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Individual variation and repeatability of the aerobic performance in Brandt's voles (*Lasiopodomys brandtii*)

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Abstract

Metabolism is thought to play an important role in shaping behaviour, ecology and physiology in animals. To study the changes of metabolism among different ages or generations as well as the repeatability during the ontogeny, we carried out the research in Brandt's voles (*Lasiopodomys brandtii*), which covered two generations' life. Meanwhile, we estimated the among-family variations to facilitate the heritability evaluation. Resting metabolic rate within the thermoneutral zone, resting metabolic rate at 5 °C, non-shivering thermogenesis and maximal metabolic rate during thermogenesis in both juveniles and adults were simultaneously measured. Population-average values of aerobic traits were generally consistent among different ages or generations; however, there was no repeatability at the level of individual variation during the ontogeny, which indicated that the aerobic traits of the young were not good indicators for that of later life. At the same time, the coefficient of intraclass correlation for full sibs failed to reach statistical significance, suggesting that heritability of aerobic traits in Brandt's voles was not high.

Keywords: Individual variation; Maximal metabolic rate; Non-shivering thermogenesis; Ontogeny; Repeatability; Resting metabolic rate

1. Introduction

Animal performance is usually described as species or group means, an approach that tends to mask the magnitude and evolutionary significance of individual variation (Bennett, 1987; Pough, 1989). Moreover, many physiological parameters themselves also show substantial within-individual variation (i.e. phenotypic plasticity) related to age, reproductive status, seasonality, acclimation or other factors (Hayes and Chappell, 1990). Metabolism is such a character that reflects the cost of living of an organism, and energy is therefore thought to play an important role in shaping behaviour, ecology and physiology in animals (Berteaux et al., 1996). A better understanding of the degree of individual variation in metabolic rate may help us understand the evolutionary pathways that shaped the metabolic capacities of organisms (Bennett, 1987).

Individual morphological (especially body mass) and physiological performance is often assumed to be consistent and repeatable (Hayes and Chappell, 1990). Repeatability, the measurement of consistent individual differences, is a critical factor to determine how a trait can evolve with natural selection (Bennett, 1987). Significant repeatability facilitates the study of selection acting on natural populations and the concept has several practical implications for identifying traits (Dohm, 2002). For example, it provides important information by setting the upper limit for heritability (Falconer and Mackay, 1996), although this may not always be the case (see Dohm, 2002).

As is known, body mass has a profound effect on almost every aspect of an animal's morphology and physiology (Calder, 1984; Peters, 1984). It is shown to be a highly repeatable trait in birds and mammals (Hayes and Chappell, 1990; Hõrak et al., 2002; Rønning et al., 2005).

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Studies on repeatability of metabolism in vertebrates have mainly been focused on maximum metabolic rate (MMR) (Chappell et al., 1995, 1996; Hayes and Chappell, 1990; Hayes and O'Connor, 1999). MMR sets an upper limit to sustainable power output during physiologically important activities such as thermoregulatory heat production, which can be intuitively related to fitness (Chappell et al., 1995). Further, studies on repeatability relevant to resting metabolic rate (RMR) (Hayes et al., 1997; Vézina and Thomas, 2000; Vézina and Williams, 2005) and basal metabolic rate (BMR) (Bech et al., 1999; Hõrak et al., 2002; Labocha et al., 2004; Rønning et al., 2005) have also accumulated rapidly. Compared with BMR, RMR is a slightly less rigorously defined measurment, but it is justified for small rodents for avoiding the hyperactivity and thermoregulating abnormality from the starvation prior to measurement (Speakman et al., 2004). Specifically, RMR measured within the thermoneutral zone (RMRt, see Speakman et al., 2004) is functionally equivalent to BMR in developing animals that by definition cannot have their BMR measured (Speakman et al., 2004). Non-shivering thermogenesis (NST) is an important mechanism of heat production in small mammals (Jansky, 1973). To our knowledge, there is no study on the repeatability of NST so far except a work of NST heritability measurement in the leaf-eared mouse (*Phyllotis darwini*) (Nespolo et al., 2003).

On the other hand, most work concerning repeatability of metabolism has been described for adult animals, although juvenile stages span considerable parts of life and juveniles are subjected to many of the same environmental factors as adults; furthermore, juveniles even experience more intense selection than adults (Chappell and Bachman, 1995). However, we are still aware of only a few studies on juveniles available (e.g. Chappell and Bachman, 1995; Chappell et al., 1996, 1999; Van Berkum et al., 1989).

Brandt's voles (*Lasiopodomys brandtii*) are typical steppe herbivores that mainly inhabit the Inner Mongolian grasslands of China, Mongolia and the region of Beigaer in Russia. Data are relatively abundant on their behaviour (Yu et al., 2004; Zhong et al., 1999), physiology (Li and Wang, 2005; Wang et al., 2003; Zhang and Wang, 2006) and population structure and dynamics (Wan et al., 2002; Zhang et al., 2003). In the present study, from an evolutionary view, we aimed to (1) measure the repeatability of metabolism and thermogenesis during the ontogeny of Brandt's voles, (2) compare values obtained in two generations of Brandt's voles and (3) estimate the correlations of metabolism and thermogenesis within full-sib families of voles, so as to provide some implications for the evolution of metabolism in Brandt's voles.

