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Seasonal adjustments in body mass and thermogenesis in Mongolian gerbils (*Meriones unguiculatus*): the roles of short photoperiod and cold

Abstract Seasonal adjustments in body mass and thermogenesis are important for the survival of small mammals during acclimatization in the temperate zone. To determine the contributions of short photoperiod and cold temperatures to seasonal changes in thermogenesis and body mass in Mongolian gerbils (*Meriones unguiculatus*), body mass, basal metabolic rate (BMR), nonshivering thermogenesis (NST), energy intake and energy digestibility were determined in seasonally acclimatized and laboratory acclimated animals. Body mass showed significant seasonal changes and decreased to a minimum in winter. Both BMR and NST increased in winter, and these changes were mimicked by exposing animals to short photoperiod or cold temperatures in the animal house. Digestible energy intake also increased significantly in winter, and also during exposure of housed animals to both short photoperiod and cold. These results suggest that Mongolian gerbils overcome winter thermoregulatory challenges by increasing energy intake and thermogenesis, and decreasing body mass to reduce total energy requirements. Short photoperiod and cold can serve as effective environmental cues during seasonal acclimatization.

Keywords Body mass · Basal metabolic rate (BMR) · Nonshivering thermogenesis (NST) · Energy intake · Mongolian gerbils (*Meriones unguiculatus*)

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Introduction

Non-hibernating small mammals in the temperate zone face the shortage of available food and increased energy demand in winter (Merritt 1995; Wang and Wang 1996; Jackson et al. 2001). Potential imbalances in food supply and energy demand pose strong selective pressure for the evolution of physiological and behavioral adaptations that enhance their probability of survival over winter (Nagy 1993a; Jackson et al. 2001).

An important physiological strategy for small mammals to cope with cold winter is to increase the capacity for heat production, particularly nonshivering thermogenesis (NST) in brown adipose tissue (Heldmaier et al. 1982; Klaus et al. 1988; Merritt and Zegers 1991; Merritt 1995; Wang and Wang 1996; Kronfeld-Schor et al. 2000). Seasonal cycles of NST have been studied in several small mammals including Djungarian hamsters (Heldmaier et al. 1982), desert spiny mice (*Acomys russatus*) (Kronfeld-Schor et al. 2000), Masked shrews (*Sorex cinereus*) (Merritt 1995), Gapper's red-backed voles (*Clethrionomys gappei*) (Merritt and Zegers 1991), plateau pikas (*Ochotona curzoniae*), and root voles (*Microtus oeconomus*) (Wang and Wang 1996). Most studies showed that increased thermogenic capacity during cold periods was due to the increased capacity of NST (Merritt et al. 2001).

Changes in body mass are the result of the balance between energy intake and expenditure and decrease in body mass is one of the means to save energy (Merritt et al. 2001). Most small mammals, such as Djungarian hamsters (*Phodopus sungorus*), South American field mice (*Abrothrix andinus*), prairie voles (*M. ochrogaster*), and meadow voles (*M. pennsylvanicus*) decrease their body mass in cold seasons (Iverson and Turner 1974; Steinlechner et al. 1983; Bartness and Wade 1985; Bozinovic et al. 1990; Voltura 1996). However, some species such as collared lemmings (*Dicrostonyx groenlandicus*), Syrian hamsters (*Mesocricetus auratus*), and Pampas mice (*Akodon azarze*) increase their body

mass by accumulating energy reserves for the coming winter (Bartness and Wade 1984; Nagy et al. 1995; Del Valle and Busch 2003). The maintenance of a constant body temperature is expensive for winter-active small mammals. However, there are relatively few data on energy budgets for seasonal acclimatized small mammals.

Photoperiod and temperature are two important environmental factors that are involved in seasonal control of body mass and thermogenesis in small mammals (Heldmaier et al. 1981, 1982; Jansky et al. 1986; Wang et al. 1999; Knopper and Boily 2000; Powell et al. 2002; Peacock et al. 2004). Generally, short photoperiod and/or cold can significantly reduce body mass and enhance thermogenic capacity in some small mammals (Dark et al. 1983; Voltura and Wunder 1998; Wang et al. 1999; Klingenspor et al. 2000; Knopper and Boily 2000; Peacock et al. 2004). Whereas with seasonal variations, short photoperiod and/or cold can significantly increase body mass in some small rodent species such as collared lemmings (Powell et al. 2002) and golden hamsters (Jansky et al. 1986).

