The maximum metabolizable energy intake and the relationship with basal metabolic rate in the striped hamster *Cricetulus barabensis*

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The maximum metabolizable energy intake (MEI_{max}) of striped hamster *Cricetulus barabensis* (Pallas, 1773) was determined in gradually lowering temperature. The MEI_{max} was gained at 0°C, 3.6 ± 0.1 kJ/(g × d) or 121.9 ± 4.9 kJ/d, which is 2.8 times the basal metabolic rate (BMR). This suggests that the actual energy budgets of striped hamsters in natural environment will keep near the upper physiological limit. As the temperature decreased, both metabolizable energy intake (MEI) and BMR increased though there was no significant correlation between the MEI and BMR or between the MEI_{max} and BMR. However, the significant correlation between MEI_{max} and BMR was found in nine species of rodents. Our results support the assimilation capacity model of the origin and evolution of endothermy at the interspecific level.

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Introduction

The metabolizable energy intake (MEI) is critical for survival, reproduction, and distribution of animals (Karasov 1986, Bozinovic 1992). In homeothermic animals, with ambient temperature decreasing, the MEI should increase to cover the increased demands of thermoregulation until it reaches the ceiling (Song and Wang 2001). A higher rate of MEI requires an increased capacity of alimentary tract and other visceral organs, and sequentially causes the increase in basal metabolic rate (BMR). The link between the metabolizable energy intake capacity and BMR represents a key element in the origin and evolution of endothermy.

The aerobic capacity model has been regarded as the most plausible interpretation for the evolution of endothermy. According to this model, the evolution of endothermy was driven by selection favouring high sustainable locomotor activity

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supported by aerobic metabolism (Taigen 1983). Daan *et al.* (1990) also suggested that BMR variation reflects the evolution of metabolic machinery necessary to generate high non-basal metabolic rates during energetically demanding periods such as reproduction, cold exposure, or sustained physical activity. Koteja (2000) proposed an alternative model, the assimilation capacity model, which emphasizes that the total daily energy expenditure must be balanced by MEI in a time-scale of hours to many days, which is different from the aerobic capacity model that refers to a time-scale of seconds to hours.

The tests of the aerobic capacity model focused on examining the correlation between the basal and maximum metabolic rates (Hayes and Garland 1995). In the assimilation capacity model an equivalent assumption is that the BMR should be correlated with a maximum rate of energy processing, which can be sustained over a long time-scale (MEI) (Koteja 2000). Numerous studies on the correlation between the maximum metabolic rate and BMR, both inter- and intraspecific, have been done (Hayes and Garland 1995). However, the relationship between BMR and cold-induced maximum metabolizable energy intake has seldom been tested.

Striped hamster *Cricetulus barabensis* (Pallas, 1773), a common species in the farmland of northern China and grassland of Inner Mongolia, is granivorous, nocturnal, and storing food in winter (Luo *et al.* 2000). There is little information on ecophysiology for this species. This study aimed to measure the cold-induced maximum metabolizable energy intake rate (MEI_{max}) in the striped hamster, and try to analyse the relationship between MEI_{max} and BMR intra- and interspecifically, with the available data for other species taken from literature.

Material and methods

Eight male and three female striped hamsters were live-captured in the farmland of Hebei Province, China, in April 20, 2000. All were adults and about one year old. They were individually caged in the laboratory under photoperiod L:D = 16:8 and temperature 23°C, and provided with a standard rat pellets chow (Beijing Ke Ao Fed. Co.) and water *ad lib.* The experiments were carried out from June 26 to July 27, 2000. Animals were housed individually in metabolic cages ($0.24 \times 0.24 \times 0.24$ m) without bedding, and were fed with pellets for one week before the experiments. Animals were consecutively exposed to the following ambient temperatures: 23, 20, 15, 10, 5, 0, and –3°C. Trials were performed consecutively. When one trial ended, the animals were fasted and BMR measured. After several hours, when the animals had recovered from the fasting states, the new trial started. Each trial lasted for 3 days. Uneaten food, feces and urine were collected each day. Food and feces were separated by hand and oven-dried at 70°C for at least 72 h. The caloric contents of food, feces, and urine were determined by Parr1281 bomb calorimeter (Parr Instrument, USA). The MEI was calculated by the following formula: MEI = C–F–U (C = Consumption, F = Faeces, U = Urine), and digested energy was calculated as C–F. We calculated the efficiencies of digestion and assimilation as $100 \times (C–F)/C$ and $100 \times (C–F–U)/C$, respectively.

