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Maximum metabolizable energy intake in the Mongolian gerbil (*Meriones unguiculatus*)

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The objective of this study was to determine the maximum metabolizable energy intake (MEI_{max}) in the Mongolian gerbil (*Meriones unguiculatus*). Metabolizable energy intake was measured with metabolic cage and induced by two cold-exposure procedures: group I was gradually exposed to cold from 23°C to −9°C, MEI_{max} was gained at 5° and kept till −9°C ($3{\cdot}40 \pm 0{\cdot}42\,kJ\,g^{-1}\,day^{-1}$), 3·31 times the basal metabolic rate (BMR); Group II was directly exposed to cold temperature (0°C and −6°C). Mongolian gerbil could maintain their MEI_{max} in a wide temperature range, suggesting that Mongolian gerbils have a greater capacity to tolerate the ambient temperature fluctuation in their natural environments. MEI of group II was lower than that of group I at 0°C and −6°C. Cold acclimation could increase the MEI_{max} and enhance the ability to cope with the cold stress. Mongolian gerbils are able to change their physiological performance to adapt to their natural environments.

Keywords: Mongolian gerbil, *Meriones unguiculatus*; maximum metabolizable energy intake, MEI_{max}

Introduction

Metabolizable energy intake has been proposed as a more likely physiological contributor to explain the differences in life history traits for animals (Derting & Austin, 1998). Maximum metabolizable energy intake rate (MEI_{max}) is critical for the survival, reproduction and distribution of mammals (Hayes & Chappell, 1986; Karasov, 1986; Weiner, 1987; Peterson *et al.*, 1990; Bozinovic, 1992), and thus has been receiving much attention (Piatkowska & Weiner, 1987; Weiner, 1987; Koteja, 1995). However, there is no report on MEI_{max} for cold desert gerbils.

Weiner (1987) found that the energy assimilation of direct cold induction is different from that of gradually lowered temperatures. Koteja *et al.* (2001)

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subsequently stated that cold acclimation might result in physiological adjustment and might also influence the maximum energy intake. Some studies have demonstrated that animals acclimated to cold could be able to achieve a higher maximum sustained energy intake rate than non-acclimated ones (Koteja, 1995; Hammond & Diamond, 1997). Therefore, it can be hypothesized that the upper limit of energy intake might be influenced by cold acclimation.

Mongolian gerbil (*Meriones unguiculatus*) is a dominant small rodent species in the cold desert and semi-arid grassland of northern China and Mongolia. Although several studies have been done on the ecophysiology for this species (Weiner & Gorecki, 1981; Sun & Jing, 1984; Wang *et al.*, 2000), no data about the metabolizable energy intake are available at present. In this study, we aimed to determine the physiological upper limit for metabolizable energy intake and to compare as to whether there is a difference between gradually lowered temperature and direct cold induction in the maximum metabolizable energy intake.

Material and methods

Mongolian gerbils were live-captured in spring 1999 in Inner Mongolia grassland and were raised in the laboratory of Institute of Zoology, the Chinese Academy of Sciences, under conditions of 12L:12D and 23°C. The standard rat pellets chow (Crude fat 6·97%, Crude protein 25·50%, acid detergent fiber 4·75%, neutral detergent fiber 12·82%, and gross energy content 18·29 kJ g^{-1}) (Beijing Ke Ao Feed Co.) and water were provided *ad lib.* The experiments were carried out during October and November. Before the experiments the animals were housed in metabolic cages (0·24 m × 0·24 m × 0·24 m) and fed rat pellets chow for a week to familiarize the environment. No shelter material was provided in the metabolic cages. The animals were divided into two groups. In group I (three females and three males), gerbils were gradually exposed to ambient temperatures of 23°C, 20°C, 15°C, 10°C, 5°C, 0°C, −3°C, −6°C, and −9°C, each trail last for 3 days. On the bases of determination on group I, it has been shown that 0°C and −6°C were within the temperature range for inducing MEI_{max}. Thus, in group II (two females and three males), gerbils were exposed from 23°C to 0°C and -6°C directly, between the trials the animals spent 3 days at 23°C for recovering. The uneaten food, feces and urine in each trial were collected. The uneaten food and feces were separated manually 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, U.S.A.). The consumed, digested, metabolizable energy intake (MEI), coefficient of assimilation and coefficient of digestion were calculated according to Drozdz (1975). Consumed energy (kJ day^{-1})=dry food ingestion (g day^{-1}) × caloric content of food (kJ g^{-1}); Digested energy (kJ day^{-1})=Consumed energy (kJ day^{-1})-energy of feces (kJ day^{-1}); Metabolizable energy intake (MEI, kJ day^{-1})=digested energy (kJ day^{-1})- energy of urine (kJ/day); coefficient of digestion = 100 × digested energy/consumed energy; Coefficient of assimilation = 100 × MEI/consumed energy.