2. Material and methods

2.1. Animals

All animal procedures were licensed under the Animal Care and Use Committee of the Institute of Zoology, Chinese Academy of Sciences. Brandt's voles (*L. brandtii*) used in this study came from a laboratory-bred colony established in May 1999 from a wild population inhabiting the Inner Mongolian grasslands of China. Twenty healthy weight-matched virgins were chosen to be paired and permitted to give birth to generation 1; at weaning, 4 juveniles (3 females and 1 males) from each family of 6–8 pups were endorsed to the experiment (a sum of 48 voles). After the third time of metabolism measurement (64–68 days of age), females were paired within 3 days to produce generation 2 (a sum of 48 voles from 12 litters with 3 females and 1 males per litter). Throughout the experiment, 2 generations were gestated and reared until weaning (at 22 days of age) with the mother, and then housed individually in plastic mouse cages ($30 \times 15 \times 20\,cm^3$), provided with sawdust as bedding and given free access to food (Commercial rabbit pellets, Beijing KeAo Feed Co.) and water. The room conditions were a photoperiod of 16L:8D (with lights on at 0500) and a mean temperature of $22 \pm 1\,^{\circ}C$.

The metabolism measurements were conducted for 3 times for generation 1, that is 26 days of age (just after a food-intake measurement at weaning in another experiment; represents the juvenile stage), 49 days of age (just attain reproductive maturation; represents the subadult stage) and 64 days of age (represents the adult stage). Metabolism was measured only once for generation 2 and performed from the age of 64 days exactly similar to the third trial of generation 1. Each measurement lasted for 5 days. The first day was to measure RMR and the second day was for the NST test. The MMR test was separated by 2 days with NST measurement for avoiding the effects of NE injection.

2.2. Metabolic trials

Metabolism was measured using an established Kalabuhov–Skovortsov closed-circuit respirometer (Gorecki, 1975; Gorecki and Kania, 1986). The chamber size is 3.6 L. The resting metabolic rate (RMRt) measurement was at $30 \pm 0.5\,^{\circ}C$ (thermal neutral zone: 28–38 °C, Wang et al., 2003) with a water bath to maintain the temperature (Li and Wang, 2005; Wang et al., 2000, 2003). Carbon dioxide and water were absorbed by KOH and silica gel, respectively. Voles were put into the metabolic chamber and permitted for a 60-min stabilization, and then metabolism was recorded for another 60 min at 5-min intervals. The two stable consecutive lowest readings were used to calculate RMRt. The next day, NST of the same animals was stimulated with a subcutaneous injection of NE (Shanghai Harvest Pharmaceutical Co. Ltd). Temperature inside the chamber to measure NST was controlled with a water bath of $25 \pm 1\,^{\circ}C$. The dosage of NE was calculated following Wunder and Gettinger (1996): NE dosage $(mg/kg) = 2.53\,M_b^{-0.4}$ (g), this dosage was confirmed to induce the maximum NST in Brandt's voles (Wang and Wang, 2006). Two stable consecutive highest

values in the 60-min recordings were taken to calculate NST (Li and Wang, 2005; Wang and Wang, 1996).

MMR was determined at moderately cold ambient temperature ($T_a = 5\,^{\circ}C$) using a gas mixture (Helox) of 79% helium and 21% oxygen to produce high rates of heat loss (Rosenmann and Morrison, 1974). The temperature inside the metabolic chamber was maintained with a modified refrigerator ($\pm 1\,^{\circ}C$). After a 45-min stabilization in air, the oxygen consumption was recorded for 60 min at 5-min intervals (RMR 5 °C), then filled the chamber with Helox of 10–15 L (Song and Wang, 2002; Wang et al., 2001) and then recording the oxygen consumption for at least 20 min (Cygan, 1985; Gorecki and Kania, 1986), until the oxygen consumption began to decrease, whereupon measurements were terminated and the rectum temperature was recorded as soon as possible. MMR was computed as the highest oxygen consumption averaged over continuous 5-min intervals (Chappell et al., 1995; Cygan, 1985; Song and Wang, 2002). All metabolic measurements were performed between 0900 and 1700 and corrected to STP conditions.

Factorial aerobic scope (FAS), the reserve for aerobic work, was calculated as MMR/RMRt (Chappell and Bachman, 1995; Chappell et al., 1996; Hinds et al., 1995; Nespolo et al., 2003) and rNST was NST minus RMRt (McDevitt and Speakman, 1996).

2.3. Statistics

Data were analysed using SPSS software (SPSS 1998). Distributions of all variables were tested for normality using the Kolmogorov–Smirnov test. Pearson's correlation was performed to determine the relationship between metabolism and body mass for all the measurements. Because metabolism is a power function of body mass, the statistics was performed based on residuals. Residual values were calculated as the measured value minus predicted value, from which the predicted value was obtained from a linear regression on body mass of each time point. We used repeated measures ANOVA to assess differences in body mass, RMRt, RMR (5 °C), MMR, FAS, NST and rNST among three trials in generation 1. All the differences in each parameter were further evaluated by LSD post-hoc tests, with the significance level adjusted to account for the number of comparisons (Bonferroni correction). Independent-samples T-test was employed to detect the differences between generations at 64 days of age.

Repeatability (coefficient of intraclass correlation, ρ_i) was calculated for 48 individuals from generation 1, based on variance components obtained in ANOVA (Dohm, 2002; Lessells and Boag, 1987; Lynch and Walsh, 1998). Within-family correlation (ρ_f) was calculated for full-sib first-litter families with 4 out of 6–8 individuals in both generations (Labocha et al., 2004). Results are presented as mean ± SE and $p < 0.05$ was considered statistically significant.