Basal metabolic rate (BMR) was measured after each food-trial by using the closed-circuit respirometer at 29°C (within thermoneutrality, D.-H. Wang, unpubl.). The animals were fasted for 3 hours and were put into the metabolic chambers for 30 min to stabilize before metabolic recordings. Oxygen consumption was recorded for 40 minutes (with 5-min intervals). The two consecutive lowest readings were taken to calculate the BMR. The oxygen consumption was converted to kJ, assuming 20.08 J/ml O_2 (Kleiber 1961).

All analyses were performed with a statistical software package (SPSS 1988). The differences of MEI at various ambient temperatures were tested by ANCOVA, body mass as covariate, with the average of body mass measured at the beginning and at the end of each food trial. The correlation between BMR and MEI was calculated for average values from all the trials. The relationship between BMR and MEI (or MEI_{max}) was tested by bivariate correlations and residual analysis. Residuals of BMR and MEI (or MEI_{max}) were calculated as (measured value – predicted value), in which the predicted value was obtained from the linear regressions of log total body mass and log value of BMR or MEI (or MEI_{max}). All data in this article were expressed as means ± SE.

Results

Body mass was not significantly influenced by temperatures in striped hamster. There was no significant change in average body mass at all temperatures except at –3°C (Table 1).

Food intake, digested energy, and MEI increased with the decrease in ambient temperatures from 23 to 0°C, and all these parameters achieved peak at 0°C, then declined (Table 1, Fig. 1). At 0°C two hamsters died. All data collected from these two hamsters were not significantly different from the others, thus they were included into the whole set of data. The maximum food intake, digested energy and MEI_{max} were: 154.1 ± 6.5 kJ/d [4.6 ± 0.1 kJ/(g×d)], 126.8 ± 5.0 kJ/d [3.8 ± 0.1 kJ/(g×d)], and 121.9 ± 4.9 kJ/d [3.6 ± 0.1 kJ/(g×d)], respectively (Table 1, Fig. 1).

With the decreasing ambient temperatures, efficiency of energy digestion and assimilation tended to decrease. The efficiency at 0°C (82.3 ± 0.3% and 79.1 ± 0.3%, respectively) and –3°C (81.8 ± 0.4% and 79.2 ± 0.3%, respectively) was significantly lower than that at 23°C (83.5 ± 0.4% and 82.5 ± 0.5%, respectively) ($p < 0.05$), but there were no significant differences among 20, 15 and 10°C ($p > 0.05$) (Table 1).

BMR increased with decreasing ambient temperatures (Fig. 1). BMR values at 0°C and –3°C (43.3 ± 3.6 kJ/d and 46.7 ± 2.8 kJ/d, respectively) were significantly higher than those recorded at 23°C (34.1 ± 1.2 kJ/d; $p < 0.05$ and $p < 0.01$,

Table 1. Food intake, digested energy, efficiencies of digestion and assimilation, body mass, and body mass changes at different ambient temperatures for the striped hamster. Body mass and body mass change are the average values for each trial. Values are means ± SE.

