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Basal metabolic rate and organ size in Brandt's voles (*Lasiopodomys brandtii*): Effects of photoperiod, temperature and diet quality

Zhi-Gang Song, De-Hua Wang *

State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, 25 Beisihuan Xilu, Zhongguancun, Beijing 100080, China

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Abstract

This study examined the effects of photoperiod (long day [16 Light:8 Dark] and short day [8 Light:16 Dark]), temperature (cold [5 °C] and warm [23 °C]), and diet quality (high-fiber diet [36% neutral-detergent fiber (NDF)] and low-fiber diet [23% NDF]) on basal metabolic rate (BMR), digestible energy intake, and organ size in the Brandt's vole (*Lasiopodomys brandtii*). Cold increased BMR and showed a significant interaction with diet quality. Cold and short photoperiod increased intake of food and digestible energy. The high-fiber diet increased food intake, but decreased digestibility, and had no effects on digestible energy intake. Voles housed in the cold had heavier liver, kidneys and gastrointestinal segments but a lighter carcass. Segments of the gastrointestinal tract tended to be heavier when voles were fed the high-fiber diet. Voles housed in short photoperiod had lighter heart and kidneys but heavier gut segments. With the effects of body mass on BMR and organs was removed, BMR was significantly related to the dry mass of heart, liver, kidneys and cecum. Digestible energy intake was significantly related to the dry mass of kidneys and stomach. These significant relationships were also detected after removing the effects of body mass, temperature, photoperiod and diet quality. There was also a significant correlation between BMR and digestible energy intake. Our results suggest that variations in BMR reflected the evolution of metabolic machinery that induces higher energy intakes. The data also support the assimilation capacity model of endothermy.
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Keywords: Basal metabolic rate; Brandt's voles (*Lasiopodomys brandtii*); Endothermy; Organ morphology

1. Introduction

The capacity for thermogenesis and energy intake are important for the survival of winter-active small mammals in their natural environment. Many small mammals show seasonal changes in basal metabolic rate (BMR), which is usually higher in winter [1–5]. These seasonal variations may be cued by environmental factors such as photoperiod, ambient temperature, and diet quality and/or quantity. Short photoperiod solely or combined with cold can increase metabolic rate, and especially BMR [6–9]. Low ambient temperature can also increase the BMR of some species [9,10]. Some species can also lower their BMR when fed on a low-quality diet [11]. Geluso and Hayes [12] found that the BMR of European starlings (*Sturnus vulgaris*) did not differ between the high- and low-quality dietary groups even though organ sizes showed great differences. The seasonal decline in ambient temperatures not only increases the cost of thermoregulation for winter-active small mammals but also increases the cost of foraging. So small mammals in cold and/or fed on high-fiber diets always tend to down-regulate their energy demand and/or increase their energy intake.

It has been hypothesized that variations in BMR in animals can be related to differences in the sizes of metabolically active organs. Daan et al. [13] found that combined masses of heart and kidney explained almost 50% of BMR variation in 22 bird species and suggested that BMR variation between species of similar body size reflects the evolution of metabolic machinery. Konarzewski and Diamond [14] found that strains of mice with high BMR tended to have large liver, heart, kidney and brain after adjusting for the effects of overall size, and the correlation

* Corresponding author. Tel.: +86 10 62613511; fax: +86 10 62565689.
E-mail address: wangdh@ioz.ac.cn (D.-H. Wang).

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between BMR and masses of metabolically active organs appeared not only between strains, but also within the same strain. In non-breeding mice selected for high and low food intake, the effects of strain on BMR were also consistent with the anticipated effect from strain differences in liver size [15]. Williams and Tieleman [16] proposed that organ sizes and BMR are influenced by the amount of food consumed, which in turn parallels energy requirements. The assimilation capacity model proposed by Koteja [17] focused on examining the correlation between BMR and maximum sustained metabolic rate. Ricklefs et al. [18] showed that the BMR and daily energy expenditure was significantly correlated across 33 species of mammals. There are different conclusions in intraspecific studies for this model [14,19] and the association between total energy expenditure and BMR is still not clear.

Brandt's vole (*Lasiopodomys brandtii*) is a small mammalian herbivore that feeds on grass leaves and is primarily distributed in the Inner Mongolia grasslands of China, Mongolia and the Beigaer region of Russia. We conducted experiments on the effects of temperature, photoperiod, and diet quality on thermogenesis in Brandt's voles, in order to (1) determine the effects of temperature, photoperiod, and diet quality on BMR, food intake, digestibility, and organ sizes; and (2) examine correlations between organ size and BMR and between digestible energy intake and BMR.

