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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 ($30 \times 15 \times 20\,\mathrm{cm}^3$), 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 $22 \pm 1\,^\circ\mathrm{C}$.

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 $30 \pm 0.5\,^\circ\mathrm{C}$ (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 $25 \pm 1\,^\circ\mathrm{C}$. 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