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Journal of Thermal Biology 31 (2006) 583–587

Journal of THERMAL BIOLOGY

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Metabolism and thermoregulation in Maximowiczi's voles (*Microtus maximowiczii*) and Djungarian hamsters (*Phodopus campbelli*)

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Received 14 March 2006; accepted 28 June 2006

Abstract

1 Metabolic rates ($V\mathrm{o}_2$), body temperature (T_b), and thermal conductance (C) were first determined in newly captured Maximowiczi's voles (*Microtus maximowiczii*) and Djungarian hamsters (*Phodopus campbelli*) from the Inner Mongolian grasslands at a temperature range from 5 to 35 °C.
2 The thermal neutral zone (TNZ) was between 25 and 32.5 °C for Maximowiczi's voles and between 25 and 30 °C for Djungarian hamsters. Mean T_b was 37.0 ± 0.1 °C for voles and 36.2 ± 0.1 °C for hamsters. Minimum thermal conductance was 0.172 ± 0.004 ml O_2/g h °C for voles and 0.148 ± 0.003 ml O_2/g h °C for hamsters.
3 The mean resting metabolic rate within TNZ was 2.21 ± 0.05 ml O_2/g h in voles and 2.01 ± 0.07 ml O_2/g h in hamsters. Nonshivering thermogenesis was 5.36 ± 0.30 ml O_2/g h for voles and 6.30 ± 0.18 ml O_2/g h for hamsters.
4 All these thermal physiological properties are adaptive for each species and are shaped by both macroenvironmental and microenvironmental conditions, food habits, phylogeny and other factors.

Keywords: Basal metabolic rate; Body temperature; Djungarian hamster (*Phodopus campbelli*); Maximowiczi's vole (*Microtus maximowiczii*); Nonshivering thermogenesis; Minimum thermal conductance

1. Introduction

Energy metabolism is a critical component for the distribution, abundance, and reproductive success of rodent species (Bozinovic and Rosenmann, 1989; Bozinovic, 1992; McNab, 2002). Basal metabolic rate (BMR) is one of the most used parameters for inter- and intraspecific comparisons of energy metabolism (Jessen, 2001). The capacity of nonshivering thermogenesis (NST) is important for small mammals to survive the cold environments and seasons. Environmental (climatic) conditions are important in shaping the ecophysiological features of a rodent (small mammal) species (Degen, 1997).

Maximowiczi's voles (*Microtus maximowiczii* Schrenk, 1859) and Djungarian hamsters (*Phodopus campbelli* Thomas, 1905) are mainly distributed in northeastern China and the adjacent areas of Russia and Mongolia. Maximowiczi's voles are mainly living in the areas of marsh, meadow and bank-forest while Djungarian hamsters mostly occupying the areas of arid steppes, semidesert, and forest-steppe (Luo et al., 2000). Both species are nonhibernating small mammals and store food in the cold season. The voles are herbivorous and mostly diurnal while the hamsters are granivorous and nocturnal (Zhong et al., 1981).

For these two species, their biological characteristics are rarely studied perhaps because of their low numbers and limited distributions. From our knowledge, no data on the ecological physiology in Maximowiczi's voles and wild Djungarian hamsters are available at present. In the previous reports it was widely accepted that *Phodopus sungorus* included two subspecies: *P.s.sungorus and P.s.campbelli* (from Weiner and Heldmaier, 1987). Weiner and Heldmaier (1987) compared the two races of hamsters

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0306-4565/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtherbio.2006.06.003

and suggested that these two races of hamsters should be separate species, which has been accepted today. The purpose of this study was to examine the metabolic characteristics for these two sympatric species with fresh-trapped individuals.

2. Materials and methods

2.1. Animals

Animals were live-trapped in the Inner Mongolian grassland Ecosystem Research Station of the Chinese Academy of Sciences (43°3′N, 116°41′E) in April 2005. The altitude is about 1100–1400 m. Mean monthly temperature ranges from −22.2 °C in January to 18.3 °C in July. Annual precipitation ranged from 264.3 to 563.8 mm. Plant growing period is about 150 days. The principal types of vegetation are meadow steppe and typical steppe (Chen, 1988).