2. Materials and methods

Voles were live-captured on Inner Mongolian grassland in the spring of 1999 and raised in our laboratory. Their first filial generations (about 5 months old) were used for this experiment. Before the experiment voles were maintained on standard rabbit pellets (Beijing Ke Ao Feed Co.) in plastic cages at 23±1 °C under a 16 Light: 8 Dark cycle with lights on at 0400 h. Food and water were available ad lib. In April 1999, animals were randomly assigned to eight experimental regimens, and then acclimated for 3 weeks to long day [16 Light:8 Dark] or short day [8 Light:16 Dark], cold [5 °C] or warm [23 °C], and a high-fiber [35.5% neutral detergent fiber (NDF)] or low-fiber diet [23.1% NDF]. The mean body masses of the 8 groups were similar before acclimation.

The high-fiber diet was prepared by grinding the standard rabbit pellets, and then thoroughly mixing them with two times the weight of alfalfa (*Medicago sativa*) powder. The dry mixture was then moistened and dried at low temperature to adhere the alfalfa powder to the other dietary components, then repelleted. The contents of neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined following Goering and Van Soest [20] after pretreatment with heat-stable α-amylase (Sigma) to remove the starch [21]. The composition of the two experimental diets is shown in Table 1; agreement between two replicate analyses were within 5%.

After 3 weeks acclimation, digestible energy intake was measured. We regarded the digestible energy intake as an index of total daily energy expenditure. During the experiment, animals were housed in stainless steel mesh metabolism cages (30 cm × 15 cm × 20 cm) and food and water were provided in excess of the animals' needs. Feces and uneaten food were collected quantitatively each day. Each collection period lasted 3 days. Food and feces were separated manually and oven-dried at 70 °C for at least 72 h. The caloric values of the food and feces were determined with a Parr1281 oxygen bomb calorimeter (Parr Instrument USA). The digestible energy intake was then calculated as gross energy intake minus the energy lost in feces. Apparent digestibility (%) was calculated as

$$[(\text{Gross energy intake} - \text{Energy lost in feces}) / \text{Gross energy intake}] \times 100$$

Basal metabolic rate was measured after the 3-day collection period in a closed-circuit respirometer at 29 °C (within thermoneutrality [5]). The metabolic chamber volume was 3.6 L and the temperatures inside the chamber were maintained with a water bath (±0.5 °C). Carbon dioxide and water in the metabolic chamber were absorbed by KOH and silica gel, respectively. Before measurement, the animals were fasted for 3 h, then stabilized for 60 min in the metabolic chamber before oxygen consumption was recorded over 5 min intervals for 60 min. The two lowest stable consecutive readings were taken to be BMR. Body temperatures of the animals were measured prior to and after the BMR measurements. All metabolic measurements were taken between 1000 and 1700 h and all metabolic data were corrected to STP.

After the metabolic measurements, the animals were killed by decapitation and the brain, heart, liver, kidneys, brown adipose tissue (BAT) and gastrointestinal tract were quickly removed. The gastrointestinal tract was dissected free of mesenteric attachments but without stretching the tissue [22]. The lengths and fresh weights without contents of stomach, intestine, cecum, and colon were measured. All the tissues and organs were weighed to the nearest ±1 mg, then were oven-dried at 60 °C for 48 h, and the dry weights recorded.

Data were analyzed using the SPSS package [23]. Distributions of all variables were tested for normality using the Kolmogorov–Smirnov test. The masses of some of the morphological components were not normally distributed, so all variables were transformed to natural logarithms to normalize them. A General Linear Model Univariate procedure was used to test the effects of temperature, photoperiod and diet on BMR, digestible energy intake, digestibility and mass of alimentary tract segments. Body mass was used as the covariate for comparisons. Assumptions of homogeneity of variance and linearity were satisfied. Regression and correlation analyses

Table 1
Composition of experimental diets

Contents	Low-fiber diet	High-fiber diet
Crude fat (%)	6.2	3.9
Crude protein (%)	20.8	19.4
Neutral detergent fiber (%)	23.1	35.5
Acid detergent fiber (%)	12.5	21.4
Ash (%)	10.0	10.5
Gross energy (kJ/g)	17.5	17.3

Composition percentages are based on dry mass.

