

Metabolism and thermoregulation in three species of rodent from Northeastern China

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Abstract

Metabolic rate, body temperature, and thermal conductance were determined in the gray red-backed vole (*Clethrionomys rufocanus*), large Japanese field mouse (*Apodemus speciosus*) and striped field mouse (*Apodemus agrarius*) at a temperature range of 5–32.5°C. Oxygen consumption was measured by using a closed circuit respirometer. The thermal neutral zone of gray red-backed vole, large Japanese field mouse and striped field mouse were 22.5–27.5°C, 25–30°C and 25–27.5°C, respectively. The mean metabolic rates within thermal zone of these species were 3.62 ± 0.18 , 2.69 ± 0.08 , and 3.29 ± 0.11 ml O₂ g⁻¹ h⁻¹, respectively, which are relatively higher than the predicted values based on their body mass. Non-shivering thermogenesis of these animals were 6.76 ± 0.12 , 5.56 ± 0.39 and 6.13 ± 0.28 ml O₂ g⁻¹ h⁻¹, respectively. Mean body temperature of the three species were 37.1 ± 0.13 °C, 36.9 ± 0.2 °C, and 37.5 ± 0.2 °C, respectively. Mean thermal conductance of the three species were 0.25 ± 0.04 , 0.23 ± 0.00 and 0.25 ± 0.00 ml O₂ g⁻¹ h⁻¹°C⁻¹, respectively. The ecophysiological properties of these species were: (1) the gray red-backed vole and large Japanese field mouse had high body temperatures and metabolic rates, median non-shivering thermogenesis, relatively wide thermal neutral zones and low lower critical temperatures, and relatively high thermal conductance. All these characteristics might constrain their distribution and extension to extreme desert, low latitudes and hot regions in China. (2) the striped field mouse had high metabolic rate, body temperature and thermal conductance, median non-shivering thermogenesis, a relatively narrow thermal neutral zone and low lower critical temperature.

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Keywords: Basal metabolic rate; Non-shivering thermogenesis; Gray red-backed vole; *Clethrionomys rufocanus*; Large Japanese field mouse; *Apodemus speciosus*; Striped field mouse; *A. agrarius*; Thermal conductance; Body temperature; Graphical distribution

1. Introduction

The study on phenotypic plasticity has become a central topic in evolutionary ecology. Elucidating the selection pressure(s) that drive the evolution of metabolic rate (MR) is fundamental to understanding the evolution of the morphology, physiology, behavior, and life histories of mammals (Lovegrove, 2003). Many

variables associated with the continuum are correlated with latitude (Lovegrove, 2001), suggesting that climate has been important in the evolution of life-history traits. During maintenance of a high and constant body temperature, endotherms primarily use mechanisms alter the rates of heat production and dissipation (McNab, 1983). Typically, as ambient temperatures decreased the energy expended to remain homeothermic increases. In mammals remain active during winter will be survival on an ability to increase cold tolerance and/or reduce energy expenditure, and may entail a variety of behavioral, morphological and physiological

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mechanisms (Heldmaier, 1989; Corp et al., 1997). Cold tolerance can be improved by an increase in thermal insulation or heat production. In some small mammals insulation is improved during winter through an increase in pelage thickness and/or density, and/or elevated levels of dermal fat (Bolshakov, 1984; Feist, 1984). However, because of their small body size the extent and thus the effectiveness of such modifications is limited. Small mammals use basal metabolic rate (BMR) and non-shivering thermogenesis (NST) as their principal mechanisms for heat production (Merritt and Zegers, 1991).

Comparing small mammals from different habitats and different habits, Haim and Izhaki (1993) have emphasized the ecological significance of BMR and NST. For example, desert and fossorial rodents typically have lower BMR than expected from their body mass according to allometric equations (McNab, 1988; Degen, 1997), and alpine and boreal high latitude small mammals have higher metabolic levels (Wang and Wang, 2002). In contrast, the NST capacity levels of desert-adapted or diurnal species are significantly higher than that of mesic or nocturnal species (Haim and Izhaki, 1993). These findings indicate that environmental conditions are very important in shaping the ecophysiological features of a species. As a result, the deviation in metabolic level in one species in a given region from the general pattern seen in other mammals can reflect the specific adaptation and evolution (Wang and Wang, 2002).