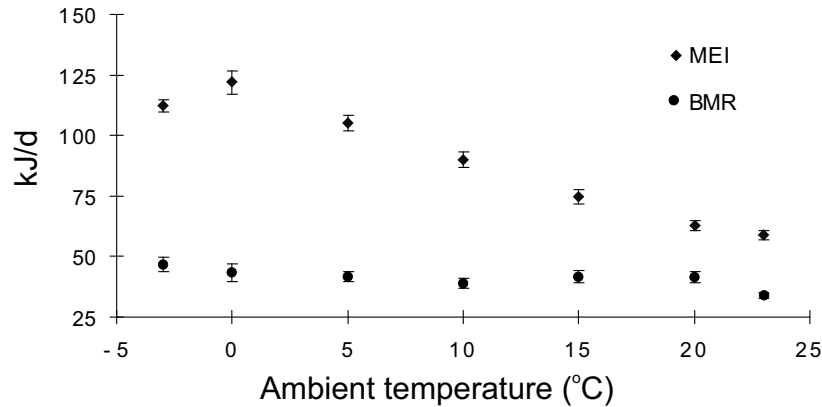| Temperature (°C)	Sample size	Food intake (kJ/d)	Digested energy (kJ/d)	Efficiency of digestion (%)	Efficiency of assimilation (%)	Body mass (g)	Body mass change (g)
23	11	71.4 ± 2.5	59.5 ± 1.8	83.5 ± 0.4	82.5 ± 0.5	33.0 ± 1.6	–0.1 ± 0.2
20	11	77.6 ± 2.9	64.0 ± 2.3	82.6 ± 0.3	80.9 ± 0.4	33.1 ± 1.6	0.2 ± 0.2
15	11	92.0 ± 4.1	77.2 ± 3.2	84.1 ± 0.5	81.3 ± 0.7	33.1 ± 1.8	–0.2 ± 0.3
10	11	110.7 ± 4.3	92.5 ± 3.6	83.6 ± 0.5	81.3 ± 0.5	32.6 ± 1.7	0.0 ± 0.4
5	11	131.9 ± 4.3	109.2 ± 3.4	82.8 ± 0.3	79.8 ± 0.4	32.9 ± 1.5	0.5 ± 0.2
0	9	154.1 ± 6.5	126.8 ± 4.9	82.3 ± 0.3	79.1 ± 0.3	34.0 ± 1.8	0.4 ± 0.3
–3	9	141.7 ± 3.3	115.9 ± 2.6	81.8 ± 0.4	79.2 ± 0.3	34.5 ± 1.7	–1.0 ± 0.3

Fig. 1. The rate of metabolizable energy intake (MEI) and basal metabolic rate (BMR) in relation to ambient temperatures in striped hamsters. Values are mean ± SE.

respectively). However, there were no significant differences between 0 and –3°C or 5°C (Fig. 1). The ratio of MEI_{max} to BMR is 2.8 at 0°C.

The relationships between MEI and BMR ($r^2 = 0.379$, $p = 0.193$, df = 5) and between residual MEI and residual BMR ($r^2 = 0.050$, $p = 0.671$, df = 5) from 23 to 0°C were not significant. We found significant correlations between the MEI_{max} and BMR at 0°C ($r^2 = 0.627$, $p = 0.011$, df = 8), however, the correlation between residual MEI_{max} and residual BMR was not significant ($r^2 = 0.060$, $p = 0.524$, df = 8).

We analysed the relationship between MEI_{max} and BMR for 9 rodent species, which have been studied so far (see Appendix). All the MEI_{max} were obtained with cold-induction methods and BMR was measured in the same individuals. We
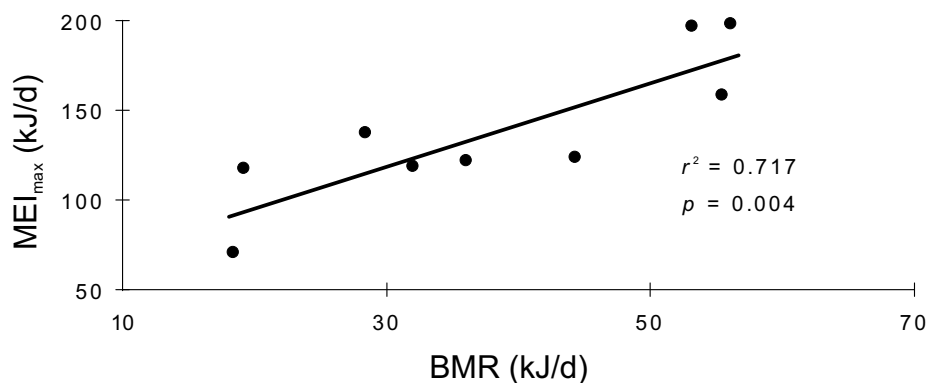

$r^2 = 0.717$

$p = 0.004$

Fig. 2. Correlation between basal metabolic rate (BMR) and maximum metabolizable energy intake (MEI_{max}), as measured by cold-induction in 9 rodent species. Data sources are listed in Appendix.

revealed a significant positive correlation between MEI_{max} and BMR ($r^2 = 0.717$, $p = 0.004$, df = 8, Fig. 2). Similar correlation was also detected between residual MEI_{max} and residual BMR for the 9 rodent species ($r^2 = 0.641$, $p = 0.010$, df = 8).