Table 2
Effects of photoperiod, temperature, and diet quality on digested energy, digestibility, energy gain, and basal metabolic rate (BMR) in Brandt's voles (*L. brandtii*)

	Long day				Short day				Effects
	High-fiber diet		Low-fiber diet		High-fiber diet		Low-fiber diet		
	Cold (n=4)	Warm (n=7)	Cold (n=8)	Warm (n=7)	Cold (n=9)	Warm (n=10)	Cold (n=10)	Warm (n=15)	
Body mass (g)	42.25 (4.70)	51.14 (4.75)	50.75 (3.00)	53.43 (3.49)	36.56 (1.72)	44.40 (2.45)	44.70 (1.59)	52.73 (2.14)	T** F**L*
Gross energy intake (kJ/day)	217.98 (18.68)	122.25 (12.23)	155.11 (11.43)	70.66 (12.58)	235.74 (20.19)	107.13 (18.67)	195.39 (10.43)	124.23 (9.51)	T*** F** L* F×L*
Digested energy (kJ/day)	107.68 (12.36)	65.72 (8.09)	105.62 (7.56)	53.63 (8.32)	122.87 (13.36)	60.35 (12.36)	133.29 (6.90)	84.63 (6.30)	T*** L*
Digestibility (%)	0.48 (0.02)	0.54 (0.01)	0.67 (0.01)	0.74 (0.01)	0.49 (0.02)	0.56 (0.02)	0.68 (0.01)	0.68 (0.01)	T*** F***
BMR (ml O_2/h)	125.99 (8.14)	100.12 (6.15)	115.21 (5.75)	121.60 (6.26)	130.41 (6.00)	103.40 (5.14)	137.25 (5.13)	116.64 (4.36)	T*** T×F*

All values are covariate-adjusted means (S.E.) except body mass. Effects: L, photoperiod; T, temperature; F, diet quality. Interactions are indicated by ×. *P<0.05, **P<0.01, ***P<0.001.

were used to test for possible associations between BMR, digestible energy intake and organ mass. To avoid repetition, further details are given in the section BMR and organs. All values are the covariate-adjusted means±S.E. except body mass in the text, and p<0.05 was taken to be statistically significant.

Table 3
Effects of photoperiod, temperature, and diet quality on morphological parameters in Brandt's voles (*L. brandtii*)