Gray red-backed vole (*Clethrionomys rufocanus* Sundevall, 1846) and large Japanese field mouse (*Apodemus speciosus* Temminck, 1845) are major pest rodents in northern China and are also distributed in Russia (Ma, 1986). The striped field mouse (*A. agrarius* Pallas, 1771) distributes extensively in China from north to south (Zhang and Wang, 1998). Within their ranges the gray red-backed vole and large Japanese field mouse preferentially occur in forest and also were found in farmland and grassland. The dominant habitats of striped field mouse are grassland, farmland, old cultivated field and hillsides, and were found in the regions inhabited by the people in winter as well (Ma, 1986). These three species are granivorous and nocturnal, non-hibernating (Ma, 1986; Zhang and Wang, 1998). Although some work has been done on the population dynamics of these species, there are no data available as yet on their energy metabolism. The purpose of this study is to measure the BMR and NST of these species and correlate them with their distribution patterns.

2. Materials and methods

2.1. Animals

Five gray red-backed voles (3 males, 2 females), six large Japanese field mice (3 males, 3 females) and seven

striped field mice (4 males, 3 females) were live-trapped in the forest regions (48°29'N, 124°51'E) at Nehe County, Heihongjiang Province in China in June 2002. The fluctuation of ambient temperature is great. The annual mean temperature is 3.4°C, average monthly air temperature in the coldest month (January) is -20.6°C, and 22.9°C in the warmest month (July). The annual temperature variation range is -32.2–35.7°C. There are seven months (October through April) in which the extreme minimum ambient temperature is below -38°C. The experiments were carried out in July 2002. The mean body mass of gray red-backed voles, large Japanese field mice and striped field mice were 23.05 ± 0.66 , 28.52 ± 3.18 and 24.37 ± 1.38 g, respectively. Animals were kept in cages ($50 \times 30 \times 25$ cm³) under natural photoperiod (14L: 10D) and temperature (16–24°C) and were fed laboratory mice chow pellets (Beijing Ke Ao Feed Co.). Food and water were supplied ad lib.

2.2. Metabolic trials

Oxygen consumption was measured using the closed-circuit respirometer according to Górecki (1975). Temperatures inside the animal chambers in a water bath were measured and maintained constant to $\pm 0.5^\circ\text{C}$. Volume of metabolic chamber size is 3.6 L. Oxygen consumption rates were measured over a temperature range of 5–32°C and each trial lasted for 60 min after the animals had been in the metabolic chamber for about 1 h to stabilize its environment. Food was removed 4 h before each test to minimize the specific dynamic action and animals were weighed to the nearest ± 0.1 g. H₂O and CO₂ were absorbed by silica gel and KOH. Recordings of oxygen consumption due to animal's activity in the chamber were discarded when computing the metabolic rate of each individual. All measurements were made daily between 8:00 and 16:00. Readings interval of O₂ consumption was 5 min. Two consecutive, stable and minimum recording were used to calculate metabolic rates. Metabolic rates were expressed as ml O₂ g⁻¹ h⁻¹ and corrected to STP conditions. Rectal temperatures (T_b) of all individuals were recorded before and after each measurement. T_b was measured with a digital thermometer (Beijing Normal University Instruments Co) in the rectum at a depth of 3 cm. Body mass was measured before and after the experiments.

2.3. Thermal conductance

Total thermal conductance (C , ml O₂ g⁻¹ h⁻¹ °C⁻¹) was calculated at temperature below the thermal neutral zone using the formula

$$C = \text{MR} / (T_b - T_a),$$

where MR is metabolic rate ($\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$), T_a is ambient temperature ($^{\circ}\text{C}$). This formula was suggested by McNab (1980a) for calculating conductance at any given T_a .

2.4. NST

NST was induced by scapular subcutaneous injection of 0.2 mg/ml norepinephrine (NE) bitartrate (Shanghai Harvest Pharmaceutical Co. LTD) at 25°C ($\pm 0.5^{\circ}\text{C}$). The dosage of NE was calculated based on preliminary experiments and the equation described by Heldmaier (1971): NE dosage (mg/kg) = $6.6M_b^{-0.458}$ (g). The two consecutive highest recordings of oxygen consumption were taken to calculate the maximum NST.

