



Journal of Thermal Biology 28 (2003) 509-514

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# Metabolism and thermoregulation in the striped hamster Cricetulus harabensis

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Received 12 December 2002; accepted 30 May 2003

#### Abstract

- (1) Basal metabolic rate (BMR), nonshivering thermogenesis (NST), and maximum metabolic rate (MMR) of *Cricetulus barabensis* were measured.
- (2) Thermal neutral zone (TNZ) was  $27-30^{\circ}$ C and BMR was  $2.20\pm0.09$  ml  $O_2$  g<sup>-1</sup> h<sup>-1</sup>. NST and MMR were  $7.27\pm0.47$  and  $14.24\pm1.16$  ml  $O_2$  g<sup>-1</sup> h<sup>-1</sup>, respectively.
- (3) The ecophysiological properties of relatively high body temperature, narrow TNZ, high BMR and thermogenic capacity enable this species to adapt to its environment.
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Keywords: Basal metabolic rate; Nonshivering thermogenesis; Maximum metabolic rate; Striped hamster; Cricetulus barabensis

### 1. Introduction

The striped hamster (*Cricetulus barabensis* Pallas, 1773) is a major pest rodent in northern China and is also distributed in Russia, Mongolia, and Korea (Zhang and Wang, 1998). Within its range the striped hamster preferentially occurs in sandy areas and has also been found on farmland, grassland, sand hills, and it mostly excavates burrows in high dry areas to avoid the rain (Zhang and Wang, 1998). The striped hamster is granivorous and nocturnal (Lu et al., 1987).

Little is known about the physiological characteristics of striped hamsters in the field. Thermogenic and thermoregulatory abilities are critical to the survival and distribution of mammals (Karasov, 1986). Bao et al. (2002) measured the basal metabolic rate (BMR) of striped hamsters from the Kubuqi Desert in Inner Mongolia, and proposed that this species is not well adapted to an arid region. The aim of this study is to

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measure the BMR, nonshivering thermogenesis (NST) and cold-induced maximum metabolic rate (MMR) in striped hamsters from farmland.

#### 2. Materials and methods

Fourteen (9 males and 5 females) striped hamsters were live trapped in Hebei Province (116.34N, 39.25E) in China in April 2000, and raised in cages  $(50\times35\times25\,\mathrm{cm}^3)$  in a room with photoperiods of 12L:12D and temperature at 23°C and fed on standard mice chow (Beijing Ke Ao Feed Co.). The habitat was a cornfield and the dominant plant species were wheat, corn and soybeans. Metabolic determinations were carried out in June 2000. Hamsters were not pregnant or lactation. Mean body mass is  $31.4\pm1.4\,\mathrm{g}$ .

Oxygen consumption was measured using a closed-circuit respirometer according to Gorecki (1975). The glass chamber, with a height of 36 cm and a diameter of 36 cm, was submerged in water bath to maintain constant temperature. Carbon dioxide and water in the

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metabolic chambers were absorbed with KOH and silica gel, respectively. 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 the experiments.

Metabolic rate measurements were made over a temperature range from 7°C to 35°C. The animals were in the chambers without bedding for about 40 min to stabilize before metabolic measurement, and each test was lasted for 60 min (with 5 min intervals). The two consecutive lowest readings were taken to calculate the resting metabolic rate (RMR). Before each test the animal was fasted for 3 h to minimize the specific dynamic action of food.

Overall thermal conductance (C, ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>) was calculated using the formula

$$C = MR/(T_b - T_a), \tag{1}$$

where MR is the metabolic rate (in ml  $O_2 g^{-1} h^{-1}$ ),  $T_b$  is the body temperature (°C), and  $T_a$  is the ambient temperature (°C). This formula was suggested by McNab (1980) as well as Bradley and Deavers (1980) for calculating conductance at any given ambient temperature.

NST was induced by scapular subcutaneous injection of  $0.2\,\mathrm{mg/ml}$  norepinephrine bitartrate (Shanghai Harvest Pharmaceutical Co. LTD) at  $25^{\circ}\mathrm{C}$  ( $\pm 1^{\circ}\mathrm{C}$ ). The dosage of NE was calculated based on our preliminary experiments and the equation described by Heldmaier (1971): norepinephrine dosage ( $\mathrm{mg/kg}$ ) =  $6.6M_{\mathrm{b}}^{-0.458}$  (g). The two consecutive highest recordings of oxygen consumption were taken to calculate the maximum NST.