	Long day				Short day				Effects
	High-fiber diet		Low-fiber diet		High-fiber diet		Low-fiber diet		
	Cold (n=3)	Warm (n=6)	Cold (n=6)	Warm (n=5)	Cold (n=3)	Warm (n=6)	Cold (n=9)	Warm (n=12)	
Body wet mass (g)	48.50 (6.50)	56.33 (3.34)	48.20 (1.93)	49.74 (3.24)	34.33 (3.84)	48.53 (4.77)	53.41 (2.31)	56.65 (2.20)	T* , F×L*
Body dry mass (g)	14.87 (2.28)	16.78 (1.03)	15.42 (0.53)	17.35 (1.14)	10.63 (1.22)	16.96 (1.59)	17.26 (0.71)	20.61 (0.85)	T* , F×L*
Carcass wet mass (g)	29.18 (3.64)	34.60 (1.91)	31.62 (1.18)	35.68 (2.17)	20.57 (2.15)	34.98 (3.21)	34.65 (1.40)	42.72 (1.55)	T***F*
Carcass dry mass (g)	11.24 (3.90)	16.02 (0.60)	13.70 (0.70)	12.15 (1.29)	14.07 (1.69)	15.63 (1.58)	16.18 (1.26)	18.70 (0.76)	T***F*
Heart wet mass (g)	0.24 (0.02)	0.36 (0.02)	0.61 (0.02)	0.25 (0.01)	0.21 (0.02)	0.21 (0.01)	0.28 (0.01)	0.26 (0.01)	T*** F*** L***
Heart dry mass (g)	0.06 (0.01)	0.09 (0.00)	0.08 (0.00)	0.07 (0.00)	0.05 (0.00)	0.05 (0.00)	0.07 (0.00)	0.06 (0.00)	
Lung wet mass (g)	0.31 (0.02)	0.39 (0.01)	0.64 (0.01)	0.32 (0.01)	0.34 (0.02)	0.34 (0.02)	0.46 (0.01)	0.41 (0.01)	T* T×F* T×L×F*
Lung dry mass (g)	0.08 (0.01)	0.09 (0.00)	0.09 (0.00)	0.08 (0.00)	0.08 (0.00)	0.08 (0.00)	0.10 (0.00)	0.10 (0.00)	
Liver wet mass (g)	2.24 (0.30)	2.04 (0.12)	2.35 (0.10)	1.81 (0.12)	1.70 (0.19)	1.76 (0.17)	2.41 (0.11)	1.96 (0.08)	T***
Liver dry mass (g)	0.76 (0.02)	0.55 (0.00)	0.64 (0.00)	0.54 (0.01)	0.46 (0.00)	0.51 (0.00)	0.69 (0.01)	0.58 (0.00)	T*** T×L×F*
BAT wet mass (g)	0.52 (0.05)	0.26 (0.01)	0.64 (0.02)	0.30 (0.01)	0.36 (0.03)	0.37 (0.03)	0.42 (0.01)	0.34 (0.01)	T** T×L*
BAT dry mass (g)	0.37 (0.07)	0.20 (0.00)	0.36 (0.01)	0.29 (0.02)	0.21 (0.01)	0.25 (0.01)	0.28 (0.01)	0.24 (0.01)	
Spleen wet mass (g)	0.02 (0.00)	0.07 (0.00)	0.26 (0.01)	0.04 (0.00)	0.03 (0.00)	0.04 (0.00)	0.04 (0.00)	0.04 (0.00)	T*** F*** L***
Spleen dry mass (g)	0.01 (0.00)	0.02 (0.00)	0.01 (0.00)	0.02 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	
Brain wet mass (g)	0.53 (0.01)	0.56 (0.01)	0.54 (0.00)	0.56 (0.00)	0.48 (0.00)	0.54 (0.00)	0.53 (0.00)	0.56 (0.00)	
Brain dry mass (g)	0.12 (0.00)	0.12 (0.00)	0.15 (0.00)	0.12 (0.00)	0.10 (0.00)	0.12 (0.00)	0.12 (0.00)	0.13 (0.00)	F*
Kidney wet mass (g)	0.72 (0.08)	0.55 (0.03)	0.96 (0.03)	0.54 (0.03)	0.57 (0.05)	0.49 (0.04)	0.71 (0.02)	0.59 (0.02)	T*** F* L** T×L*
Kidney dry mass (g)	0.20 (0.00)	0.15 (0.00)	0.19 (0.00)	0.15 (0.00)	0.14 (0.00)	0.12 (0.00)	0.16 (0.00)	0.15 (0.00)	T*** L***
Stomach length (cm)	2.92 (0.07)	3.05 (0.03)	3.19 (0.02)	2.70 (0.03)	1.90 (0.06)	2.39 (0.04)	2.39 (0.02)	2.33 (0.02)	L***
Stomach wet mass (g)	0.23 (0.02)	0.49 (0.02)	0.13 (0.00)	0.16 (0.01)	0.36 (0.02)	0.34 (0.02)	0.43 (0.01)	0.30 (0.01)	F*** L*** T×L*** L×F*
Stomach dry mass (g)	0.07 (0.00)	0.07 (0.00)	0.04 (0.00)	0.04 (0.00)	0.09 (0.00)	0.07 (0.00)	0.08 (0.00)	0.07 (0.00)	T* F* L***
SI length (cm)	38.05 (0.69)	31.52 (0.26)	32.41 (0.17)	31.17 (0.28)	29.32 (0.62)	27.97 (0.37)	30.62 (0.18)	27.80 (0.15)	T*** F* L***
SI wet mass (g)	0.15 (0.01)	0.65 (0.01)	0.11 (0.00)	0.13 (0.00)	0.69 (0.02)	0.39 (0.01)	0.75 (0.01)	0.43 (0.00)	F*** L*** T×F*** L×F***
SI dry mass (g)	0.05 (0.00)	0.07 (0.00)	0.04 (0.00)	0.04 (0.00)	0.18 (0.00)	0.06 (0.00)	0.11 (0.00)	0.09 (0.00)	F* L** T×L***
Cecum length (cm)	20.69 (0.49)	16.57 (0.18)	18.22 (0.13)	16.87 (0.20)	17.50 (0.49)	15.28 (0.27)	16.14 (0.13)	13.48 (0.09)	T*** F* L***
Cecum wet mass (g)	0.40 (0.01)	0.55 (0.01)	0.16 (0.00)	0.22 (0.00)	0.59 (0.02)	0.46 (0.01)	0.53 (0.01)	0.41 (0.00)	T* F*** L***
Cecum dry mass (g)	0.09 (0.00)	0.07 (0.00)	0.05 (0.00)	0.06 (0.00)	0.06 (0.00)	0.05 (0.00)	0.07 (0.00)	0.07 (0.00)	
Colon length (cm)	31.34 (1.63)	28.17 (0.65)	28.46 (0.43)	26.56 (0.68)	24.91 (1.52)	23.43 (0.90)	24.43 (0.42)	21.86 (0.33)	T* F* L***
Colon wet mass (g)	0.18 (0.01)	0.43 (0.01)	0.14 (0.00)	0.10 (0.00)	0.38 (0.02)	0.37 (0.02)	0.37 (0.01)	0.29 (0.01)	F* L***
Colon dry mass (g)	0.04 (0.00)	0.05 (0.00)	0.04 (0.00)	0.03 (0.00)	0.06 (0.00)	0.06 (0.00)	0.06 (0.00)	0.06 (0.00)	L*