Statistical analysis was performed using SPSS. The effect of temperature was assessed by repeated measures ANOVA. The data were tested by one-way ANOVA for the effect of gender on all the parameters, and no significant difference was found, thus data for both sexes were put together for analysis. Statistical differences between complete sets of values for groups of gerbils were tested by repeated measures ANOVA, followed by LSD comparison. The differences between groups I and II were tested by the independent sample t-test. All data were expressed with mean ± S.E. in this text. $p < 0·05$ was taken as significance.

Results

Body mass

Body mass showed significant differences under different temperatures in group I (df. = 8, 5; $F = 169.201$, $p < 0.001$), but no significant differences were found between the changed mass(df. = 8, 5; $F = 0{\cdot}008$, $p = 0{\cdot}933$). Compared with 23°C, the body mass decreased significantly at −6°C and −9°C (LSD, $p = 0{\cdot}022$ and 0·012, respectively). This result suggested an unbalance of energy budget in gerbils under cold stress. In addition, there were significant differences between 0°C and −6°C for body mass of gerbils in group II (df. = 1, 4; $F = 285{\cdot}242$, $p < 0{\cdot}001$).

Energy consumption

Temperature affected the energy consumption significantly in group I (df = 8, 5; F = 797·056, $p < 0{\cdot}001$). The consumed energy increased with the decreasing temperature and reached the peak value at −6°C (4·30 ± 0·13 kJ $g^{-1}day^{-1}$). The high level of consumed energy could be maintain from 5°C to −9°C. In group II, there is a significant difference between 0°C and −6°C for consumed energy (df. = 1, 4, $F = 211{\cdot}121$, $p < 0{\cdot}001$). Compared with group I, the consumed energy was significantly less both at 0°C (independent *t*-test: df. = 9, $t = 4{\cdot}246$, $p < 0{\cdot}001$) and at −6°C(df. = 9, $t = 3{\cdot}969$, $p = 0{\cdot}003$, Table 1).

Coefficient of digestion

In group I, there were significant differences in digestive coefficients among different temperatures (df. = 8, 5; $F = 6195{\cdot}146$, $p < 0{\cdot}001$). The highest value was obtained at 23°C (87·8 ± 2·0%), while the minimum was at −9°C (71·6% ± 2·0%) (Table 1). Within the temperature range from 20°C to 0°C, the digestive coefficients had no significant differences (LSD). Compared with 23°C, the digestive coefficients of group II decreased significantly both at 0°C and at −6°C (df. = 1, 4; $F = 4927{\cdot}235$, $p < 0{\cdot}001$). A similar trend was found in assimilated coefficients for groups I and II.

Maximum metabolizable energy intake

Metabolizable energy intake (MEI) increased with decreasing temperature decreasing in both groups I and II. In group I, the MEI increased significantly from 23°C to 5°C (df. = 8, 5; $F = 523{\cdot}755$, $p < 0{\cdot}001$). The peak value was achieved at 5°C (3.396 ± 0.424 kJ day^{-1} g^{-1}), and the high value was retained to −9°C (Fig.1). In group II, MEI were significantly lower than that in group I both at 0°C and at 6°C (independent *t*-test, df. = 9, $t = 4{\cdot}710$, $p = 0{\cdot}001$; df. = 9, $t = 4{\cdot}223$, $p = 0{\cdot}002$, respectively).