Mongolian gerbils (*Meriones unguiculatus*) mainly live in the Inner Mongolian grasslands of China, Mongolia, and the region of Beigaer in Russia (Zhang and Wang 1998). In these regions, winter lasts for more than 6 months. It has been reported that free-living Mongolian gerbils show seasonal changes in NST but a relatively stable BMR (Wang et al. 2003). Mongolian gerbils have a wide thermal neutral zone (TNZ) and can maintain maximal energy intake over a wide range of ambient temperatures, in contrast to other cold desert mammals (Wang et al. 2000; Liu et al. 2002). Short photoperiod or cold can induce an increase in BMR, NST, and energy intake, but cannot cause the change in body mass alone (Li et al. 2001, 2003, 2004). No data are available on the energy intake of seasonally acclimatized and laboratory acclimated Mongolian gerbils so far. We hypothesized that Mongolian gerbils can enhance their winter survival by adjusting body mass, energy intake, and thermogenesis seasonally. We predicted that they can increase thermogenic capacity and energy intake, and decrease body mass in short photoperiod or cold conditions. In the present study, we traced seasonal changes in body mass, energy intake, basal metabolic rate (BMR), and nonshivering thermogenesis (NST) in Mongolian gerbils in an outdoor enclosure and determined the effects of photoperiod and temperature in the laboratory for 4-week acclimated animals.

Material and methods

Animals and experimental designs

The animals were the offspring of adult Mongolian gerbils captured in Inner Mongolian Grasslands in May 1999 and transported to the Institute of Zoology, Chinese Academy of Sciences in Beijing, China. Gerbils were housed in groups (3–5) in plastic cages ($30 \times 15 \times 20$ cm^3 high) with sawdust bedding. All the animals were maintained under 16L:8D photoperiod with light on at 0400 h, and room temperature was kept at $23 \pm 1°C$. Subjects were fed ad libitum with standard rat chow and water.

Experiment I To test for seasonal changes in body mass, energy intake, and thermogenesis, we moved the gerbils (70–90 days of age) from the animal house to an outdoor enclosure, and held them individually in plastic cages ($30 \times 15 \times 20$ cm^3 high). After 1 month stabilization in the outdoor enclosure, body mass was monitored at 15-day intervals, and environmental temperature, energy intake, BMR, and NST were measured in August, October, and December of 2001, and February, May and June of 2002.

Experiment II To test for photoperiod and temperature effects on seasonal changes in the physiological parameters measured in Experiment I, gerbils (70–90 days of age) were randomly assigned to the following four experimental regimes in the animal house: long photoperiod (LD, 16L:8D) and warm (23°C); long photoperiod (LD, 16L:8D) and cold (5°C); short photoperiod (SD, 8L:16D) and warm (23°C); short photoperiod (SD, 8L:16D) and cold (5°C). The animals were acclimated for 4 weeks. Body mass was monitored every 3 days and energy intake, BMR, and NST were measured at the start and end of the experiments as described previously. This experiment was conducted from March to May in 2001.

Metabolic trials

Basal metabolic rate was measured by using an established closed-circuit respirometer (Gorecki 1975; Song and Wang 2003a; Liu et al. 2004) at 29°C within their thermal neutral zone (Li et al. 2001; Wang et al. 2003). Briefly, the metabolic chamber volume was 3.6L and the temperature inside the chamber was maintained by a water bath ($\pm 0.5°C$). KOH and silica gel were used to absorb carbon dioxide and water respectively in the metabolic chamber. Gerbils were fasted for 3 h before being moved into the metabolic chambers. After 60 min in the chambers, oxygen consumption was recorded for a further 60 min at 5 min intervals. The two stable consecutive lowest readings were taken to calculate BMR and corrected to standard temperature and pressure (STP) (Song and Wang 2003a; Liu et al. 2004). Body temperature was measured before and after each test. All metabolic measurements were taken between 10:00 and 17:00 h to minimize any effects of circadian rhythms.