3. Results

3.1. Metabolic rate

Correlation analysis demonstrated that the RMRt, RMR (5 °C), MMR, NST and rNST of 2 generations on which a total of 4 trials carried out were positively correlated with body mass (RMRt: $r = 0.675$, $p < 0.001$; RMR (5 °C): $r = 0.467$, $p < 0.001$; MMR: $r = 0.578$, $p < 0.001$; NST: $r = 0.511$, $p < 0.001$; rNST: $r = 0.212$, $p < 0.01$, respectively; Fig. 1a, b, c, e and f), while FAS showed negative correlation with body mass ($r = -0.466$, $p < 0.001$ Fig. 1d), which suggested that FAS grew smaller with the increase of body mass or age.

In the process of development, there were no significant differences in any parameters except body mass ($p < 0.001$) (Table 1). Between generations, all the parameters except body mass of males ($p = 0.011$) still showed no differences, which demonstrated the consistency of population-average characters (Table 1).

3.2. Effects of sex

The sexual difference detection based on the residuals of four trials showed that most of the characters failed to reach statistical significance except body mass ($t = 4.609$, $df = 190$, $p < 0.001$). Males showed higher body mass than females in Brandt's voles.

3.3. CV and repeatability

The observed variations in body mass (6.8–20.7%) and metabolism were very high (between 6.8% in MMR and 31.6% in NST) (Table 2). No significant repeatability in body mass, RMRt, RMR (5 °C), MMR, FAS, NST and rNST was found for each sex as well as for both sexes pooled during the ontogeny in Brandt's voles (the longest measurement interval was 23 days) (Table 2).

As for the variation among families, body mass varied significantly and was highly correlated within families at 26 days of age in generation 1 ($\rho_f = 0.79$, $p < 0.001$). No other ages or generation had differences among families in body mass. MMR had differences among families at 26 days too (MMR: $\rho_f = 0.34$, $p = 0.017$), while RMRt and FAS showed significant differences among families at 64 days of age (RMRt: $\rho_f = 0.45$, $p = 0.003$; FAS: $\rho_f = 0.36$, $p = 0.013$). There was no significant correlation within families in generation 2 in any of the parameters referred here (Table 3).

4. Discussion

4.1. Equipment reliability

To ascertain equipment reliability, we performed two RMRt trials (2 h between tests for avoiding physiological changes' occurrence in animals) for the same 16 animals.