All values are covariate-adjusted means (S.E.) except body mass. Effects: L, photoperiod; T, temperature; F, diet quality. BAT, brown adipose tissue. SI, small intestine. Interactions are indicated by ×. *P<0.05, **P<0.01, ***P<0.001.

3. Results

3.1. Body mass

Body mass of voles exposed to cold was lower than those exposed to warm ($F=10.77$, $P=0.002$). Short photoperiod ($F=5.27$, $P=0.025$) and low diet quality ($F=10.63$, $P=0.002$) decreased the body mass (Table 2).

3.2. Basal metabolic rate

Voles exposed to cold had a 13% greater BMR than those exposed to warm ($F=14.28$, $P<0.001$). BMR was not significantly affected by photoperiod ($F=2.11$, $P=0.151$) or diet quality ($F=3.01$, $P=0.088$). The interaction between temperature and diet quality was significant ($F=5.52$, $P=0.022$) and showed that animals exposed to cold and fed the high-fiber diet had a greater BMR than did voles fed the low-fiber diet (Table 2).

3.3. Food intake and digestibility

Food intake was significantly affected by temperature ($F=76.40$, $P<0.001$), diet quality ($F=10.54$, $P=0.002$), and photoperiod ($F=5.18$, $P=0.028$). The interaction between photoperiod and diet quality was significant ($F=4.93$, $P=0.032$). Animals housed in the cold ate 90% more dry matter than those in the warm. Voles on the short-day regime showed 17% greater food intake than those on the long-day regime. Food intake was 25% greater in voles fed the high-fiber diet than the low-fiber diet. The significant interaction between temperature and diet quality indicated that the differences in food intake between the two diets were more pronounced under cold than warm conditions (Table 2).

Photoperiod affected digestible energy intake ($F=5.96$, $P=0.019$). Animals on the short-day regime digested more energy than those on the long-day regime. Voles housed in the cold ate 77% more digestible energy than those housed in the warm ($F=50.86$, $P<0.001$). Digestible energy intake was not significantly affected by diet quality ($F=0.54$, $P=0.468$; Table 2).

Voles exposed to the warm showed a 9% greater energy digestibility than those under cold conditions ($F=16.90$, $P<0.001$). There was no significant difference in energy digestibility between the day lengths ($F=0.25$, $P=0.620$). Energy digestibility was 25% greater on the high-fiber than the low-fiber ($F=218.69$, $P<0.001$; Table 2).

3.4. Organ mass

Nearly all measured organ sizes and gut segments were significantly affected by photoperiod, temperature, and diet quality. Animals exposed to cold showed heavier heart, kidneys, and gut segments (Table 3), but their lean body mass was significantly lower than that in warm. Voles fed the high-fiber diet had longer small intestine, cecum, and colon (Table 3) than animals fed the low-fiber diet. The masses of stomach, small intestine, cecum, and colon were greater in voles fed the high-fiber diet than the low-fiber diet. The lean body mass, liver mass, and kidney mass were lower on the high-fiber diet (Table 3).

Voles on the short-day regime had smaller heart and kidneys than those on the long-day regime. The lengths of gut segments were less, but the masses were greater than on the long-day regime. The masses of heart, kidneys and small intestine were significantly affected by the interaction of temperature, photoperiod and diet quality (Table 3).