Wang *et al.* (2000) reported that basal metabolic rate (BMR) of Mongolian gerbils was 1·027 ± 0·067 (kJ day^{-1} g^{-1}). If we take this BMR value, the MEI_{max} in group I was 3·31 × BMR (at 5°C). In group II, the values of MEI were 1·85 × BMR at 0°C and 2·53 × BMR at −6°C, which significantly differ from that of group I (3·07 × BMR at 0°C and 3·21 × BMR at −6°C). A similar change trend was found for energy digestion (Table 1).

Table 1. *The body mass, consumed energy, digested energy, metabolizable energy intake, digestive and assimilated coefficients and changed mass at different ambient temperature(T_a) in Mongolian gerbils (mean ± S.E.)*

T_a (°C)	Group	Body mass (g)	Consumed energy		Digested energy		Metabolizable energy intake (MEI) ($kJ\,g^{-1}\,day^{-1}$)	Digestive coefficient (%)	Assimilated coefficient (%)	Changed mass (%)
			($kJ\,g^{-1}\,day^{-1}$)	($kJ\,day^{-1}$)	($kJ\,g^{-1}\,day^{-1}$)	($kJ\,day^{-1}$)				
23	I	55·78 ± 5·05	1·973 ± 0·194	106·982 ± 9·085	1·733 ± 0·170	93·819 ± 7·630	1·701 ± 0·169	87·8 ± 0·5	86·2 ± 0·7	0·87 ± 0·32
20	I	57·51 ± 5·63	2·303 ± 0·007	132·307 ± 13·455	1·894 ± 0·169	94·161 ± 8·263	1·868 ± 0·175	83·0 ± 4·1	81·8 ± 4·5	2·58 ± 1·52
15	I	58·46 ± 5·48	2·659 ± 0·186	151·950 ± 11·195	2·133 ± 0·146	121·392 ± 6·693	2·088 ± 0·146	80·4 ± 1·8	78·7 ± 1·8	−0·68 ± 0·97
10	I	57·93 ± 4·80	3·001 ± 0·196	172·566 ± 15·818	2·347 ± 0·142	133·874 ± 8·412	2·326 ± 0·144	78·5 ± 2·2	77·8 ± 2·1	−0·37 ± 0·61
5	I	57·83 ± 4·59	4·187 ± 0·423	208·476 ± 7·679	3·453 ± 0·409	171·812 ± 10·943	3·396 ± 0·424	82·3 ± 3·3	80·9 ± 3·4	0·17 ± 0·58
0	I	58·49 ± 4·27	4·275 ± 0·318	246·660 ± 18·579	3·257 ± 0·157	188·270 ± 10·847	3·154 ± 0·201	77·1 ± 3·3	74·4 ± 3·4	1·15 ± 0·45
−3	I	57·28 ± 3·45	3·982 ± 0·169	225·750 ± 7·801	3·258 ± 0·169	184·126 ± 6·848	3·201 ± 0·178	81·1 ± 0·5	79·6 ± 0·7	−1·12 ± 0·94
−6	I	56·65 ± 3·45	4·301 ± 0·125	241·826 ± 9·046	3·353 ± 0·130	188·173 ± 6·649	3·294 ± 0·131	77·9 ± 1·2	76·5 ± 1·3	−0·13 ± 0·38
−9	I	55·43 ± 3·30	3·750 ± 0·391	205·229 ± 19·748	2·701 ± 0·305	147·877 ± 15·566	2·661 ± 0·302	71·7 ± 1·4	70·6 ± 1·5	−2·32 ± 0·91
0	II	60·18 ± 3·83	2·444 ± 0·277	145·337 ± 16·068	1·938 ± 0·222	114·792 ± 11·449	1·899 ± 0·216	79·5 ± 1·4	77·8 ± 1·4	0·32 ± 1·21
−6	II	64·68 ± 3·44	3·444 ± 0·184	215·059 ± 9·952	2·651 ± 0·089	165·733 ± 5·456	2·598 ± 0·087	77·3 ± 1·9	75·7 ± 1·8	3·52 ± 1·07

Note: Group I indicates gradually cold induction and group II indicates direct cold exposure.