Nonshivering thermogenesis was measured on the next day and induced with subcutaneous injections of norepinephrine (NE) (Shanghai Harvest Pharmaceutical

Co. LTD) at $25 \pm 1°C$ which is near the lower critical temperature (Wang et al. 2003; Li et al. 2004). The dosage of NE was calculated according to the equation described by Heldmaier (1971): NE dosage (mg/kg) $= 6.6\ M_b^{-0.458}$ (g), where M_b is body mass in gram. Oxygen consumption was recorded for 60 min with 5 min intervals. The two consecutive highest recordings of oxygen consumption were taken to calculate the maximum NST (Wang and Wang 1996; Wang et al. 1999; Li et al. 2001), and corrected to the STP conditions.

Energy intake and digestibility

Energy intake was measured for 3-day intervals as described previously (Song and Wang 2001, 2002; Liu et al. 2002). During each test, gerbils were housed individually in stainless steel mesh metabolic cage ($0.24 \times 0.24 \times 0.24\ m^3$ high), in which food and water were provided ad libitum. Uneaten food and feces were collected after the 3-day test, and separated manually and oven-dried at 70°C for at least 72 h. The caloric values of food and feces were determined by Parr1281 oxygen bomb calorimeter (Parr Instrument, USA). Dry matter intake, gross energy intake, digestible energy, and digestibility were calculated by the following equations (Grodzinski and Wunder 1975; Song and Wang 2001;

$$\text{Gross energy intake (kJ/day)} = \text{Dry matter intake (g/day)} \times \text{Food caloric value (kJ/g dry matter)}$$
$$\text{Feces energy (kJ/day)} = \text{Dry feces (g/day)} \times \text{Feces caloric value (kJ/g dry matter)}$$
$$\text{Digestible energy intake (kJ/day)} = \text{Gross energy intake (kJ/day)} - \text{Feces energy (kJ/day)}$$
$$\text{Digestibility (\%)} = \text{Digestible energy intake (kJ/day)}/\text{Gross energy intake (kJ/day)} \times 100\%$$

Liu et al. 2002, 2003):
It should be noted that all digestibilities are apparent digestibilities.

Data analysis

Data analysis was carried out using SPSS package (SPSS 1998). Distributions of all variables were tested for normality using the Kolmogorov-Smirnov test. Abnormally distributed data were transformed to natural logarithms for normalization. Seasonal data such as body mass, BMR, NST, and energy intake were obtained from the same animals and were analyzed by general linear model (GLM) repeated measures ANO-VA, followed by an LSD post-hoc test for individual comparisons. To remove the effect of body mass on these parameters, BMR, NST, and energy intake were scaled to the 0.67 power of body mass ($M_b^{0.67}$) as proposed for rodents (Hayssen and Lacy 1985; Pei et al. 2001). Two-way ANCOVA was used to detect the effects of photoperiod and temperature on body mass, BMR, NST, and energy intake, using body mass as the covariate. Differences among groups were detected by LSD post-hoc tests. All values in the text are expressed as mean $\pm$ SEM, and $P < 0.05$ was considered to be statistically significant.

Results

Mean, maximum and minimum ambient temperatures during seasonal acclimatization are shown in Table 1.

Experiment I

Body mass

Body mass of Mongolian gerbils showed significant seasonal changes ($F_{(20,\ 100)} = 18.907$, $P < 0.01$, Fig. 1). Body mass remained stable from July to September (LSD, $P > 0.05$) and then decreased from September to a minimum in November (LSD, $P < 0.05$, Fig. 1). After that, body mass began to increase and reached a maximum in June. Compared with November, body mass of gerbils in June increased by 47% (LSD, $P < 0.05$, Fig. 1).