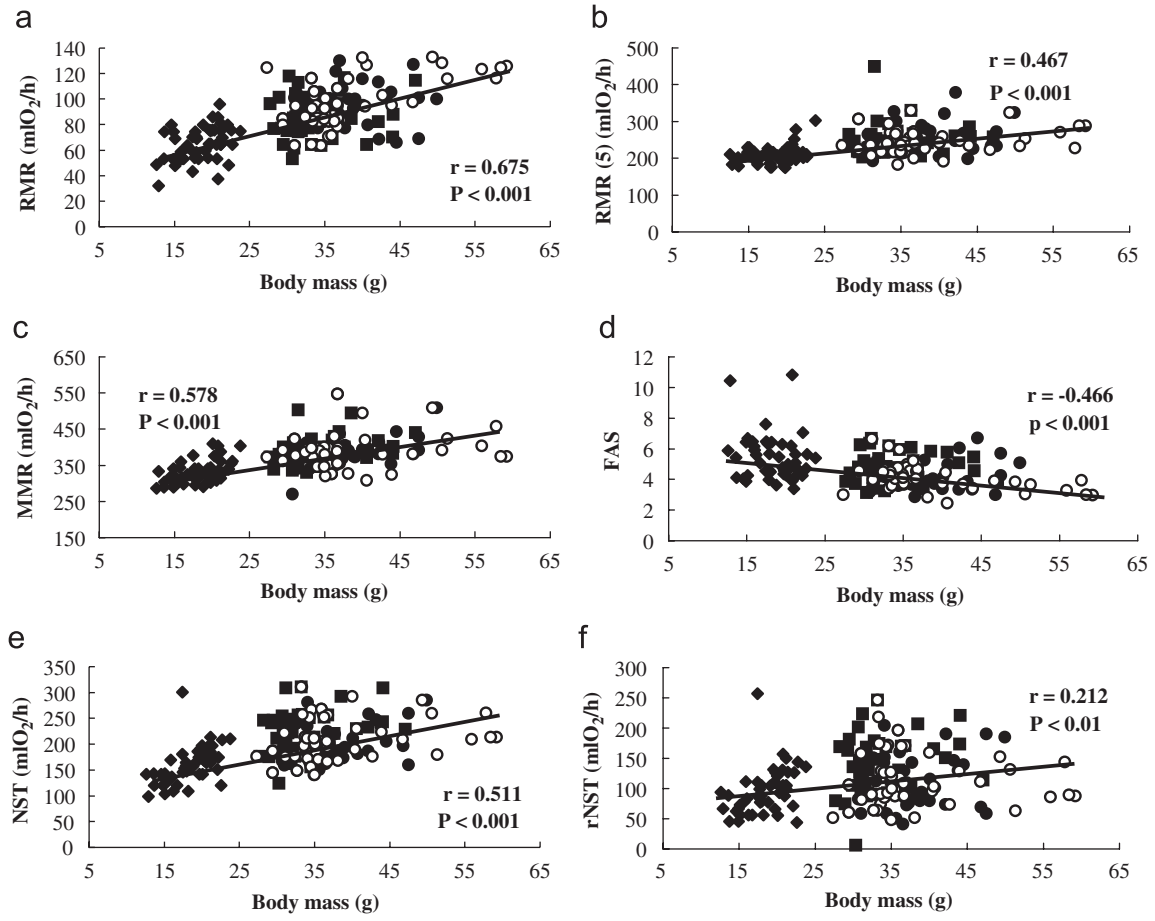

Fig. 1. Relationships between metabolism or metabolic capacity and body mass in Brandt's voles. Correlation analysis demonstrated that the RMRt, RMR (5 °C), MMR, NST and rNST of two generations were positively correlated with body mass (a, b, c, e and f), while FAS showed negative correlation with body mass (d). $p<0.05$ was considered to be significantly correlated. Filled diamond, trial 1; filled square, trial 2; filled circle, trial 3; open circle, trial 4. The line represents the relationship between parameters for all the trials.

Table 1
p Values of body mass and metabolism among different ages or generations in Brandt's voles

	Size	Body mass	RMRt	RMR (5 °C)	MMR	FAS	NST	rNST
Trials								
Male	36	**<0.001**	0.645	0.710	0.592	0.419	0.804	0.754
Female	108	**<0.001**	0.733	0.788	0.673	0.675	0.944	0.117
Total	144	**<0.001**	1.000	1.000	1.000	1.000	1.000	0.316
Generations								
Male	24	**0.011**	0.845	0.938	0.912	0.206	0.704	0.795
Female	72	0.168	0.868	0.948	0.932	0.347	0.832	0.892
Total	96	0.399	0.434	0.297	0.796	0.929	0.296	0.520

Trials' comparison is among different ages of generation 1 with repeated measures ANOVA; generations' comparison is between data of generation 1 at 64 days of age and that of generation 2 with independent-samples *T*-test. The Bonferroni correction was applied to the significance level. Significant differences at the 95% confidence level are in bold type. The bold type means significantly different among trials or generations.

We found that the correlation between repeats was high ($r = 0.95$, $p<0.001$) and the error variance (coefficient of variation in repeated trials) in measurements was about 7%. The measurement error therefore contributes only a small fraction to the total variance, which ensured the biological information rather than noise of our data.

4.2. Comparison of population-average characters among different ages or generations

With the somatic growth, RMRt, RMR (5°C), MMR, NST and rNST increased. It might be a result of the increasing metabolic organs that contribute to metabolic

Table 2
CV and ρ_i of metabolism at different ages or generations in Brandt's voles

	CV (%)												ρ_i			*p* Value		
	Trial 1 (26 d)			Trial 2 (49 d)			Trial 3 (64 d)			Generation 2 (64 d)								
	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total
Body mass	16.0	15.3	15.4	14.5	9.8	12.8	11.6	9.2	13.3	14.7	6.8	20.7	0.00	0.00	0.00	1.00	1.00	1.00
RMRt	19.1	21.6	20.7	19.8	15.8	17.8	21.3	13.6	16.5	12.3	16.1	19.5	0.16	0.14	0.15	0.17	0.08	0.04
RMR (5 °C)	13.7	10.8	11.7	8.8	19.1	17.1	19.1	12.1	14.3	13.5	12.4	12.7	0.05	0.19	0.14	0.38	0.03	0.05
MMR	8.7	9.4	9.1	6.8	9.4	8.8	9.7	10.7	10.9	14.6	9.9	11.5	−0.01	0.01	0.01	0.68	0.43	0.53
FAS	19.9	29.6	27.3	20.9	16.6	17.8	27.1	16.8	20.0	15.3	17.9	20.0	0.17	0.13	0.13	0.14	0.11	0.07
NST	31.6	18.1	22.5	19.8	18.0	18.3	17.7	18.4	18.3	16.6	21.4	20.4	−0.01	0.09	0.03	0.61	0.18	0.35
RNST	55.1	30.7	38.9	39.6	31.2	33.2	44.3	39.0	40.2	28.2	42.7	39.3	0.02	0.12	0.08	0.44	0.11	0.17

CVs are of absolute values of parameters. ρ_i and *p* values are of statistics for residuals of parameters. ρ_i was calculated based on variance components obtained in ANOVA performed on generation 1. The Bonferroni correction was applied to the significance level.

Table 3
The variations of metabolism among families at different ages or generations in Brandt's voles

	Body mass		RMRt		RMR (5 °C)		MMR		FAS		NST		rNST	
	ρ_f	*p* value	ρ_f	*p* value	ρ_f	*p* value	ρ_f	*p* value	ρ_f	*p* value	ρ_f	*p* value	ρ_f	*p* value
Trial 1 (26 d)	**0.79**	**<0.001**	0.25	0.060	0.31	0.028	**0.34**	**0.017**	0.17	0.138	0.27	0.044	0.29	0.036
Trial 2 (49 d)	0.01	0.877	0.03	0.403	0.03	0.583	0.03	0.402	0.10	0.250	0.11	0.232	0.21	0.096
Trial 3 (64 d)	0.01	0.805	**0.45**	**0.003**	0.16	0.154	0.24	0.065	**0.36**	**0.013**	0.09	0.278	0.24	0.071
Generation 2 (64 d)	0.00	0.996	0.16	0.145	0.01	0.914	0.03	0.837	0.10	0.255	0.16	0.145	0.21	0.094

ρ_f was calculated based on variance components obtained in ANOVA performed on both generations of pooled data. The Bonferroni correction was applied to the significance level. The bold type means significantly different among families.