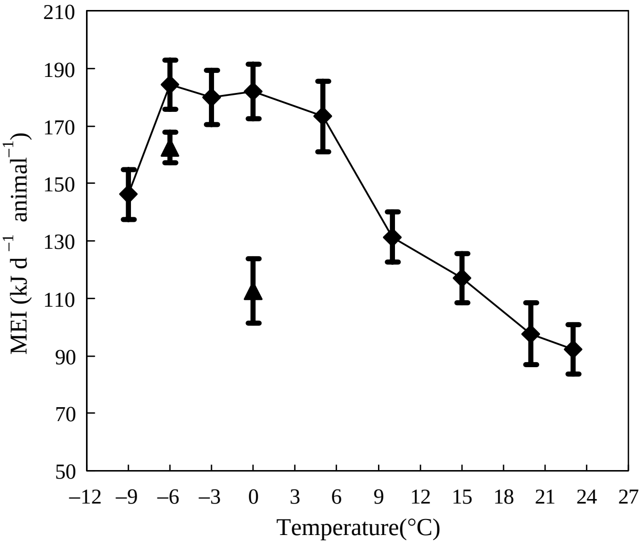

Figure 1. Metabolizable energy intake (MEI, kJ day^{-1} animal^{-1}) in Mongolian gerbils (*Meriones unguiculatus*) at different temperatures. Data are mean ± S.E. (—◆—) Group I; (▲) Group II.

Discussion

Mongolian gerbil could maintain their MEI_{max} in a wide temperature range. MEI_{max} was reached and maintained within the temperature range from 5°C to −9°C. All the individuals survived after the determination at −9°C. Cold acclimation could increase the MEI_{max} and enhance the ability to cope with the cold stress in Mongolian gerbils. The hypothesis that cold acclimation can influence the metabolizable energy intake is supported.

Cold-induced MEI_{max} has been reported for several small mammals. Different species revealed different temperatures or temperature ranges to induce MEI_{max} (Table 2). This suggests that different species have different survival ability under cold

Table 2. *Comparison of temperature or temperature ranges to induce and maintain MEI_{max} for some small mammals species*

Species	Body mass (g)	Temperature range of MEI_{max}	Mortality and temperature	References
Meriones unguiculatus	57·2	5°C to −9°C	0% (−9°C)	Present study
Apodemus flavicollis	27·8	0°C to −10°C	20% (−10°C)	Koteja, (1995)
Microtus pinetorum	22·7	5°C	75% (3°C)	Derting & Austin (1998)
Mus domesticus	28·4	2°C	80%(−8°C)	Manning & Bronson (1990)
Acomys cahirinvs	40·6	12°C to −15°C	50%(12°C)	Koteja (1994)
Phodopus sungorus	37·6	−2°C	—	Weiner (1987)
Clethrionomys glareolus	19·0	5°C	60% (0°C to −5°C)	Piatkowska & Weiner (1987)
Microtus agrestis	25·1	5°C	40% (−5°C)	McDevitt & Speakman (1994)
Microtus brandti	42·4	5°C to −3°C	50% (−6°C)	Song & Wang (2001)
Microtus oeconomus	22·1	5°C	40% (3°C)	Wang *et al.* (1996)

stress. Similar to Mongolian gerbils, Koteja (1995) found that the temperature to achieve MEI_{max} in yellow-necked mice (*Apodemus flavicollis*) was from 0°C to −10°C and the mortality was 20% at −10°C. Generally, the temperature ranges to induce and maintain the MEI_{max} in small rodent species are relatively narrow (Table 2). Weiner (1987) reported that half of the hamsters (*Phodopus sungorus*) indicated negative energy balance at −2°C. The bank voles (*Clethrionomys glareolus*) reached their MEI_{max} at 5°C and over 60% of individuals died from 0°C to −5°C (Piatkowska & Weiner, 1987). The spiny mice (*Acomys cahirinus*) could not maintain their energy balance below 15°C, and MEI_{max} was obtained from 15°C to 5°C(Koteja *et al.*, 1994). Furthermore, the temperature range to maintain MEI_{max} in a sympatric species to Mongolian gerbil, Brandt's vole (*Microtus brandti*), is from 5°C to −3°C (Song & Wang, 2001). Thus Mongolian gerbils have a wide temperature range to maintain their $MEI_{max.}$