The mean body mass of Maximowiczi's voles (four males and four females) is 41.67 ± 1.56 g ($\pm$SE) and Djungarian hamsters (four males and four females) is 39.18 ± 1.62 g in this study. Animals were raised in cages ($50 \times 35 \times 25\,\mathrm{cm}^3$) in a room at the field research station with natural photoperiods (around 16L:8D) and temperature (15–20 °C). Fresh China Aneurolepidium (*Aneurolepidium chinense*), Schmidt Sedge (*Carex schmidtit*) and a few slices of carrot were supplied to Maximowiczi's voles everyday. Additional food was composed of standard rabbit pellets (Beijing Ke Ao Feed Co.). The main food of Djungarian hamsters consisted of fresh grasses, wheat with commercial rat pellets (Beijing Ke Ao Feed Co.) as additional food. Food and water were supplied ad libtium. The experiments were carried out from April to May in 2005. No pregnancy and lactation individuals were used in the experiments. All animal procedures were licensed under the Animal Care and Use Committee of Institute of Zoology, the Chinese Academy of Sciences.

2.2. Metabolic trials

$V\mathrm{o}_2$ rate was measured using an established closed-circuit respirometer as described previously (Gorecki, 1975; Wang and Wang 1996; Li and Wang, 2005). The chamber size is 3.6 L and the temperature inside the chamber was maintained with a water bath. Carbon dioxide and water in the metabolic chambers were absorbed with KOH and silica gel. Rectal temperatures (T_b) of animals were recorded before and after each measurement. T_b was measured by a digital thermometer (Beijing Normal University Instruments Co.) in the rectum at a depth of 3 cm. Body mass was measured before and after each metabolic test.

$V\mathrm{o}_2$ rate was measured over a temperature range from 5 to 35 °C. Animals were in the chambers without bedding for more than 60 min for stabilization. Each test lasted for 60 min and oxygen consumption were recorded at 5 min intervals. The two consecutive lowest readings were taken to calculate the resting metabolic rate (RMR) (Li and Wang, 2005). Before each test animals were fasted for 3 h to minimize the specific dynamic action of food.

Norepinephrine-induced heat production can be a measure of NST as it is equivalent to cold-induced NST (Böckler et al., 1982). NST was induced by subcutaneous injection of norepinephrine bitartrate (Shanghai Harvest Pharmaceutical Co. LTD) at 25 °C (±1 °C). The dosage of NE was calculated based on our preliminary experiments (Wang and Wang, 2006, Li and Wang 2005a, Zhao and Wang 2005) and the equation described by Heldmaier (1971): norepinephrine dosage $(\mathrm{mg/kg}) = 6.6\mathrm{Mb}^{-0.458}\,(\mathrm{g})$ (Mb is body mass in gram). Oxygen consumption was measured as RMR described above. The two consecutive highest recordings were taken to calculate the maximum NST (Wang and Wang, 1996; Li and Wang, 2005b). Maximum NST usually occurred between 15 and 40 min after NE injection (Wang and Wang, 2006). All the data of metabolic rates were corrected to standard (STP) conditions and were expressed in $\mathrm{ml\,O_2/g\,h}$.

2.3. Thermal conductance

Overall thermal conductance (C, $\mathrm{ml\,O_2/g\,h\,°C}$) at any given ambient temperature was calculated using the formula suggested by McNab (1980) and Bradley and Deavers (1980):

$$C = \mathrm{MR}/(T_\mathrm{b} - T_\mathrm{a})$$

where MR is the metabolic rate ($\mathrm{ml\,O_2/g\,h}$), T_b is the body temperature (°C), and $\mathrm{T_a}$ is the ambient temperature (°C). Overall thermal conductance includes the heat loss by evaporation.

2.4. Statistics

Data were analyzed using the SPSS package (version 12.0 for windows). Differences between groups were determined by one-way repeated measures analysis of variance (ANOVA). Regression analysis was determined by the method of least squares using the mean values of the parameters measured at each temperature point. All values were presented as mean±SE in the text and $P < 0.05$ was taken as statistically significant.

3. Results

Mean T_b of Maximowiczi's vole ranged from 36.9 ± 0.1 °C at 5 °C to 37.9 ± 0.1 °C at 35 °C. T_bs were fairly constant between 5 and 30 °C with a mean of 37.0 ± 0.1 °C and increased as T_a above 32.5 °C (37.7 ± 0.1 °C) (Fig. 1A). Djungarian hamsters maintained stable T_bs within the range of 5–27.5 °C with a mean of 36.2 ± 0.1 °C. Within the range of 27.5–35 °C, Djungarian hamsters increased T_b with T_a and reached 39.4 ± 0.4 °C at T_a of 35 °C (Fig. 2A).