rate (Bech et al., 1999; Even et al., 2001; Meerlo et al., 1997; Song and Wang, 2003). Surprisingly, however, FAS decreased with increased body mass in Brandt's voles, which was contradictory with the observations for free-living Belding's ground squirrels (*Spermophilus beldingi*) (Chappell and Bachman, 1995). In the latter species, FAS of weaning pups was 5.4 while that of adults was 7.5, the author speculated that the change in FAS might occur at least partially through exercise conditioning and acclimatization to cold after juveniles leave their sheltered natal burrows and become active above ground (Chappell and Bachman, 1995). In our animals, however, it decreased from 5.4 of weaning pups to 4.2 of 64-day-old animals. If FAS was under the selection, we might imagine that juveniles may experience more intense selection than adults (Chappell and Bachman, 1995). Few data on the ontogeny of FAS in mammals are available, so it is unclear whether this is a species-specific phenomenon.

The stability of most parameters in the process of development demonstrated that the average mass-independent performance did not differ during the maturation. The results between two generations also suggested the consistency of population-average characters, which was similar to the BMR in bank voles (*Clethrionomys glareolus*) (Labocha et al., 2004). Further, the inexplainable changes in body mass of males might result from the small samples in the present study. Generally, population-average traits showed consistency among different ages or between generations in Brandt's voles.

Our sexual difference analysis showed that males had higher body mass but similar metabolism with females in Brandt's voles. Consistently, Chappell and Bachman (1995) found no effect of sex on RMR but on both thermogenic and exercise MMR in Belding's ground squirrels. Females had an MMR that averaged 6.7% and 6.3% higher than males for cold exposure and exercise, respectively. In another work on red junglefowl (*Gallus gallus*), Chappell et al. (1996) found that FAS in adult males (9.6) was higher than in females (5.6), which was considered to be an adaptation to support intense, prolonged inter-male aggression.

4.3. Repeatability of metabolism during the ontogeny at the level of individual variation

The CV of body mass was 6.8–20.7% in Brandt's voles, which was greater than that of house mice (*Mus*

domesticus) (10–15%, Dohm et al., 2001). The highest CV in aerobic performance was 31.6% for NST in male Brandt's voles, which was much higher than the common magnitude of 10% generally observed in other mammals for BMR and MMR (e.g. Chappell and Bachman, 1995). The average CV of 6.8–14.6% for MMR in Brandt's voles was fairly similar to variance in sprint speed in lizards (*Sceloporus merriami* and *Sceloporus occidentalis*) (Huey and Dunham, 1987; Van Berkum et al., 1989) and MMR in deer mice (*Peromyscus maniculatus*) (cited from Chappell and Bachman, 1995) as well as *Mus musculus* (Dohm et al., 2001; Friedman et al., 1992). On the other hand, Bryant and Furness (1995) found that the CV of BMR in kittiwakes from Svalbard (*Rissa tridactyla*) was as high as 31.5%. Another example, 23% of BMR and 27% of PMR (MMR), was found in nine-banded armadillos (*Dasypus novemcinctus*) (Boily, 2002).

To our knowledge, the only estimate of the repeatability of RMR in a non-domestic mammal has been reported for captive Merriam's kangaroo rats (*Dipodomys merriami*) (Hayes et al., 1997), in which repeatability was measured across a 21-day interval. They were 0.69 for absolute RMR and 0.68 for mass-independent values. Meanwhile, the only measurement of the repeatability for BMR in a non-domestic mammal has been reported for the first and second laboratory-bred offsprings of free-living bank voles (Labocha et al., 2004). The ρ_i was 0.70 for absolute log-transformed values and 0.56 for mass-independent values (Labocha et al., 2004). Compared with them, the non-significant repeatability of RMR in our experiment was contradictory. But the one thing that should be kept in mind is that the repeatability measurement mentioned above was performed in adults, which might make a difference from our measurement during the ontogeny in Brandt's voles. Consequently, the RMR in juveniles was not a good indicator of the RMR in adulthood in Brandt's voles.

Similar to our non-significant repeatability in MMR in Brandt's voles during the development, Chappell et al. (1996) also found no repeatability of MMR in red junglefowl during the growth, and no repeatability of MMR in Belding's ground squirrels (Chappell et al., 1995). However, in the lizards, speed is significantly repeatable across considerable ontogenic growth (Huey and Dunham, 1987; Van Berkum et al., 1989). This is the only work we are aware of that showed significant repeatability during the development. Just as Chappell et al. (1996) addressed that the lack of repeatability during the growth was problematic, and begs the question of whether adult metabolic rate was heritable. It is a subject of quantitative genetics studies. Yet, without the quantitative study, we can only conclude here that it is not valid to use the performance of a young to predict its capabilities after maturation in Brandt's voles. In a broader sense, developmental stages should be taken into account when making comparisons between different experiments and even different species.