BMR and NST

Both BMR and NST showed significant seasonal changes (BMR, $F_{(5,\ 25)} = 8.854$, $P < 0.01$; NST, $F_{(5, 25)} = 17.879$, $P < 0.01$, Fig. 2). Scaling the data to $M_b^{-0.67}$ resulted in the same statistical outcome (not shown in Fig. 2). From August through December, BMR and NST increased significantly, reached a peak in December and February (BMR: 118.3 ± 3.7 mlO$_2$/h; NST: 361.0 ± 32.9 O$_2$/h) respectively, then declined to a mini-

Table 1 Average, extreme minimum and maximum ambient temperatures (in °C) during seasonal acclimatization in Mongolian gerbils

	May	Jun	Aug	Oct	Dec	Feb
Mean	22.2 ± 1.3	32.4 ± 0.3	28.3 ± 2.1	18.3 ± 1.2	1.7 ± 0.3	6.4 ± 1.0
Extreme minimum	2.6	10.5	11.4	−3.5	−15.6	−16.0
Extreme Maximum	36.8	39.2	36.1	29.2	19.5	17.4

Fig. 1 Seasonal changes in body mass of Mongolian gerbils. Values are expressed as mean ± SEM ($n=6$)
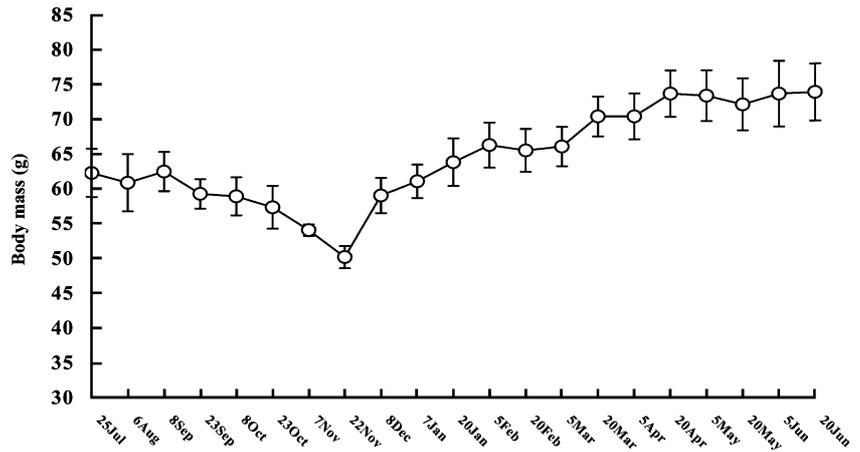
mum in June(BMR: 98.2 ± 8.0 mlO$_2$/h; NST: 228.9 ± 50.0 O$_2$/h). Compared with December, BMR and NST decreased by 17 and 31% in June, respectively (LSD, $P < 0.05$, Fig. 2).

Energy intake and digestibility

Gross energy intake varied significantly over the seasons ($F_{(5,\ 25)}=2.977$, $P<0.05$, Table 2). Energy intake in February increased by 51% compared with that in June (LSD, $P<0.05$). Similar patterns were seen in digestible energy intake ($F_{(5,\ 25)}=2.638$, $P<0.05$), which was the highest in February and lowest in June (LSD, $P<0.05$, Table 2). Digestibility showed no significant seasonal variation.

Experiment II

Body mass

Prior to acclimation, no differences were found in the body mass of Mongolian gerbils between groups. During acclimation, no significant changes were observed among the other three groups, even though animals in warm and short photoperiod conditions increased their

body mass significantly ($t= -3.560$, $P<0.01$, Table 3). At the end of the experiment, no effect of photoperiod and temperature on final body mass was detected (photoperiod, $F=0.057$, $P>0.05$; temperature, $F=0.446$, $P>0.05$; interaction, $F=0.507$, $P>0.05$, Table 3).

BMR and NST

Initial BMR and NST showed no differences among groups. During acclimation, NST increased by 41% under short photoperiod and cold conditions ($t= -8.661$, $P<0.01$, Table 3). At the end of acclimation, temperature had a significant effect on BMR, with cold inducing a 16% higher BMR than that after warm acclimation conditions ($F=8.153$, $P<0.01$), but there was no effect of photoperiod, and no significant interaction between photoperiod and temperature (photoperiod, $F=0.732$, $P>0.05$; interaction, $F=0.246$, $P>0.05$). Both short photoperiod and cold caused NST to increase by 11 and 21% respectively (photoperiod, $F=4.978$, $P<0.05$; temperature, $F=18.570$, $P<0.01$, Table 3). There was no significant interaction between photoperiod and temperature on NST ($F=3.015$, $P>0.05$).