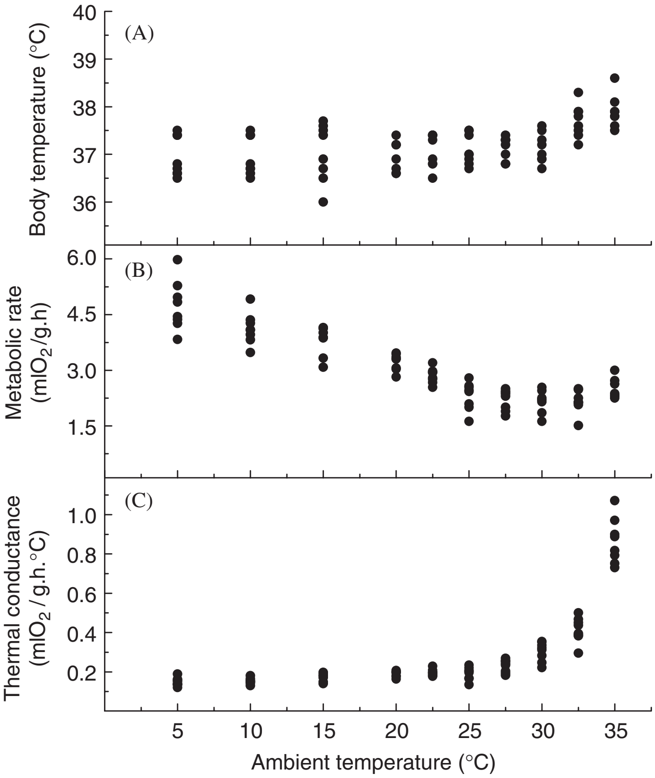

Fig. 1. Body temperature (A), metabolic rate (B) and overall thermal conductance (*C*, including the evaporative heat loss) of Maximowiczi's voles (*Microtus maximowiczii*) at different ambient temperatures.

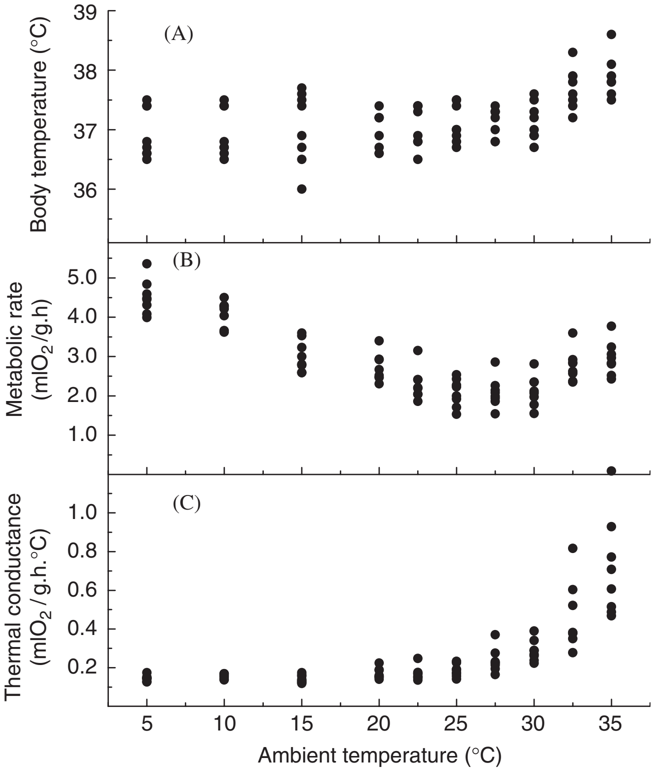

Fig. 2. Body temperature (A), metabolic rate (B) and overall thermal conductance (*C*, including the evaporative heat loss) of Djungarian hamsters (*Phodopus campbelli*) at different ambient temperatures.

There were no significant differences in metabolic rates in Maximowiczi's vole within the temperature range between 25 and 32.5 °C ($F_{(3,\ 21)} = 1.819$, $P = 0.175$), so we considered it as the thermal neutral zone (TNZ) which was 25–32.5 °C (Fig. 1B). The mean metabolic rate within the TNZ (regarded as the RMR) was 2.21 ± 0.05 ml O_2/g h Below the TNZ, RMRs increased linearly as T_as declined and can be described as: RMR (ml O_2/g h) = 5.211 (±0.214)–0.130 (±0.014) T_a (°C) ($R^2 = 0.969$, df = 5, $P < 0.001$) (Fig. 1B).