4.4. Relationship between repeatability and heritability

Rønning et al. (2005) asked a valuable question of over what timescale the trait had to be repeatable to consider the possibility that natural selection was working upon it. Work done on lizard (Huey and Dunham, 1987) and zebra finch (*Taeniopygia guttata*) (Rønning et al., 2005) obtained the high significant repeatability in which the measurement period was as long as their lifespan. However, a trait with high repeatability might have a heritability of zero (Merilä and Sheldon, 2001). The few studies on heritability of BMR, NST (NSTmax-BMR; NSTmax in Nespolo's work is the same as our defined NST), MMR and FAS indicated that the heritability might be very low (Nespolo et al., 2003). Our experiment in body mass and residuals of metabolism did not differ significantly across families at 64 days of age and the coefficient of intraclass for full sibs did not differ from zero except the RMRt and FAS of generation 1 (not very high), which suggested that heritability of these traits in Brandt's voles was not high. Labocha et al. (2004) showed evidence that in bank voles BMR did not differ significantly across families, which implied that heritability of BMR in bank voles was low. All these agreed well with available estimates of narrow-sense heritability of RMR in other vertebrates (humans, Bogardus et al., 1986; Rice et al., 1996). In contrast, significant among-litter variability for mass-specific RMR existed in armadillos (Bagatto et al., 2000) and lizards (*Chalcides ocellatus*) (Pough and Andrews, 1984). Dohm et al. (2001) found a fairly high heritability of exercise-induced MMR in house mice but low heritability for BMR; however, heritability of BMR in the bank vole was relatively high (Sadowska et al., 2005).

An important advantage of laboratory studies is that genealogy is easy to record and, after accumulating sufficient data, heritability of the traits can be estimated (Labocha et al., 2004). Further, measurement on laboratory animals is helpful for eliminating the confounding effects of natural variations in ecological conditions. Many performances such as aerobic traits in many species are known to change rapidly when individuals are manipulated to conditioning regimes or acclimatization (e.g. Li and Wang, 2005, Brandt's voles). This plasticity may fundamentally influence the magnitude of repeatability and hence how selection acts (Chappell et al., 1995). But our present study only supplies tentative evidence of this subject because of the relatively small samples.

Taken together, population-average values of aerobic performance were consistent among different ages or generations in Brandt's voles; however, there was no repeatability at the level of individual variation during the ontogeny, which indicated that a single measure of metabolism in a certain time did not represent the true value of the individual throughout its life. At the same time, mass-independent data did not differ significantly

across families, and the coefficient of intraclass correlation for full sibs failed to reach statistical significance, suggesting that heritability of aerobic traits in Brandt's voles was relatively low.

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Appendix

See Table A1.

Table A1
Descriptive data for body mass and metabolism at different ages or generations in Brandt's voles

Source	Generation 1			Generation 2
	Trial 1 (26 d)	Trial 2 (49 d)	Trial 3 (64 d)	Trial (64 d)
Sample size				
Male	12	12	12	12
Female	36	36	36	36
Total	48	48	48	48
Body mass (g)				
Male	18.7±0.8	36.8±1.5	42.3±1.4	49.0±2.0
Female	18.4±0.5	32.4±0.5	35.0±0.5	34.0±0.4
Mean	18.5±0.4	33.6±0.6	37.0±0.7	38.1±1.1
RMRt (ml O_2/h)				
Male	65.5±3.5	92.5±5.1	99.0±5.9	116.7±4.0
Female	64.5±2.3	82.2±2.2	91.7±2.1	89.0±2.4
Mean	64.8±1.9	85.0±2.2	93.7±2.2	96.5±2.7
RMR (5 °C) (ml O_2/h)				
Male	214.2±8.1	235.5±5.7	258.8±13.7	252.7±9.4
Female	207.0±3.8	245.3±7.9	248.9±5.1	241.3±5.0
Mean	209.0±3.5	242.6±6.0	251.6±5.2	244.4±4.5
MMR (ml O_2/h)				
Male	330.9±8.0	400.4±7.6	408.6±10.9	403.5±16.3
Female	332.8±5.3	386.2±6.1	378.4±6.9	383.5±6.4
Mean	332.3±4.4	390.1±5.0	386.6±6.1	388.9±6.5
FAS				
Male	5.2±0.3	4.5±0.3	4.3±0.2	3.5±0.1
Female	5.5±0.3	4.8±0.1	4.2±0.1	4.4±0.1
Mean	5.4±0.2	4.7±0.1	4.2±0.1	4.2±0.1
NST (ml O_2/h)				
Male	166.2±14.6	219.8±12.1	211.6±10.4	226.4±10.4
Female	159.3±4.9	221.6±6.7	198.1±6.2	204.4±7.4
Mean	161.2±5.2	221.1±5.8	201.8±5.3	210.4±6.2
RNST (ml O_2/h)				
Male	100.7±15.4	127.3±14.0	112.5±13.8	109.8±8.6
Female	94.9±4.9	139.3±7.3	106.4±7.0	115.4±8.3
Mean	96.4±5.4	145.2±6.5	108.1±6.3	113.9±6.5

Descriptive data are absolute values of parameters (mean±SE).

References

Bagatto, B.D.A., Crossley, I.I., Burggren, W.W., 2000. Physiological variability in neonatal armadillo quadruplets: within- and between-litter differences. J. Exp. Biol. 203, 1733–1740.

Bech, C., Langseth, I., Gabrielsen, G.W., 1999. Repeatability of basal metabolism in breeding female kittiwake *Rissa tridactyla*. Proc. R. Soc. London B 266, 2161–2167.

Bennett, A.F., 1987. Interindividual variability: an underutilized resource. In: Feder, M.E., Bennett, A.F., Burggren, W.W., Huey, R.B. (Eds.), New Directions in Ecological Physiology. Cambridge University Press, New York, pp. 1–8.

Berteaux, D., Thomas, D.W., Bergeron, J.-M., Lapierre, H., 1996. Repeatability of daily field metabolic rate in female meadow voles (*Microtus pennsylvanicus*). Funct. Ecol. 10, 751–759.