Fig. 2 Seasonal changes in basal metabolic rate (*BMR*) and nonshivering thermogenesis (*NST*) in Mongolian gerbils. Values are expressed as Mean ± SEM ($n=6$). Different letters identify statistically significant differences
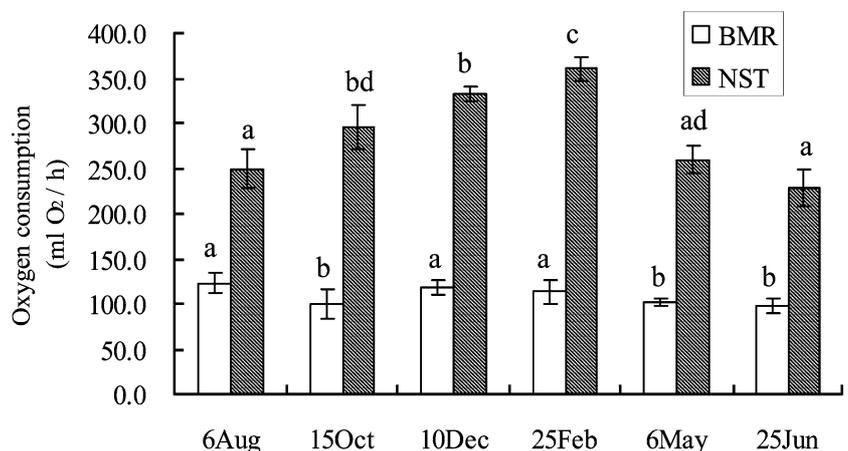
Table 2 Energy intake and digestibility in seasonal acclimatized Mongolian gerbils

	6 Aug	15 Oct	10 Dec	25 Feb	6 May	25 Jun
Sample size	6	6	6	6	6	6
Body mass (g)	61.7 ± 3.6^a	58.8 ± 2.2^{ab}	56.4 ± 2.2^b	66.7 ± 3.3^{ac}	71.2 ± 3.5^d	74.2 ± 4.2^d
Dry matter intake						
g/ d	4.73 ± 0.82^a	5.80 ± 0.44^a	6.35 ± 0.34^{ab}	7.56 ± 0.60^b	6.08 ± 0.64^{ab}	5.00 ± 0.72^a
$g/g^{0.67}$ d	0.29 ± 0.04^{ac}	0.38 ± 0.03^{abc}	0.43 ± 0.02^{ab}	0.45 ± 0.03^b	0.35 ± 0.04^{abc}	0.29 ± 0.05^c
Gross energy intake						
kJ/ d	85.94 ± 14.97^a	105.54 ± 7.93^a	115.51 ± 6.20^{ab}	137.46 ± 10.88^b	110.58 ± 11.66^{ab}	90.92 ± 13.03^a
$kJ/g^{0.67}$ d	5.32 ± 0.71^{ac}	6.90 ± 0.53^{abc}	7.77 ± 0.44^{ab}	8.27 ± 0.62^b	6.36 ± 0.66^{abc}	5.19 ± 0.85^c
Digestible energy intake						
kJ/ d	73.44 ± 14.68^{ac}	81.99 ± 6.99^{ac}	93.65 ± 6.13^a	113.51 ± 9.16^b	89.60 ± 12.33^{abc}	66.77 ± 11.49^c
$kJ/g^{0.67}$ d	4.53 ± 0.71^{ab}	5.36 ± 0.47^{ab}	6.30 ± 0.44^b	6.83 ± 0.54^b	5.15 ± 0.71^{ab}	3.82 ± 0.73^a
Digestibility (%)	84.0 ± 1.8	77.3 ± 1.9	80.8 ± 1.1	82.6 ± 8.9	79.8 ± 2.8	71.4 ± 5.3