Cold-induced MMR was elicited by the mixture of 80% He:20% O<sub>2</sub>. Since helium conducts heat four times faster than that of nitrogen, heat loss in the mixture is considerably higher than air. Maximum oxygen consumption can, therefore, be elicited at relatively high

temperatures (Rosenmann and Morrison, 1974). The temperature of the chamber was gradually lowered until the animals' oxygen consumption did not increase or start to decrease. The cold-induced MMR was defined as the highest oxygen consumption that animals could maintain within 10 min.

All measurements were made daily between 11:00 and 17:00 h. Metabolic rates were expressed as ml  $O_2 g^{-1} h^{-1}$  and corrected to STP conditions.

The data were analyzed using the SPSS (1988) package. Differences between groups were determined by repeated measure ANOVA, and p < 0.05 was taken to be statistically significant. Regression equations were determined by the method of least squares using the mean value at each temperature. All values in the test were presented as mean + SE.

#### 3. Results

 $T_{\rm b}$ 's were fairly constant between 7°C and 30°C and mean  $T_{\rm b}$  was 37.9±0.1°C.  $T_{\rm b}$  increased above 30°C (Fig. 1), and three animals died at the end of metabolic determination at 35°C due to hyperthermia ( $T_{\rm b}$  reached to 39.6°C).

The relationship between metabolic rates and  $T_a$ 's are shown in Fig. 2. There was no significant difference in metabolic rates between 27°C and 30°C. Metabolic rates between 25°C and 27°C showed a significant difference, and the difference between 30°C and 32°C was also significant. Above 30°C, the metabolic rate significantly increased and thus was regarded as the upper critical temperature. The thermal neutral zone (TNZ) of striped hamsters was from 27°C to 30°C. The mean BMR within the TNZ is  $2.20\pm0.09\,\mathrm{ml}$   $O_2\,\mathrm{g}^{-1}\,\mathrm{h}^{-1}$ , which is 170% (Fig. 4) predicted values by McNab (1988), (BMR (ml  $O_2\,\mathrm{g}^{-1}\,\mathrm{h}^{-1}$ )=  $3.45\,M_\mathrm{b}^{-0.287}$  (g)) and 145% by Hayssen and Lacy (1985), (BMR (ml  $O_2\,\mathrm{g}^{-1}\,\mathrm{h}^{-1}$ )=  $3.289\,M_\mathrm{h}^{-10.226}$  (g)). Below the TNZ, RMRs of hamsters

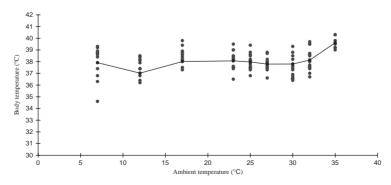


Fig. 1. Body temperature of the striped hamster *Cricetulus barabensis* at different ambient temperatures. Means were plotted and lined. n = 14.

increased linearly with  $T_a$ :

RMR (ml 
$$O_2 g^{-1} h^{-1}$$
) =  $-0.17T_a(^{\circ}C) + 6.84$   
( $P < 0.001, R^2 = 0.993, df = 5$ ).

The variations of overall thermal conductance with  $T_a$ for the striped hamster are shown in Fig. 3. At temperatures below TNZ, the overall thermal conductances showed no significant difference. The minimum thermal conduction  $(C_{\rm m})$  was calculated as  $0.20\pm$ 0.00 ml  $O_2$  g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup>, which is 11% higher than the predicted value by Bradley and Deavers (1980), ( $C_{\rm m}$  (ml  $O_2$  g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>) = 0.76 $M_{\rm b}^{-0.426}$  (g)), based on body mass. Within and above the TNZ, C increased significantly with  $T_a$ , and sharply increased from 32°C  $(0.43 \pm 0.02 \text{ ml } O_2 \text{ g}^{-1} \text{ h}^{-1} \circ \text{C}^{-1})$ , reaching  $0.81 \pm 0.09 \text{ ml}$  $O_2 g^{-1} h^{-1} \circ C^{-1}$  at 35°C.

The maximum NST of the striped hamster is  $7.27 \pm 0.47 \,\text{ml O}_2 \,\text{g}^{-1} \,\text{h}^{-1}$  (n = 11), 15% higher than the

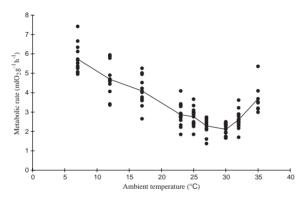


Fig. 2. Relationship between RMRs and ambient temperatures in the striped hamster Cricetulus barabensis. The means were plotted and lined. n = 14.