Mongolian gerbils live in the cold desert and semi-arid habitat, face the large seasonal temperature fluctuations and great temperature variety between day and night (Wang *et al.*, 2000). Then a wide temperature range to maintain MEI_{max} is beneficial for their survival. Pei *et al.* (2001*a*,*b*) also demonstrated that the digestive strategies are different between Mongolian gerbils and Brandt's voles, mean retention time of digesta in gut is longer in Mongolian gerbils than Brandt's vole. Some studies have shown that Mongolian gerbils have a relatively wide thermal neutral zone (30–40°C, Robinson, 1959; 26–38°C, Wang *et al.*, 2000), which addresses a good ability to cope with high temperature. Steffen & Roberts (1977) have reported that Mongolian gerbils have a largely great capacity to tolerate the wide ambient temperature fluctuation.

Cold acclimation could improve the thermogenic performance, thus increasing food intake and peak metabolic rate (Oufara *et al.*, 1987). Nespolo *et al.* (1999) reported that the maximum metabolic rates of small mammals increased by 25–94% after cold acclimation. Our study presented that energy budgets of gradually cold-exposed gerbils were significantly higher than that of directly cold-exposed gerbils at the same temperatures.

The physiological adjustments induced by a physiologically stressful situation may result in an increased performance under a different energy-demanding condition (Koteja *et al.*, 2001). Therefore, the individuals acclimated to a condition, such as cold stress, lactation, low-quality food and the locomotion activity, required to increase their energy expenditure (Weiner, 1987; Koteja, 1995; Hammond & Diamond, 1997; Koteja *et al.*, 2001). Our experiment also showed that cold acclimation improved the energy assimilation ability, therefore enhanced the cold tolerance capacity in Mongolian gerbil.

In general, Mongolian gerbils could maintain their MEI_{max} in such a wide temperature range that they have a greater capacity to tolerate the ambient temperature fluctuation in their natural environments. Cold acclimation could increase the MEI_{max} and then enhance the ability to cope with the cold stress. Mongolian gerbils are able to change their physiological performance to adapt to their natural environments.

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References

Bozinovic, F. (1992). Scaling of basal and maximum metabolic rate in rodents and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology*, **65**: 921–932.