2.5. Statistics

The data were analyzed using SAS package (2001). Differences between groups are determined by repeated measurement ANOVA and $p < 0.05$ was taken to be statistically significant. All results were expressed as mean \pm SE, and linear regression analysis was used to analyze the relationship between energetic parameters and T_a .

3. Results

3.1. *Clethrionomys rufocanus*

Mean T_b was $38.2 \pm 0.2^{\circ}\text{C}$ after experiments and ranged from a mean of $36.5 \pm 0.3^{\circ}\text{C}$ at 5°C to $40.7 \pm 0.3^{\circ}\text{C}$ at 32.5°C . T_b s were fairly constant between 5°C and 22.5°C ($37.1 \pm 0.1^{\circ}\text{C}$), but increased above 25°C (Fig. 1).

There was no significant difference in metabolic rates within the temperature range 22.5 – 27.5°C , so we considered the thermal neutral zone (TNZ) as being 22.5 – 27.5°C . The BMR was $3.62 \pm 0.18 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$. Below the TNZ, metabolic rates increased with decreasing T_a (Fig. 1), the relationship between RMR and T_a can be described by the equation

$$\text{RMR}(\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}) = 8.73(\pm 0.39) - 0.22(\pm 0.22)T_a(^{\circ}\text{C})$$

($P < 0.0001$, $R^2 = 0.771$) (Fig. 1). Above 27.5°C metabolic rate increased markedly with temperature.

The maximum NST of gray red-backed vole was $6.76 \pm 0.12 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1}$, which is 1.87 times of BMR (Fig. 4).

Within the temperature range of 5 – 25°C , gray red-backed vole could keep their thermal conductance (C) stable and the average C was $0.25 \pm 0.04 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1} \text{ } ^{\circ}\text{C}^{-1}$. Within and above the TNZ, C increased significantly with increasing T_a , and attained $0.61 \pm 0.03 \text{ ml O}_2 \text{g}^{-1} \text{h}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ at T_a of 32.5°C (Fig. 1).

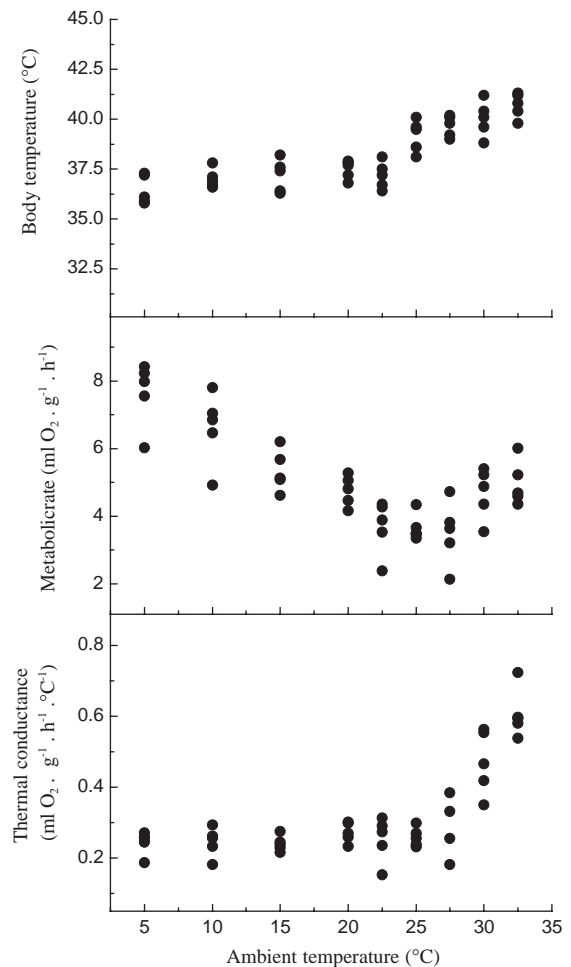


Fig. 1. Changes of body temperature, metabolic rates and thermal conductance with ambient temperatures in *Clethrionomys rufocanus*.

3.2. *Apodemus speciosus*

The large Japanese field mouse maintained stable T_b s within T_a range of 5 – 22.5°C , at which the T_b was $36.9 \pm 0.2^{\circ}\text{C}$. Within the range of 25 – 32.5°C , Japanese field mouse increased T_b with increasing in T_a , and reaching to $40.8 \pm 0.3^{\circ}\text{C}$ at T_a of 32.5°C (Fig. 2).