predicted value based on body mass by Heldmaier (1971) (NST (ml  $O_2g^{-1}h^{-1}$ ) =  $30M_b^{-0.454}$  (g)) (Fig. 4). The metabolic rate in the gas mixture of He–O<sub>2</sub> was

measured at four temperatures, 15°C, 10°C, 5°C and

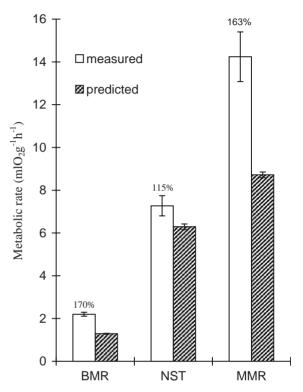


Fig. 4. BMR, NST and MMR of Cricetulus barabensis and percentages of predicted values by McNab (1988) (BMR (ml  $O_2 g^{-1} h^{-1}$ ) = 3.45 $M_b^{-0.287}$  (g), n = 14), by Heldmaier (1971) (NST (ml  $O_2 g^{-1} h^{-1}$ ) = 30 $M_b^{-0.454}$  (g), n = 11) and by Bozinovica and Rosenmann (1989), MMR(ml  $O_2 g^{-1} h^{-1}$ ) = 28.3 $M_b^{-0.338}$ (g), n = 11). Values are Mean  $\pm$  SE.

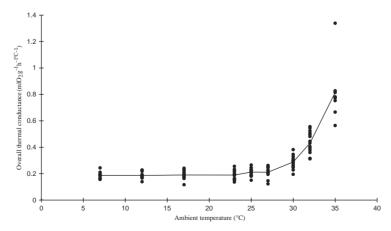


Fig. 3. Overall thermal conductance of the striped hamster Cricetulus barabensis at different ambient temperatures. The means were plotted and lined. n = 14.

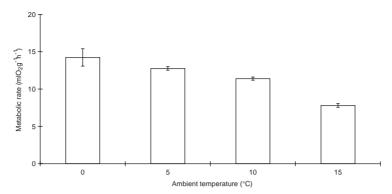


Fig. 5. Metabolic rates measured in He-O<sub>2</sub> mixture (80%:20%) at different ambient temperatures in the striped hamster *Cricetulus barabensis*. Values are Mean+SE. n = 11.

 $0^{\circ}$ C. With the decrease in  $T_a$ , the metabolic rate in the gas mixture increased (Fig. 5). The metabolic rates at  $15^{\circ}$ C and  $10^{\circ}$ C are significantly lower than at  $5^{\circ}$ C. The metabolic rates at  $5^{\circ}$ C and  $0^{\circ}$ C are not significantly different, so they are regarded as the MMR. The mean MMR is  $14.24 \pm 1.16 \,\text{ml} \,\text{O}_2 \,\text{g}^{-1} \,\text{h}^{-1}$ , which is  $1.63 \,\text{times}$  the predicted values by Bozinovic and Rosenmann (1989) (MMR (ml  $O_2 \,\text{g}^{-1} \,\text{h}^{-1}) = 28.3 M_b^{-0.338}$  (g)) (Fig. 4). The ratio of MMR to BMR is 6.9.

## 4. Discussion

#### 4.1. Basal metabolic rate

This study showed that the striped hamster had higher metabolic rates relative to that predicted (145% of that predicted by Hayssen and Lacy, 1985; 170% of that predicted by McNab, 1988). Similar results were reported in the striped hamster from the Kubuqi Desert in Inner Mongolia. BMR is 172% of that predicted by Hayssen and Lacy and 200% of that predicted by McNab (Bao et al., 2002). So it seems that the high level of metabolism is a specific characteristic, regardless of whether it is distributed in the Hebei farmland or in the Inner Mongolian desert. Compared to other *Cricetulus* species, the BMR value of the striped hamster is higher than *Cricetulus triton* (1.23 ml  $O_2 g^{-1} h^{-1}$ , Wang and Wang, 2002) and *Cricetulus migratorius* (1.43 ml  $O_2 g^{-1} h^{-1}$ , Haim and Izhaki, 1993).

Most of the variation in the basal rate of metabolism in eutherians can be accounted for by the combined influences of body mass, food habits, behavior and climate (McNab, 1986). The striped hamster is generally distributed in boreal high latitude regions, thus a high metabolic level is advantageous as an adaptation to the cold. High dietary quality and nocturnal habits could be important factors that cause the high metabolic rates in the granivorous striped hamster. And its high metabolic

rates may be related to its solitary lifestyle as well. The solitary species usually cost more energy for thermoregulation than social species (McNab, 1988).

# 4.2. Thermal conductance and body temperature

The minimum thermal conductance in the striped hamster below the TNZ is slightly higher (11%) than that predicted in the equation of Bradley and Deavers (1980). It is lower than that of *C. triton* (145% of that predicted, Wang and Wang, 2002) and *C. migratorius* (144% of that predicted, Haim and Izhaki, 1993).