Values are expressed as absolute mean $\pm$ SE

*Different superscripts in each row means significantly different ($P < 0.05$). Because all energetic parameters were measured with the same animals, we detected the differences among different times by repeated measure ANOVA

Energy intake and digestibility

There were no significant effects of photoperiod and temperature on dry matter intake, gross energy intake, digestible energy intake or digestibility before acclimation ($P > 0.05$). However, dry matter intake (Photoperiod, $F = 4.400$, $P < 0.05$, temperature, $F = 46.725$, $P < 0.01$), gross energy intake (Photoperiod, $F = 4.400$, $P < 0.05$, temperature, $F = 46.725$, $P < 0.01$), digestible energy intake (Photoperiod, $F = 1.872$, $P > 0.05$, temperature, $F = 44.692$, $P < 0.01$), and digestibility (Photoperiod, $F = 18.844$, $P < 0.01$, temperature, $F = 7.771$, $P < 0.01$) under short photoperiod and/or cold increased more than under long photoperiod and warm conditions after 3 days of acclimation (Table 4), and there was a significant interaction between photoperiod and temperature ($P < 0.01$). The effect of temperature persisted to the end of acclimation (dry matter intake, $F = 324.297$, $P < 0.01$; gross energy intake, $F = 324.297$, $P < 0.01$; digestible energy intake, $F = 3245.300$, $P < 0.01$; digestibility, $F = 2.441$, $P > 0.05$, Table 4). At the end of acclimation, dry matter intake, gross energy intake, and digestible energy intake in the two cold groups increased by 70 and 71%, 70 and 71%, 73 and 71% respectively compared with that of the initial. There were no significant differences in digestibility.

Discussion

In the present study, it was clear that Mongolian gerbils showed seasonal changes in body mass, which was lowest in winter and highest in summer. This pattern is similar to a sympatric species—Brandt's voles (*M. brandtii*) (Li and Wang 2005), and other small mammals in temperate zones (Iverson and Turner 1974; Steinlechner et al. 1983; Klaus et al. 1988; Bozinovic et al. 1990; Merritt 1995; Wang and Wang 1996). In the Djungarian hamster, body mass in winter decreased by 30% compared with summer (Steinlechner et al. 1983). Iverson and Turner (1974) reported that mean body mass of *M. pennsylvanicus* also decreased by 30–40% from August (summer) to February (winter). Winter-active small mammals have great energy demands in cold periods and it has been thought that a decrease in body mass helps them to cope with winter stress by reducing their total energy requirements (Merritt and Zegers 1991; Merritt 1995; Merritt et al. 2001). The decrease in body mass could result from changing energy reserves and/or thermoregulatory heat production (Klaus et al. 1988; Voltura and Wunder 1998; Merritt et al. 2001; Bartness et al. 2002). However, a decrease in body mass will increase the ratio of surface-to-volume,

Table 3 Effect of photoperiod and temperature on body mass, basal metabolic rate (BMR), and nonshivering thermogenesis (NST) in Mongolian gerbils

Values are expressed as mean $\pm$ SE*Different superscripts in each row means significantly different ($P < 0.05$). Differences among groups were detected using ANCOVA and body mass as covariate

	Long photoperiod		Short photoperiod	
	23°C	5°C	23°C	5°C
Sample size	9	6	9	9
Body mass (g)				
Initial	55.5 ± 1.1	57.0 ± 1.3	54.2 ± 2.1	53.6 ± 1.4
Final	58.3 ± 1.7	57.2 ± 1.9	60.0 ± 2.9	56.7 ± 2.4
BMR (mlO_2/ h)				
Initial	109.7 ± 5.7	121.0 ± 7.0	119.0 ± 5.7	119.5 ± 5.7
Final	119.7 ± 8.4^a	132.5 ± 10.3^{ab}	125.0 ± 8.4^a	141.3 ± 8.4^b
NST (mlO_2/h)				
Initial	277.9 ± 11.9	271.0 ± 14.3	241.0 ± 11.7	243.4 ± 11.7
Final	266.4 ± 13.0^a	301.1 ± 16.0^a	276.7 ± 13.0^a	352.6 ± 13.0^b

