading to lower self-maintenance costs of homeothermy are not possible or adequate, the animal uses heterothermy and operates at a wider range of T_b. However, more experimental studies are needed to better understand this phenomenon and distinguish whether it is a result of phenotypic plasticity or natural selection.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest statement

The authors declare no competing or financial interests.

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