The body temperature (37.9°C) of the striped hamster in this study is higher than that in the Kubuqi Desert (37.0°C) and is also higher than *C. triton* (36.6°C, Wang and Wang, 2002), but similar to *C. migratorius* (38.1°C, Haim and Izhaki, 1993). Bao et al. (2002) found that the body temperature in summer is 1–2°C higher than that in spring and autumn. In summer, the high body temperature increased the temperature difference between body and hot air in burrow and increases the ability to dissipate heat.

Bao et al. (2002) proposed that the properties of high metabolic level and narrow TNZ in the striped hamster in the Kubuqi Desert are similar to those of non-desert and mesic-adapted species, but somewhat different from those of desert species. The wider TNZ in desert species implies a high tolerance for hot and dry environments, while the narrow TNZ in the striped hamster perhaps limits its distribution in extremely hot and dry environments.

# 4.3. Nonshivering thermogenesis

Bockler 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 this study, the contribution of NST to MMR is 51%, 3.4 times BMR. Degen (1997) reported that the ratio of NST/BMR

ranged between 1.0 and 5.8 in desert rodents. In species distributed in northern temperature zones in China, the ratio of NST/BMR in the striped hamster is higher than that of *Microtus brandti* (1.4), *Spermophilus dauricus* (1.6), *Ochotona curzoniae* (1.6), and *Meriones unguiculatus* (2.2) (Li et al., 2001).

Haim and Izhaki (1993) proposed that species that have low BMR values show high values of NST. However, the striped hamster has a high BMR and also has a high NST. It may be interpreted as the effect of habitat and habits on NST. Haim and Izhaki (1993) proposed that diurnal species have a significantly higher NST/BMR ratio (4.2) than nocturnal species (2.5), and the NST/BMR ratios of mesic species (2.5) are significantly lower than those of arid species (3.7). The NST/BMR ratio of the striped hamster (3.4) is in the middle of nocturnal species and diurnal species but close to the mesic species. This support the hypothesis that the striped hamster is more adapted to mesic habitats than to arid habitats (Bao et al., 2002).

#### 4.4. Cold-induced maximum metabolic rate

The mean MMR is 1.63 times of the predicted value by Bozinovic and Rosenmann (1989). It is higher than the sympatric Brandt's voles (1.49, M. brandti) (Song and Wang, unpublished date) and Mongolian gerbils (1.47, M. unquiculatus) (Song and Wang, 2002). With this MMR, the striped hamster has a high tolerance to low temperatures and is able to withstand an effective minimum temperature of  $-33^{\circ}$ C (Derived from Eq (1), on the assumption that  $C_{\rm m}$  and  $T_{\rm b}$  were stable). The aerobic factorial scope (ratio of MMR to BMR) (6.9) in the striped hamster is higher than the mean values in eutherians (5.1, Hinds et al., 1993) and in rodents (6, Bozinovic, 1992). We also calculated the aerobic factorial scope listed by Hinds and Rice-Warner (1992) and found the average aerobic factorial scope was 5.70 in Cricetidae. The aerobic factorial scope of the striped hamster in this study is significantly higher than the scopes of other rodents. To our knowledge, the aerobic factorial scope of the striped hamster is one of the two highest aerobic factorial scopes in Cricetidae species, only lower than Calomys ducilla (7.7, Rosenmann and Morrison, 1974).

Thus, the ecophysiology properties for the striped hamster were (1) the high  $T_{\rm b}$  and BMR, and slightly high  $C_{\rm m}$ , (2) a narrow TNZ and low upper critical temperature, and (3) high NST and MMR. These characteristics were closely related to their living habits. The higher  $T_{\rm b}$  and BMR may imply that the striped hamster is more adaptable to cold rather than to hot. The high NST and high MMR can enable the striped hamster to withstand cold and increase the foraging time and food collection at low temperatures, this is very important for the survival of the striped hamster, which

has a high BMR. The ecophysiological characteristics of the striped hamster might constrain their distribution and extension to extreme desert, low latitudes and hot regions in China.

#### Acknowledgements

We wish to thank Professor Zhi-Bin Zhang and Dr. Jian-Xu Zhang for supplying the hamsters for this study. This study was financially supported by the National Natural Science Foundation of China (No. 30070125) and the Chinese Academy of Sciences (Nos. KSCX2-SW-103, KSCX2-1-03, KSCX3-IOZ-06 and STZ-01-06). We also thank the suggestions of the two anonymous reviewers.

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