Metabolic rates of mice over the T_a range from 5 to 32.5°C are shown in Fig. 2. There was no significant difference for metabolic rates between 25°C and 30°C . Metabolic rates between 22.5°C and 25°C showed a significant difference, and the difference between 30°C and 32.5°C was also significant. Above the 30°C , the metabolic rate significantly increased and thus was regarded as the upper critical temperature. The TNZ of this species was from 25°C to 30°C . The mean BMR

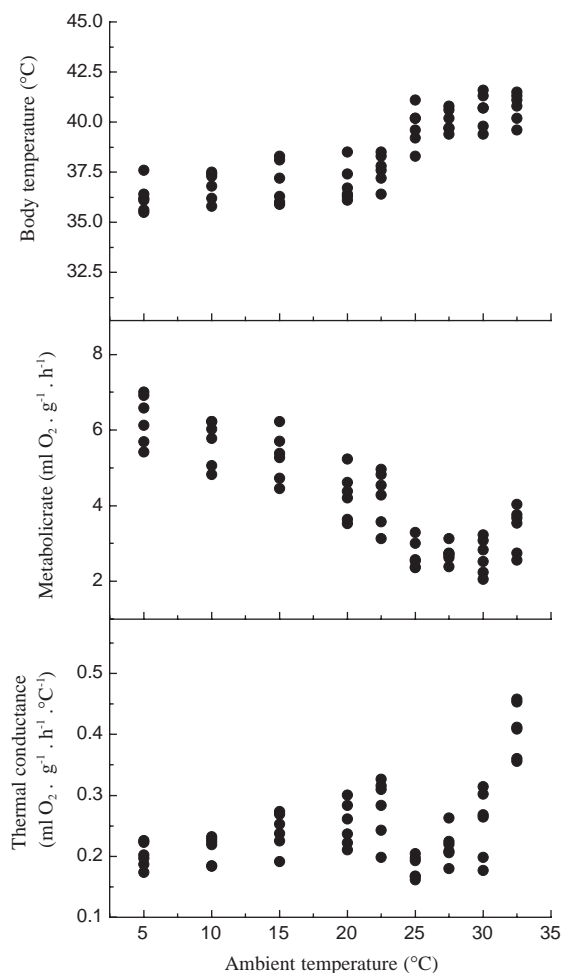


Fig. 2. Changes of body temperature, metabolic rates and thermal conductance with ambient temperatures in *Apodemus speciosus*.

within the TNZ was $2.69 \pm 0.08 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$. Below the TNZ, RMRs increased linearly with T_a and was described as

$$\text{RMR}(\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 6.96 (\pm 0.29) - 0.12 (\pm 0.01)T_a(^\circ\text{C})$$

($P < 0.0001$, $R^2 = 0.624$) (Fig. 2).

The NST of large Japanese field mouse was $5.56 \pm 0.39 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, the ratio of NST to BMR is 2.07 (Fig. 4).

The changes of overall thermal conductance with T_a for large Japanese field mouse are shown in Fig. 2. At temperatures below and within the TNZ, the C s showed no significant difference. The C was calculated as $0.23 \pm 0.00 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Above the TNZ, C increased significantly with T_a , and reaching to $0.41 \pm 0.02 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at 32.5°C (Fig. 2).

3.3. *Apodemus agrarius*

T_b in striped field mouse tended to decrease with the decreasing in T_a . T_b was $36.1 \pm 0.3^\circ\text{C}$ at 5°C and $40.9 \pm 0.3^\circ\text{C}$ at 32.5°C . They maintained stable T_b s within T_a range of $5\text{--}22.5^\circ\text{C}$, at which the T_b was $37.5 \pm 0.2^\circ\text{C}$ (Fig. 3).

The TNZ was from 25°C to 27.5°C (Fig. 3). Mean BMR was $3.29 \pm 0.11 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$. The relationship between metabolic rats and T_a below TNZ (from 5 to 25°C) was described as the follow equation:

$$\text{RMR}(\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 8.33 (\pm 0.27) - 0.19 (\pm 0.02)T_a(^\circ\text{C})$$

($P < 0.0001$, $R^2 = 0.789$) (Fig. 3).