In Djungarian hamsters, metabolic rates kept relatively constant within the range of 25–30 °C, thus this temperature range was regarded as TNZ (Fig. 2B). Mean RMR within TNZ was 2.01 ± 0.07 ml O_2/g h. Below the TNZ, RMR increased linearly with T_a and can be expressed as: RMR (ml O_2/g h) = 5.25 (±0.112)–0.104 (±0.007) T_a (°C) ($R^2 = 0.986$, df = 5, $P < 0.001$). Above 30 °C, the metabolic rate increased markedly with T_a.

Below the TNZ, Maximowiczi's voles kept thermal conductance (*C*) relatively stable and the average minimum *C* was 0.172 ± 0.004 ml O_2/g h °C. Within and above the TNZ, *C* increased with increasing T_a, and reached up to 0.87 ± 0.04 ml O_2/g h °C at T_a of 35 °C (Fig. 1C). Within the temperature range of 5–15 °C, Djungarian hamsters kept *C* relatively stable and the average minimum *C* was 0.148 ± 0.003 ml O_2/g h °C. From 20 to 35 °C, *C* increased with T_as and the relationship can be described by the equation: *C* (ml O_2/g h °C) = 0.585(±0.215)–0.033(±0.008) T_a (°C) ($R^2 = 0.784$, df = 5, $P = 0.008$). Thermal conductance can reach up to 0.714 ± 0.091 ml O_2/g h °C at T_a of 35 °C (Fig. 2C).

The maximum NST is 5.36 ± 0.30 ml O_2/g h for Maximowiczi's voles and 6.30 ± 0.18 ml O_2/g h for Djungarian hamsters, which are 2.4 and 3.0 times their RMR, respectively.

4. Discussion

4.1. Metabolic rates

Many factors can affect metabolism in mammals, such as body size, food habits, climate, activity and phylogeny (McNab, 1979a, b, 1986, 2002). According to the allometric equation proposed by Hayssen and Lacy (1985) for rodents ($\mathrm{BMR} = 4.98\mathrm{Mb}^{-0.331}$, BMR is in ml O_2/g h and Mb is body mass in gram), measured RMR for Maximoviczi's vole is 153% of the predicted values based on their body mass and 136% for Djungarian hamster, which are similar to other sympatric species in their ecosystem, such as Brandt's vole (*Lasiopodomys(Microtus) bandtii*) (147%, Wang et al., 2003), Desert hamster (*Phodopus roborovskii*) (142%, Zhan and Wang, 2004), and Mongolian gerbils (*Meriones unguiculatus*) (166%, Wang et al., 2000, 2003) (Table 1). It has been suggested that climate conditions is one of the most important factors to affect metabolic levels (Lovegrove, 2003). The metabolic similarities for these sympatric rodent species can be regarded as the convergent adaptation to the macroenviroment of Inner Mongolian grasslands.

The relative high RMR in Maximoviczi's voles can be interpreted as the effects of geography and phylogeny. Hayssen and Lacy (1985) and McNab (1992) proposed that Arvicolidae species have high BMRs. Arvicolinae species are generally distributed in boreal high latitude regions and thus high metabolic level is an adaptive characteristic (McNab 1992). It has been suggested that an elevated BMR for small mammals inhabiting cold high latitude regions allowed higher thermogenic capacity (Wunder et al., 1977; Heldmaier et al., 1989). Weiner and Heldmaier (1987) reported that *P. campbelli* showed lower endurance capacity to cold than *P. sungorus*.

4.2. Nonshivering thermogenesis

Generally, species inhabiting cold-temperate climate have high NST levels. NST of Maximowiczi's voles and Djungarian hamsters in spring (this study) are 96% and 109% of expected NST based on body mass ($NST = 30Mb^{-0.45}$, where NST is in ml O_2/g h and Mb in gram, Heldmaier, 1971), respectively (Table 1). Haim and Izhaki (1993) proposed that species with high RMR values show low NST, and diurnal species have high ratios of NST/RMR than nocturnal species, and the NST/RMR ratios of arid species are higher than those in mesic species. In our study, the ratio of NST/RMR for Maximowiczi's voles is 2.4 and 3.1 for Djungarian hamsters, which is consistent with the prediction of Haim and Izhaki (1993). For other sympatric species, similar results were found such as the ratio of NST/RMR in *Phodopus roborovskii* (3.3, low BMR, nocturnal and living in arid microenvironment) (Zhan and Wang 2004), *Lasiopodomys bandtii* (2.9) and *Meriones unguiculatus* (2.1) (both species are diurnal with high BMR (Wang et al., 2003; Table 1).