Bogardus, C., Lillioja, S., Ravussin, E., Abbott, W., Zawadzki, J.K., Young, A., Knowler, W.C., Jacobowitz, R., Moll, P.P., 1986. Familial dependence of the resting metablic rate. N. Engl. J. Med. 315, 96–100.

Boily, P., 2002. Individual variation in metabolic traits of wild nine-banded armadillos (*Dasypus novemcinctus*), and the aerobic capacity model for the evolution of endothermy. J. Exp. Biol. 205, 3207–3214.

Bryant, K.L., Furness, R.W., 1995. Basal metabolic rate of North Atlantic seabirds. Ibis 127, 219–226.

Calder, W.Z., 1984. Size, Function and Life History. Harvard University Press, Massachusetts.

Chappell, M.A., Bachman, G.C., 1995. Aerobic performance in Belding's ground squirrels (*Spermophilus beldingi*): variance, ontogeny, and the aerobic capacity model of endothermy. Physiol. Zool. 68, 421–442.

Chappell, M.A., Bachman, G.C., Odell, J.P., 1995. Repeatability of maximal aerobic performance in Belding's ground squirrels, *Spermophilus beldingi*. Funct. Ecol. 9, 498–504.

Chappell, M.A., Zuk, M., Johnsen, T.S., 1996. Repeatability of aerobic performance in red junglefowl: effects of ontogeny and nematode infection. Funct. Ecol. 10, 578–585.

Chappell, M.A., Bech, C., Butteer, W.A., 1999. The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. J. Exp. Biol. 202, 2269–2279.

Cygan, T., 1985. Seasonal changes in thermoregulation and maximum metabolism in the yellow-necked field mouse. Acta Theriol. 30, 115–130.

Dohm, M.R., 2002. Repeatability estimates do not always set an upper limit to heritability. Funct. Ecol. 16, 273–280.

Dohm, M.R., Hayes, J.P., Garland Jr., T., 2001. Quantitative genetics of maximal and basal rates of oxygen consumption in mice. Genetics 159, 267–277.

Even, P.C., Rolland, V., Roseau, S., Bouthegourd, J.C., Tome, D., 2001. Prediction of basal metabolism from organ size in the rat: relationship to strain, feeding, age, and obesity. Am. J. Physiol. 280, R1887–R1896.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, fourth ed. Longman, London.

Friedman, W.A., Garland, T., Dohm, M.R., 1992. Individual variation in locomotor behaviour and maximal oxygen consumption in mice. Physiol. Behav. 52, 97–104.

Gorecki, A., 1975. Kalabukhov–Skvortsov respirometer and resting metabolic rate measurement. In: Grodzinski, W., et al. (Eds.), Methods for Ecological Energetics. Blackwell Scientific, Oxford, pp. 309–313.

Gorecki, A., Kania, Z., 1986. Maximum metabolism and thermoregulation in laboratory mice. Acta Theriol. 31, 97–105.

Hayes, J.P., Chappell, M.A., 1990. Individual consistency of maximal oxygen consumption in deer mice. Funct. Ecol. 4, 495–503.

Hayes, J.P., O'Connor, C.S., 1999. Natural selection on thermogenic capacity of high-altitude deer mice. Evolution 53, 1280–1287.

Hayes, J.P., Bible, C.A., Boone, J.D., 1997. Repeatability of mammalian physiology: evaporative water loss and oxygen consumption of *Dipodomys merriami*. J. Mammal. 79, 445–485.

Hinds, D.S., Baudinette, R.V., MacMillen, R.E., Halpern, E.A., 1995. Maximum metabolism and the aerobic factorial scope of endotherms. J. Exp. Biol. 182, 41–56.

Hõrak, P., Saks, L., Ots, I., Kollist, H., 2002. Repeatability of conditions indices in captive greenfinches (*Carduelis chloris*). Can. J. Zool. 80, 636–643.

Huey, R.B., Dunham, A.T., 1987. Repeatability of locomotor performance in natural populations of the lizard, *Sceloporus merriami*. Evolution 41, 1116–1120.

Jansky, L., 1973. Nonshivering thermogenesis and its thermoregulatory significance. Biol. Rev. 48, 85–132.

Labocha, M.K., Sadowska, E.T., Baliga, K., Semer, A.K., Koteja, P., 2004. Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionmys glareolus*. Proc. R. Soc. London B 271, 367–372.

Lessells, C.M., Boag, P.T., 1987. Unrepeatable repeatabilities: a common mistake. Auk 104, 116–121.

Li, X.S., Wang, D.H., 2005. Regulation of body weight and thermogenesis in seasonally acclimatized Brandt's voles (*Microtus brandtii*). Horm. Behav. 48, 321–328.

Lynch, M., Walsh, J.B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer, Sunderland, MA.

McDevitt, R.M., Speakman, J.R., 1996. Summer acclimatization in the short-tailed field vole, *Microtus agrestis*. J. Comp. Physiol. B 166, 286–293.

Meerlo, P., Bolle, L., Visser, G.H., Masman, D., Daan, S., 1997. Basal metabolic rate in relation to body composition and daily energy expendicture in field vole, *Microtus agrestis*. Physiol. Zool. 70, 362–369.

Merilä, J., Sheldon, B.C., 2001. Avian quantitative genetics. In: Nolan, Jr., V., Thompson, C.F. (Eds.), Current Ornithology, vol. 16. Kluwer Academic/Plenum Publishers, New York, pp. 179–255.