3.5. BMR and organs

We pooled the data from all treatments and examined the relationships between individual variations in BMR and the mass of each organ. To remove the effect of body mass, we used the residuals of BMR, digestible energy, and organs for analysis. Residuals were calculated according to the regression equations between each parameter and body mass. BMR residuals were significantly correlated with the residuals of dry heart mass ($r=0.337$, $P=0.024$, $n=45$), dry liver mass ($r=0.505$, $P<0.001$, $n=45$), dry kidney mass ($r=0.394$, $P=0.008$, $n=44$), and dry cecum mass ($r=0.315$, $P=0.035$, $n=45$). The relationships between residuals of digestible energy intake and dry masses of liver ($r=0.384$, $P=0.014$, $n=40$), spleen ($r=-0.320$, $P=0.047$, $n=39$), kidneys ($r=0.409$, $P=0.010$, $n=39$), stomach ($r=0.314$, $P=0.048$, $n=40$) and colon ($r=0.361$, $P=0.022$, $n=40$) were also significant. BMR residuals versus dry body masses were significantly correlated with digestible energy intake ($r=0.448$, $P=0.004$, $n=40$).

The preceding analyses did not separate the effects of between-treatment variations (induced by temperature, photoperiod and diet quality) from the effects of within-treatment variation. To determine whether the correlations still exist after removing the effects of differences in body mass and treatments we coded each treatment as a "dummy variable" by assigning 0 for cold and 1 for warm, 0 for short day and 1 for long day, 0 for low-diet quality and 1 for high-diet quality according to Konarzewski and Diamond [14]. We computed the multiple regression equations in which

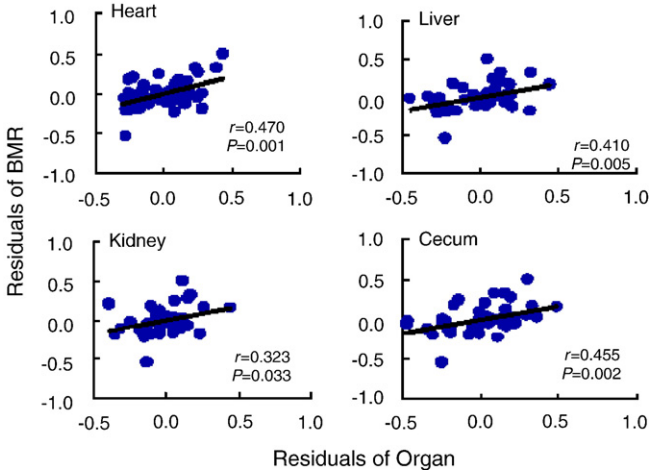

Fig. 1. Residual variation in BMR (ordinate) plotted against residual variation in organ dry masses (abscissa) after accounting for differences in dry body mass, photoperiod, temperature and diet quality.

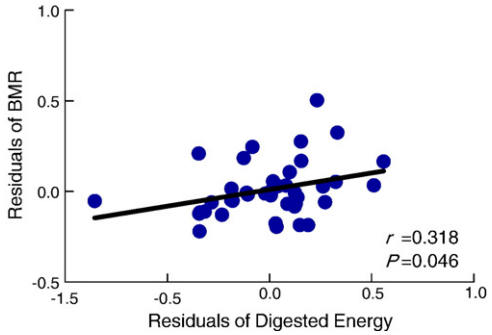

Fig. 2. Residual variation in BMR (ordinate) plotted against residual variation in digestible energy intake (abscissa) after accounting for differences in dry body mass, photoperiod, temperature and diet quality.

BMR, digestible energy intake and dry and wet organ masses were the dependent variables, while dry and wet body mass and the block of dummy variables were the independent variables. The correlations between residuals of BMR from the multiple regressions and residuals of dry mass of heart (r=0.470, P=0.001, n=45), liver (r=0.410, P=0.005, n=45), kidneys (r=0.323, P=0.033, n=44), and cecum (r= 0.455, P=0.002, n=45) were also significant (Fig. 1). The residuals between digestible energy intake and dry mass of kidneys (r=0.422, P<0.001, n=39) and stomach (r=0.419, P=0.007, n=40) were significant as well, but the correlations between residuals of digestible energy intake and residuals of the dry mass of liver, pancreas, and colon disappeared. BMR residuals and dry body masses were significantly correlated with digestible energy intake (r=0.318, P=0.046, n=40; Fig. 2).