4.3. Thermal conductance and body temperature

The mean minimum thermal conductance is 111% for Maximowiczi's vole and 93% for Djungarian hamster of their predicted values based on their body mass. Djungarian hamster showed the similar adaptive features with desert small mammals and similar to the sympatric species of desert hamster (Zhan and Wang, 2004; Table 1). Weiner and Heldmaier (1987) reported that *P. campbelli* was more variable in T_b and C values in the cold than *P. sungorus*. For Maximowiczi's vole, relatively high C values are advantageous to avoid hyperthermy during the daily high temperature period (Wang et al., 2000).

Djungarian hamsters have relatively low T_b values (36.2 °C). Low T_b can be beneficial for Djungarian hamster to reduce energy loss while they are active at night. For the relatively high T_b in Maximowiczi's vole (37.1 °C), McNab (1992) has proposed that high T_b values

Table 1
Some metabolic and thermoregulatory variables measured for some rodent species in Inner Mongolian grassland of China

Species	Habitat[1]	Habit[2]	BM (g)	TNZ[3] (°C)	T_b^4 (°C)	C^5 (ml O_2/g h °C)	% Bradley and Deavers[6]	BMR[7] (ml O_2/g h)	% Hayssen and Lacy[8]	% McNab[8]	NST[9] (ml O_2/g h)	% Heldmaier[10]	Reference
Arvicolinae													
Lasiopodomys brandtii	M	D	43.3	30–34	37.0	0.21	—	2.11	147	174	6.09	110.6	Wang et al., 2003 and unpublished data
Microtus maximowiczii	M	D	41.7	25–32.5	37.0	0.172	110.9	2.21	153	180	5.36	95.7	Present study
Cricetinae													
Phodopus campbelli	A	N	39.1	25–30	36.2	0.148	92.8	2.01	136	161	6.30	109.3	Present study
Phodopus roborovskii	A	N	20.3	25–33	35.7	0.210	98	2.61	142	168	8.53	110.2	Zhan et al., 2004
Gerbillinae													
Meriones meridianus	A	N	38.7	27–35	—	—	—	2.12	143	169	3.47	59.9	Bao et al., 2002a, b
Meriones unguiculatus	A	D	58.1	26–38	38.4	0.179	133	2.15	166	196	4.43	91.8	Wang et al., 2000, 2003

Note: 1. Habitat: A—semi-arid or arid; M: mesic; 2. Habit: D—Diurnal; N—Nocturnal; 3. TNZ: thermal neutral zones; 4. T_b: body temperature during TNZ; 5. Overall minimal thermal conductance measured by using the formula $C = MR/(T_b–T_a)$; 6. Allometric equation $C = 0.76Mb^{-0.426}$ (Bradley and Deavers, 1980); 7. BMR: basal metabolic rate; 8. Allometric equation $BMR = 4.98Mb^{-0.331}$ (Hayssen and Lacy, 1985) or $BMR = 4.18Mb^{-0.329}$ (McNab, 1988); 9. NST: maximal oxygen consumption as a response to noradrenaline injection; 10. Allometric equation $NST = 30Mb^{-0.45}$ (Heldmaier, 1971).

are one of the characteristics in Arvicolidae because of their high BMRs. Further, the relative low T_{lc} values for both species are advantageous for reducing the energy expenditure in the cold.

In summary, we first reported the metabolic properties for wild Maximowiczi's voles and Djungarian hamsters. Both species showed similar thermal physiological characteristics (such as relatively high metabolic levels) to their sympatric species of Inner Mongolian grasslands, suggesting a convergent adaptation to the same macroenvironment (cold and dry). Further, the species-specific differences in ecophysiological properties for these two rodent species may arise from their microenvironment, phylogeny, food habits, and other factors.

Acknowledgements

We thank Dr. Xin-Rong Wan for his help to this study. Thanks to Qing-Sheng Chi, Li-Na Zhang, Xue-Ying Zhang, Gang-Bin Tang and Jian-Guo Cui for their critical reading of the draft. This study was financially supported by the National Natural Foundation of China (No. 30430140 and 30470279).

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