Derting, T.L. & Austin, M.W. (1998). Change in gut capacity with lactation and cold exposure in a species with low rates of energy use, the pine vole (*Microtus pinetorum*). *Physiological Zoology*, **71**: 611–623.
Drozdz, A. (1975). Metabolic cages for small rodents. In: Grodzinski,W., Klekowski, R. Z. & Duncan, A. (Eds.), *Methods for Ecological Bioenergetics,* pp. 346–351. Oxford: Blackwell Scientific. 367 pp.
Hammond, K.A. & Diamond, J. (1997). Maximal sustained energy budgets in humans and animals. *Nature*, **386**: 457–462.
Hayes, J.P. & Chappell, M.A. (1986). Effect of cold acclimation on maximum oxygen consumption during cold exposure and treadmill exercise in deer mice, *Peromyscus maniculatus*. *Physiological Zoology*, **59**: 473–481.
Karasov, W. H. (1986). Energetics, physiology and vertebrate ecology. *Trends in Ecology and Evolution*, **1**: 101–104.
Koteja, P. (1995). Maximum cold-induced energy assimilation in a rodent, *Apodemus flavicollis*. *Comparative Biochemistry and Physiology*, **112A**: 479–485.
Koteja, P., Krol, E. & Stalinski, J. (1994). Maximum cold- and lactation-induced rate of energy assimilation in *Acomys cahirinus*. *Polish Ecological Studies*, **20**: 369–374.
Koteja, P., Swallow, J.G., Carter, P.A. & Garland Jr, T. (2001). Maximum cold-induced food consumption in mice selected for high locomotor activity: implications for the evolution of endotherm energy budgets. *Journal of Experimental Biology*, **204**: 1177–1190.
Manning, J.M. & Bronson, F.H. (1990). The effects of low temperature and food intake on ovulation in domestic mice. *Physiological Zoology*, **63**: 938-948.
McDevitt, R.M. & Speakman, J.R. (1994). Central limits to sustainable metabolic rate have no role in cold acclimation of the short-tailed field vole (*Microtus agrestis*). *Physiological Zoology*, **67**: 1117–1139.
Nespolo, R.F., Opazo, J.C., Posenmann, M. & Bozinovic, F. (1999). Thermal acclimation, maximum metabolic rate, and nonshivering thermogernsis of *Phyllotis xanthopygus* (Rodentia) in the andes mountains. *Journal of Mammalogy*, **80**: 742–748.
Oufara, S., Barre, H., Rouanet, J.-L. & Chatonnet, J. (1987). Adaptation to extreme ambient temperatures in cold-acclimated gerbils and mice. *American Journal of Physiology*, **253**: R39–R45.
Pei, Y.X., Wang, D.H. & Hume, I.D. (2001*a*). Selective digesta retention and coprophagy in Brandt's vole (*Mictorus brandti*). *Journal of Comparative Physiology B,* **171**: 457–464.
Pei, Y.X., Wang, D.H. & Hume, I.D. (2001*b*) Effects of dietary fibre on digesta passage, nutrient digestibility, and gastrointestinal tract morphology in the granivorous Mongolian gerbil (*Meriones unguiculatus*). *Physiological and Biochemical Zoology,* **74**: 742–749.
Peterson, C.C., Nagy, K.A. & Diamond, J. (1990). Sustained metabolic scope. *Proceedings of the National Academy of Sciences of the United States of America*, **87**: 2324–2329.
Piatkowska, K. & Weiner, J. (1987). Maximum rate of energy assimilation in the bank vole. *Acta Theriologica*, **32**: 45–50.
Robinson, P.F. (1959). Metabolic of the gerbil, *Meriones unguiculatus*. *Science*, **130**: 502–503.
Song, Z.G. & Wang, D.H. (2001). Maximum energy assimilation rate in Brandt's vole (*Microtus Brandti*) from Inner Mongolia Grassland. *Acta Theriologica Sinica* (published in Chinese with English abstract), **21**: 271–278.
Steffen, J.M. & Roberts, J.C. (1977). Temperature acclimation in the Mongolian gerbil (*Meriones unguiculatus*): biochemical and organ weight changes. *Comparative Biochemistry and Physiology*, **58B**: 237–242.
Sun, R.Y. & Jing, S. (1984). Relationship between average daily metabolic rate and resting metabolic rate of the Mongolian gerbil (*Meriones unguiculatus*). *Oecologia*, **65**: 122–124.
Wang, D.H., Sun, R.Y. & Wang, Z.W. (1996). Maximum energy assimilation in the root vole (*Microtus oeconomu*). *Acta Zoologica Sinica*, (Published in Chinese with English abstract), **42**: 35–41.
Wang, D.H., Wang, Y.S. & Wang, Z.W. (2000). Metabolism and thermoregulation in the Mongolian gerbil (*Meriones unguiculatus*). *Acta Theriologica*, **45**: 183–192.
Weiner, J. (1987). Maximum energy assimilation rate in the Djungarian hamster (*Phodopus sungorus*). *Oecologia*, **72**: 297–302.
Weiner, J. & Gorecki, A. (1981). Standard metabolic rate and thermoregulation in five species of Mongolian small mammals. *Journal of Comparative Physiology B*, **145**: 127–132.