NST of striped field mouse was $6.11 \pm 0.29 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, which is 1.86 times of BMR (Fig. 4).

Below and within the TNZ, the mean C of striped field mouse was $0.25 \pm 0.00 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Above the TNZ, C increased significantly with the increasing in T_a ,

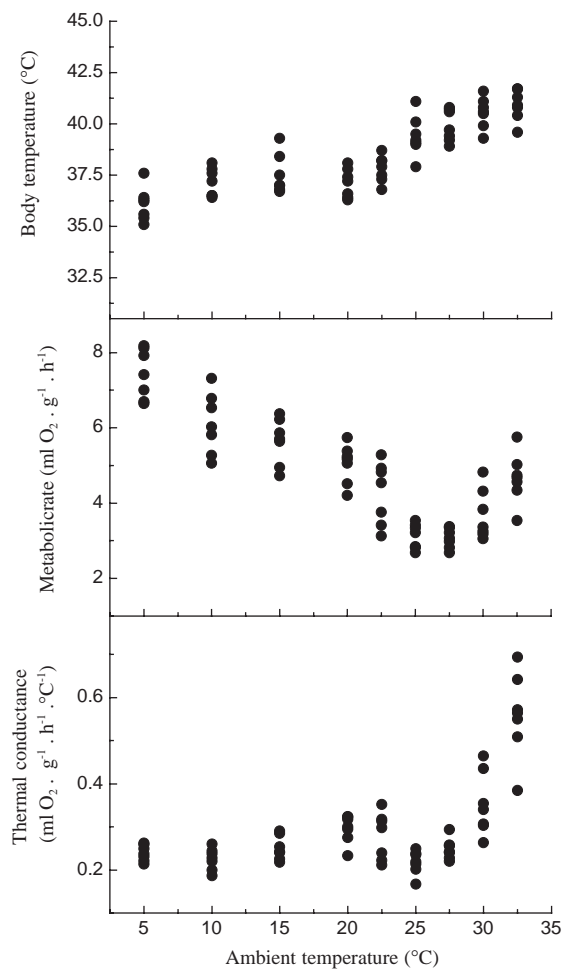


Fig. 3. Changes of body temperature, metabolic rates and thermal conductance with temperatures in *Apodemus agrarius*.

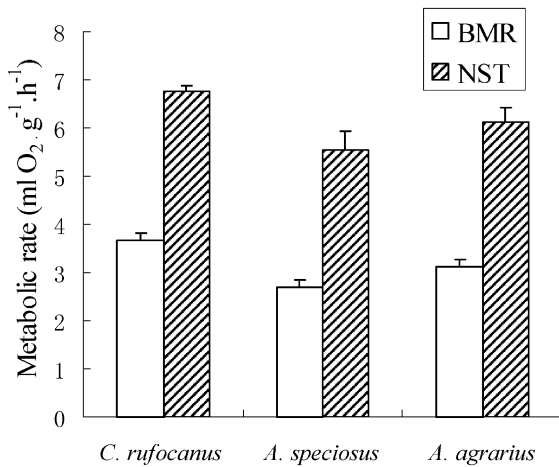


Fig. 4. BMR and NST of *Clethrionomys rufocanus*, *Apodemus speciosus* and *A. agrarius*.

and reaching to $0.60 \pm 0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at T_a of 32.5°C (Fig. 3).

4. Discussion

4.1. BMR

Hayssen and Lacy (1985) and McNab (1988) reviewed the BMRs of 293 and 321 mammal species, respectively, and obtained the allometric equations for mammals. According to the allometric equations of Hayssen and Lacy (1985), $\text{BMR} = 6.966M_b^{-0.332}$ for rodents, the BMR for the gray red-backed voles, large Japanese field mice and striped field mice are 147%, 117% and 128%, respectively, of the values as predicted from body mass. McNab (1988) also described the allometric relationship as $\text{BMR} = 7.79M_b^{-0.352}$ for rodents, accordingly the BMR of these three species are 137%, 109% and 119%, respectively, of their predicted values. Gray red-backed voles, large Japanese field mice and striped field mice are all higher than the values predicted on the basis of allometric equations for rodents. Compared to other *Clethrionomys* and *Apodemus* species, the BMR of gray red-backed voles, large Japanese field mice and striped field mice are higher than *A. flavicollis* (74% of that predicted by Hayssen and Lacy, 1985; 69% of predicted by McNab, 1988; Haim et al., 1996); *A. hermonensis* (74% and 69%, respectively, Haim et al., 1993); *C. glareolus* (97% and 90%, respectively, Górecki, 1968) and *C. gapperi* (85% and 79%, respectively, Deavers and Hudson, 1981), similar to values for *A. agrarius* (125% and 116%, respectively, Górecki, 1969); *C. californicus* (126% and 117%, respectively, McNab, 1992) and *C. rutilus* (119% and 111%, respectively, Rosenmann et al., 1975).