Discussion

The present study showed that, in the striped hamster, cold-induced MEI_{max} was achieved at 0°C, and it was 2.8 × BMR. Many studies have been designed to estimate MEI_{max} in small mammals (Koteja 1995). For instance, during cold--exposure MEI_{max} was 4.7 × BMR in mice *Mus musculus* (Konarzewski and Diamond 1994), 3 × BMR in bank voles *Clethrionomys glareolus* (Weiner 1987), and 3.2–3.5 × BMR in root vole *Microtus oeconomus* (Wang *et al*. 1996). For almost all mammalian species and all types of energy expenditure examined to date, the range of MEI_{max} was 1.4 to 7.0 (mostly 2 to 5) times BMR (Peterson *et al*. 1990, Hammond and Diamond 1997). Our results (2.8 × BMR) fall in the range.

The MEI_{max} represents the maximum potential energy budgets for a longer period in the striped hamster. Based on the doubly labeled water technique, the daily energy budgets of 9 free-living small mammals were 2 to 5 times BMR (average 3 × BMR) (Karasov 1981). Accordingly, Weiner (1987) proposed a hypothesis that the actual energy budgets of small mammals in their natural environments could be kept fairly near to their upper physiological limits. The results of our study support this hypothesis.

Although no significant relationship between residual MEI and residual BMR was found as temperature decreased, MEI and BMR showed the same trend of increase. As the food intake increased, the efficiencies of digestion and assimilation did not significantly differed among 20, 15, and 10°C, suggesting that the gut size enlarged. The changes of viscera can lead to variations in BMR. The correlation between residual BMR and residual MEI_{max} was not significant in this study. Similarly, no such correlation was found in *Apodemus flavicollis* (Koteja 1995) or *Peromyscus maniculatus* (Koteja 1996). So the intraspecific correlation between MEI_{max} and BMR was seldom detected, similar to the detection on the correlation between maximum metabolic rate and BMR described by Hayes and Garland (1995).

According to the assimilation capacity model of endothermy, natural selection acts in favour of increased routine locomotor activity. More active individuals should have their daily energy expenditure (which must be balanced by MEI) increased, and ingest more food. Consequently, the key organs (such as liver, heart, and kidneys) are stimulated to hypertrophy. These organs have high metabolic intensity, therefore BMR increases. A higher BMR will contribute to a further increase in the daily energy expenditure, which reinforces the BMR and daily energy expenditure again. The correlation between daily energy expenditure and BMR is a key element of the assimilation capacity model (Koteja 2000). Our results

showed a significant interspecific correlation between MEI and BMR and this supports the assimilation capacity model of origin and evolution of endothermy.

In conclusion, MEI_{max} of striped hamsters induced by cold was achieved at 0°C, and approached $2.8 \times BMR$, suggesting that their actual energy budgets in natural environment will keep fairly near to the upper physiological limit. Review of the available data for other rodent species, suggests that the assimilation capacity model of endothermy applies also to interspecific level.

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Appendix. The cold-induced maximal metabolizable energy intake (MEI_{max}) and basal metabolic rate (BMR) in 9 rodent species.

Species	MEI_{max} (kJ/d)	BMR (kJ/d)	Body mass (g)	Reference
Microtus agrestis	158.32	55.46	23.7	McDeviit and Speakman 1994
Microtus oeconomus	121.11	36.15	22.1	Wang *et al*. 1996
Microtus brandti	197.53	56.20	41.6	Song and Wang 2001
Apodemus flavicollis	118.14	32.09	28.4	Koteja 1995
Peromyscus maniculatus	116.63	19.26	21.4	Koteja 1996
Acomys cahirinus	69.74	18.52	37.8	Koteja *et al*. 1994
Mus musculus	136.92	28.51	26.9	Konarzewski and Diamond 1994
Meriones unguiculatus	196.39	53.20	57.8	Liu *et al*. in press
Cricetulus barabensis	122.85	44.36	34.0	This study