Nespolo, R.F., Bacigalupe, L.D., Bozinovic, F., 2003. Heritability of energetics in a wild mammal, the leaf-eared mouse (*Phyllotis darwini*). Evolution 57, 1679–1688.

Peters, R.H., 1984. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Pough, F.H., 1989. Organismal performance and Darwinian fitness: approaches and interpretations. Physiol. Zool. 62, 199–236.

Pough, F.H., Andrews, R.M., 1984. Individual and sibling-group variation in metabolism of lizards: the aerobic capacity model for the origin of endothermy. Comp. Biochem. Physiol. A 79, 415–419.

Rice, T.A., Tremblay, O., Deriaz, L., Perusse, D.C., Rao, D.C., et al., 1996. Genetic pleiotropy for resting metabolic rate with fat-free mass and fat mass: the Quebec family study. Obes. Res. 4, 125–131.

Rønning, B., Moe, B., Bech, C., 2005. Long-term repeatability makes basal metabolic rate a likely heritable trait in the zebra finch *Taeniopygia guttata*. J. Exp. Biol. 208, 4663–4669.

Rosenmann, M., Morrison, P., 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He–O_2. Am. J. Physiol. 226, 490–495.

Sadowska, E.T., Labocha, M.K., Baliga, K., Stanisz, A., Wrblewska, A.K., Jagusiak, W., Koteja, P., 2005. Genetic correlations between basal and maximum metabolic rates in a wild rodent: consequences for evolution of endothermy. Evolution 59, 672–681.

Song, Z.G., Wang, D.H., 2002. Relationships between metabolic rates and body composition in the Monglian gerbils (*Meriones unguiculatus*). Acta Zool. Sin. 48, 445–451.

Song, Z.G., Wang, D.H., 2003. Relationship between metabolic rate and organ size in Brandt's voles (*Microtus brandti*). Acta Theriol. Sin. 23, 230–234.

Speakman, J.R., Król, E., Johnson, M., 2004. The functional significance of individual variation in basal metabolic rate. Physiol. Biochem. Zool. 77, 900–915.

Van Berkum, F.H., Huey, R.B., Tsuji, J.S., Garland, T., 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard, *Sceloporus occidentalis* (Baird and Girard). Funct. Ecol. 3, 97–105.

Vézina, F., Thomas, D.W., 2000. Social status does not affect resting metabolic rate in wintering dark-eyed juncos (*Junco hyemalis*). Physiol. Biochem. Zool. 73, 231–236.

Vézina, F., Williams, T.D., 2005. The metabolic cost of egg production is repeatable. J. Exp. Biol. 208, 2533–2538.

Wan, X.R., Wang, M.J., Wang, G.H., Liu, W., Zhong, W.Q., 2002. The reproduction parameters in the marked populations of Brandt's vole. Acta Theriol. Sin. 22, 116–122.

Wang, D.H., Wang, Z.W., 1996. Seasonal variations in thermogenesis and energy requirements of plateau pikas *Ochotona curzoniae* and root voles *Microtus oeconomus*. Acta Theriol. 41, 225–236.

Wang, D.H., Wang, Y.S., Wang, Z.W., 2000. Metabolism and thermoregulation in the Mongolia gerbils (*Meriones unguiculatus*). Acta Theriol. 45, 183–192.

Wang, D.H., Wang, Z.W., Wang, Y.S., Yang, J.C., 2003. Seasonal changes of thermogenesis in Mongolian gerbils (*Meriones unguiculatus*) and Brandt's voles (*Microtus brandtii*). Comp. Biochem. Physiol. A Mol. Integr. Physiol. 134, S96.

Wang, J.M., Wang, D.H., 2006. Comparison of nonshivering thermogenesis induced by dosages of norepinephrine from 3 allometric equations in Brandt's voles (*Lasiopodomys brandtii*). Acta Theriol. Sin. 26, 84–88.

Wang, Y.S., Wang, D.H., Wang, Z.W., 2001. Maximum metabolic rate in plateau pikas (*Ochotna curzoniae*) and root voles (*Microtus oeconomus*). Acta Zool. Sin. 47, 601–608.

Wunder, B.A., Gettinger, R.D., 1996. Effects of body mass and temperature acclimation on the nonshivering thermogenic response of small mammals. In: Geiser, F., Hulbert, A.J., Nicol, S.C. (Eds.), Adaptations to the Cold: Tenth International Hibernation Symposium. University of New England Press, New South Wales, pp. 131–139.

Yu, X.D., Sun, R.Y., Fang, J.M., 2004. Effect of kinship on social behaviours in Brandt's voles (*Microtus brandti*). J. Ethol. 22, 17–22.

Zhang, X.Y., Wang, D.H., 2006. Effects of cold acclimation and rewarming on energy metabolism and body mass regulation in Brandt's voles (*Lasiopodomys brandtii*). Horm. Behav. 50, 61–69.

Zhang, Z.B., Pech, R., Davis, S., Shi, D.Z., Wan, X.R., Zhong, W.Q., 2003. Extrinsic and intrinsic factors determine the eruptive dynamics of Brandt's voles *Microtus brandtii* in Inner Mongolian, China. Oikos 100, 299–310.

Zhong, W.Q., Wang, M.J., Wan, X.R., 1999. Ecological management of Brandt's vole in Inner Mongolia, China. In: Singleton, G., Hinds, L., Leirs, H., Zhang, Z.B. (Eds.), Ecologically-Based Management of Rodent Pests. Australian Centre for International Agricultural Research, Canberra, pp. 199–214.