Many factors have been considered to affect the metabolic levels of animals, such as body size, phylogeny, climate conditions, activity and feeding habits (McNab, 1986). Lovegrove (2003) suggested that climate conditions are one of the most important factors. Cold-adapted rodents typically have higher BMR values than warm- or desert-adapted rodents (Haim and Izhaki, 1993). Our results support these findings, as the BMR relative to expected values of gray red-backed voles, large Japanese field mice and striped field mice are higher. These three species are generally distributed in boreal high-latitude regions, and inhabits some parts of Siberia (Ma, 1986), thus a high metabolic level is advantageous as an adaptation to the cold areas (Song and Wang, 2003).

Feeding habits are also one of the important factors that affect the metabolic rates of animals. Animals feeding on grass and herbs would have high metabolic rates. High metabolic level was considered to be closely related to the consistency and abundance of food resources in animal's environment (McNab, 1986). The gray red-backed voles, large Japanese field mice and striped field mice mainly feed on plant seeds, roots, stems, leaves, and some flowers and insects (Ma, 1986).

The most provocative recent ideas have focused on the search for a so-called "energetic definition of fitness" (EDF models) (Kozłowski and Weiner, 1997), and one study in particular illustrates the potential role of BMR variance in terms of optimizing reproductive power (Kozłowski and Weiner, 1997). From an evolutionary point of view, a high reproductive potential is for responsible for relatively high metabolic rates (Wang and Wang, 2002). McNab (1980b) indicated that a population of a species with a higher intrinsic growth rate should have a high metabolic level. The mean litter sizes for gray red-backed voles, large Japanese field mice and striped field mice are 6.5, 7.5, and 7, respectively, but the maximum can reach 12, 11, and 13 (Ma, 1986), respectively, equal or higher than other rodent species (Hasler, 1975). Furthermore, their living habits and behavior are also important for shaping their metabolic rates, i.e. being burrowing, nocturnal and solitary. The nocturnal habits and solitary behavior usually cost more energy for thermoregulation than social species (McNab, 1988; Song and Wang, 2003). So the reasons why gray red-backed voles, large Japanese field mice and striped field mice have relatively high metabolic rates are as follows: they (1) live in cold areas; (2) do not hibernate and remain active throughout winter; (3) eat plants; (4) have high reproductive rates; (5) are nocturnal; and (6) live solitary in burrows.

4.2. Body temperature and thermal conductance

The T_b s of gray red-backed vole (37.1°C), large Japanese field mouse (36.9°C) and striped field mouse

(37.5°C) are higher than *A. flavicollis* (35.7°C, Haim et al., 1996), but similar to *A. hermonensis* (38.1°C, Haim et al., 1993), *C. glareolus* (37.2°C, Górecki, 1968) and *C. gapperi* (37.9°C, Deavers and Hudson, 1981). Lovegrove (2003) describe the relationships of T_{bs} for 267 mammal species and conclude that Nearctic and Palaearctic small mammals have high T_{bs} , and thus a high T_{bs} are advantageous as an adaptation to the boreal high latitude regions. The temperature differences between the animal and its environment are great because of their nocturnal, solitary and burrowing habits. In summer, the high T_{bs} increase the temperature difference between body and hot air in burrow and increase the ability to dissipate heat (Song and Wang, 2003).