Table 4 Effect of photoperiod and temperature on dry matter intake, gross energy intake, digestible energy intake, and digestibility in Mongolian gerbils

	Long photoperiod			Short photoperiod	
	23°C	5°C		23°C	5°C
Sample size	9	6		9	9
Body mass (g)					
0 day	56.5 ± 1.3	57.0 ± 1.0		54.6 ± 2.0	53.7 ± 1.4
3 days	56.4 ± 1.3	57.0 ± 1.1		54.6 ± 2.0	53.7 ± 1.4
27 days	58.0 ± 1.6	57.3 ± 1.8		59.3 ± 3.0	55.7 ± 2.3
Dry matter intake (g / d)					
0 day	6.87 ± 0.19	6.97 ± 0.25		6.64 ± 0.20	6.59 ± 0.20
3 days	6.88 ± 0.33[a]	10.38 ± 0.41[b]		7.21 ± 0.33[a]	8.13 ± 0.33[c]
27 days	6.27 ± 0.52[a]	11.85 ± 0.85[b]		6.47 ± 0.52[a]	11.29 ± 0.52[b]
Gross energy intake (kJ / d)					
0 day	121.30 ± 3.34	123.17 ± 4.48		117.24 ± 3.54	116.35 ± 3.54
3 days	121.50 ± 5.89[a]	183.46 ± 7.21[b]		127.41 ± 5.89[ac]	143.62 ± 5.88[c]
27 days	110.86 ± 9.13[a]	209.35 ± 11.18[b]		114.35 ± 9.13[a]	199.43 ± 9.13[b]
Digestible energy intake (kJ / d)					
0 day	102.04 ± 3.34	103.83 ± 4.48		98.13 ± 3.55	96.59 ± 3.55
3 days	102.24 ± 4.69[a]	150.90 ± 5.74[b]		110.46 ± 4.69[a]	122.62 ± 4.69[c]
27 days	95.83 ± 8.56[a]	179.18 ± 10.48[b]		98.88 ± 8.56[a]	165.53 ± 8.56[b]
Digestibility (%)					
0 day	84.2 ± 0.9	84.3 ± 1.2		83.5 ± 1.0	82.9 ± 1.0
3 days	84.2 ± 0.4[a]	82.4 ± 0.6[b]		86.7 ± 0.5[c]	85.4 ± 0.5[ac]
27 days	86.5 ± 0.5	85.6 ± 1.6		85.9 ± 1.2	84.1 ± 3.1

Values are expressed as mean ± SE

*Different superscripts in each row means significantly different ($P < 0.05$). Differences among groups were detected using ANCOVA and body mass as covariate

which can cause greater heat loss, and thus increase living costs. Generally, small mammals possess less cooling resistance than large mammals and, therefore, imposed much more cost for endothermy, especially for winter-active small mammals (Merritt 1995; Merritt et al. 2001).

Short photoperiod and/or cold can cause a decrease in body mass of some small mammals (Iverson and Turner 1974; Heldmaier et al. 1982; Steinlechner et al. 1983; Bartness and Wade 1985; Klingenspor et al. 2000; Knopper and Boily 2000; Zhao and Wang 2005). For Djungarian hamsters, the decrease in body mass in winter was mainly caused by short photoperiod (Knopper and Boily 2000), while in species of *Microtus*, such as *M. pennsylvanicus*, it resulted mainly from lack of food (Iverson and Turner 1974). In the present study, both short photoperiod and cold had no significant effects on body mass in 4-week acclimated Mongolian gerbils. We recently reported that under constant long photoperiod, cold can increase BMR, NST, and energy intake in this species, but not body mass (Li et al. 2004). We have also found that short photoperiod alone can increase BMR and energy intake in Brandt's voles, but not body mass and NST (Zhao and Wang 2005). There is also evidence that acclimation time and photoperiod history can influence responses to environmental factors (Nagy 1993; Veloso and Bozinovic 2000).