Bradley and Deavers (1980) found the relationship between C and body mass for 192 mammal species to be $C = 0.760M_b^{-0.54}$ and for cricetid rodents to be $C = 1.03M_b^{-0.54}$. The mean total C of the gray red-backed vole, large Japanese field mouse and striped field mouse below the TNZ are 0.25, 0.23 and 0.25 ml O₂ g⁻¹ h⁻¹ °C⁻¹, respectively, which are 123%, 123% and 128% of the predicted value for total mammals, respectively and 133%, 133% and 136% of that for cricetid rodents, respectively. They are lower than that of *A. flavicollis* (157% of that predicted for total mammals and 166% of that for cricetid rodents, Haim et al., 1996); similar to *A. hermonensis* (118% and 123%, respectively, Haim et al., 1993) and *C. californicus* (116% and 118%, respectively, McNab, 1992); but higher than *A. agrarius* (102% and 107%, respectively, Górecki, 1969), *C. rutilus* (97% and 105%, respectively, Rosenmann et al., 1975) and *C. gapperi* (85% and 79%, respectively, Deavers and Hudson, 1981).

4.3. Thermal neutral zone

According to the definition, TNZ is the range of ambient temperature at which temperature regulation is achieved only by control of sensible heat loss, without regulatory changes in metabolic heat production or evaporative heat loss (IUPS Thermal Commission, 1987). The TNZ of gray red-backed vole, large Japanese field mouse and the striped field mouse are 22.5–27.5°C, 25–30°C, and 25–27.5°C. The low lower critical temperatures of gray red-backed vole, large Japanese field mouse and the striped field mouse are lower than *Cricetulus triton* (29°C, Wang and Wang, 2002) and *C. barabensis* (29°C, Song and Wang, 2003). Animals that have high BMR, low lower critical temperature, and wider TNZ are typical characteristics of adaptation to cold; and they have high C and narrow TNZ are advantageous for them to live in the hot regions (Wang and Wang, 2002). Low lower critical temperature and wider TNZ are advantageous for animals to decrease the expenditure of energy in the cold, and high upper critical temperature is a beneficial adaptation for animals, specifically for water conservation during hot time.

4.4. NST

Böckler et al. (1982) found that NE-induced heat production was equivalent to that of cold-induced NST. So it can be a measure of NST. In our study, the NST of gray red-backed vole, large Japanese field mouse and striped field mouse are 6.76, 5.56 and 6.13 ml O₂ g⁻¹ h⁻¹, respectively, and are 1.87, 2.07 and 1.86 times BMR, respectively. Haim and Izhaki (1993) reported that the ratio of NST/BMR was 2.5 in nocturnal and mesic species and 3.7 in arid species. In species distributed northern temperature zones in China, the ratio of NST/BMR in the gray red-backed vole, large Japanese field mouse and striped field mouse are higher than that of *Microtus brandti* (1.4), similar to that of *Spermophilus dauricus* (1.6), and *Meriones unguiculatus* (2.2) (Li et al., 2001). Haim and Izhaki (1993) proposed that species that have high BMR values show low values of NST, and proposed that diurnal species have a significantly higher NST/BMR ratio (4.2) than nocturnal species (2.5), and the NST/BMR ratios of arid species (3.7) are higher than mesic species. This supports the prediction that the three species are more adapted to cold and/or mesic habitats than to arid habitats.

4.5. Metabolic properties and distribution

The gray red-backed vole and large Japanese field mouse are distributed mainly in the northern China, These two species are absent from extremely arid, low latitudes and hot regions. However, the striped field mouse is distributed widely in China from south to north. According to our study, we propose that ecophysiological characteristics of these species are one of the important factors constraining their distribution in China. For gray red-backed vole and large Japanese field mouse: (1) they have high BMR, low lower critical temperature, and wider TNZ—all typical characteristics of adaptation to cold; (2) The food resources in their environments should be abundant because of their high metabolic levels, so it is difficult for them to live in low productivity regions. The ecophysiological characteristics of the gray red-backed vole and large Japanese field mouse might constrain their distribution and extension to extreme desert, low latitudes and hot regions in China. For the striped field mouse: (1) This species has a high BMR and C , a relatively low lower critical temperature and narrow TNZ—adaptive characteristics of both “south” and “north” species; (2) The food resource is also one of important limiting factors for this species because of its high-metabolic rates. Our results support the conclusion that Zhang and Wang (1998) proposed that *A. agrarius* is not a true “north” form. Perhaps severe climate is the main selective force faced by the striped field mouse during their evolution with their macroenvironments.

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