Small mammals cope with cold mainly by increasing their capacity for thermogenesis (Heldmaier 1982; Klaus et al. 1988; Merritt and Zegers 1991; Merritt 1995; Wang and Wang 1996; Kronfeld-Schor et al. 2000; Li

and Wang 2005). In the present study, Mongolian gerbils increased BMR and NST in winter, consistent with previous findings in the laboratory and field (Li et al. 2001; Wang et al. 2003) and similar to other rodent species living in cold regions (Heldmaier et al. 1982; Wang and Wang 1996; Li and Wang 2005). Spiny mice living in a hot rocky desert also increased NST capacity by 112–170% higher in winter than in summer (Kronfeld-Schor et al. 2000). Heldmaier et al. (1982) showed that the NST capacity of Djungarian hamsters increased by 71% in winter compared with summer. Plateau pikas and root voles living in Qinghai-Tibet alpine meadow (Wang and Wang 1996) and Brandt's voles in Inner Mongolian grasslands (Li and Wang 2005) also showed similar patterns. Enhancement of thermogenesis in winter is common for temperate and arctic small mammals (Rosenmann et al. 1975; Heldmaier et al. 1982; Merritt and Zegers 1991; Merritt 1995; Merritt et al. 2001).

During seasonal acclimatization many factors such as temperature, photoperiod, and food quality and quantity can all affect NST capacity in small mammals (Heldmaier et al. 1982; Wunder and Gettinger 1996; Nespolo et al. 1999; Wang et al. 1999). Cold appears to be the dominant factor in the inducion of increased NST capacity, while short photoperiod can also stimulate the development of NST (Heldmaier and Steinlechner 1981; Heldmaier et al. 1982). In the present study, both short photoperiod and cold induced a significant enhancement in BMR and NST in Mongolian gerbils, as has been shown in some other small

mammals (Heldmaier et al. 1982; Wang et al. 1999; Zhao and Wang 2005). The high BMR has been found to be due to the increased development of body organs, especially the gastrointestinal tract, associated with the processing of high food intakes (Speakman et al. 2000; Song and Wang 2002, 2003b). The high NST is due to the increased thermogenic properties of brown adipose tissue mitochondria, such as increased cytochrome c oxidase activity and increased contents of uncoupling protein (Heldmaier et al. 1981, 1982; Klaus et al. 1988; Klingenspor et al. 1989; Zhao and Wang 2005; Li and Wang 2005). Speakman (1996) suggested that small mammals entering winter have a choice of thermoregulatory strategies. They can choose low BMR/low NST, which results in low total energy demands and therefore high survival in mild winters. Alternatively, they can maintain high BMR/high NST in severe cold winters, as suggested by the results of this study with Mongolian gerbils, which enable them to survive long cold periods in extreme climates.

The balance between energy acquisition and expenditure is critical to an animal's survival and reproductive success (Bozinovic et al. 2004; Nagy and Negus 1993). This balance depends on the interplay among energy intake, digestion processing, and the energy allocation to alternative functions such as thermoregulation, growth, reproduction, and others (Nagy and Negus 1993; Wang and Wang 1996; Bacigalupe and Bozinovic 2002). In Mongolian gerbils, energy intake increased during winter and cold conditions, partly in response to increases in BMR and NST in winter. Liu et al. (2002) also found that Mongolian gerbils increase food intake in cold conditions. Collared lemmings housed at 5°C had a 37% higher food intake than those housed at 18°C (Nagy and Negus 1993). We found that in Brandt's voles, the winter decrease in body mass was accompanied by increased energy intake and enhanced NST as well as by decreased body fat mass and reduced levels of circulating leptin: we suggest that leptin may serve as a starvation signal in the regulation of energy balance (Li and Wang 2005).

In summary, Mongolian gerbils decreased body mass and increased BMR, NST, and energy intake in winter. Short photoperiod and cold seem to be the environmental cues involved. The increase in energy intake and thermogenesis under cold conditions can enhance winter survival. Decreased body mass also helps by lowering total energy requirements. Another possible interpretation for the seasonal variations in body mass is that Mongolian gerbils are hyperphagic in late winter and early spring to fatten before breeding ensues. This possibility needs to be further investigated.

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