4. Discussion

4.1. Temperature

The higher BMR in the cold may have resulted from the greater mass and activity of visceral organs in Brandt's voles. BMR, food intake and digestible energy intake were all higher in the cold than in the warm, which probably stimulated the enlargement of organs such as the liver, heart, and intestine. Hammond and Kristan [24] found that cold exposure caused increases in masses of the small intestine, kidneys and heart. Some of these organs, such as liver and kidneys, have high metabolic activities [25].

Animals with relatively high BMR have relatively large masses of metabolically active tissues and organs. Konarzewski and Diamond [14] acclimated nude house mice (*Mus musculus*) at either 23 °C or 30 °C for 8 days and found that the low temperature mice had higher BMRs and larger liver, intestine, kidneys and heart. Williams and Tieleman [16] indicated that larks in the cold tended to have larger liver, kidneys and intestine, and higher BMR than in warm.

4.2. Diet quality

Voles fed the high-fiber diet had greater gut size and mass [26]. Bozinovic et al. [27] observed that the South American rodent *Octodon degus* compensated for nutritionally poor food by increased gut content volume. Pei et al. [28] also found in Brandt's voles that total length and total gut tissue mass, and the length and tissue mass of the cecum and colon were significantly greater on a higher fiber diet. Nagy and Negus [29] proposed that the greater gut length and mass were necessary to increase or maintain digestive efficiency. The potential benefits of increasing gut size include: (1) an increase in the retention time of food, which increases digestive efficiency if food intake remains constant [30] and maintains the digestive efficiency if food intake increases [31]; and (2) an increase in the rate of digestion and absorption through an increase in the number of nutrient transporters [32]. Pei et al. [28] found in Brandt's voles that total tract mean retention time (MRT) of a solute marker was significantly greater than that of a particle marker on the low-fiber diet, and in the same direction on the high-fiber diet. Examination of marker concentrations in gut organs indicated that the marker was recycled to the stomach by coprophagy [28]. Thus, an increase in gut capacity, selective digesta retention, and recycling of digesta via coprophagy enables Brandt's voles to utilize diets of higher fiber content by maintaining relatively constant intakes of digestible energy on low- and high-fiber diets.

McNab [33] suggested that mammals that utilized foods with relatively low available energy had evolved lower BMR to survive the periods of reduced food quality and availability. Cork [34] hypothesized that animals may lower their basal energy expenditure to survive on diets of poor quality. Available data for small mammals provide only limited support for this hypothesis. For example, Veloso and Bozinovic [11] demonstrated that herbivorous degus maintained on a low-quality diet for 190 days had a significantly lower BMR than on a high-quality diet. Nevertheless, Bozinovic [35] reported that after 10 days of acclimation to high, medium and low dietary fiber, the BMR of degus did not change. Choshniak and Yahav [36] indicated that Levant voles (*Microtus guenteri*) had a low BMR after 35 days of acclimation to a diet of low quality. Koteja [37] reported that deer mice (*Peormyscus maniculatus*) decreased their BMR after 10 days acclimation to low-quality diets. In the present study, we found no decrease in BMR after 3 weeks of acclimation to low food quality in Brandt's voles. Geluso and Hayes [12] found no effect of diet quality on BMR in European starlings. Apparently, acclimation time plays a major role in determining changes in BMR in response to changes in diet quality. This was demonstrated by Veloso and Bozinovic [11]; rodents on low-quality diets maintained a constant BMR through time, but increased BMR on a high-quality diet after 30 days. After 120 days acclimation, individuals on the high-quality diet had even higher BMRs [38].

4.3. Photoperiod

Some species of rodent showed decreases in growth rate and body mass when exposed to short days, and increases when exposure to long days [39]. For example, Siberian hamsters (*Phodopus sungorus*) decreased body mass under short days [7,40]. Knopper and Boily [41] proposed that body mass loss

might be caused by a voluntary decrease in food intake when *P. sungorus* were exposed to short days. Meadow voles (*Microtus pennsylvanicus*) exposed to short days reduced body mass by 20% and food intake by 30% when compared with long day animals [42]. In the present study, Brandt's voles decreased body mass on short days even though food intake and digestible energy intake increased. Zhao and Wang [43] also found that Brandt's voles increased energy intake but decreased body mass under short days because the adaptive thermogenesis (such as nonshivering thermogenesis), as a means of energy expenditure, increased.

The effect of photoperiod on digestible energy intake cannot be explained by the difference in BMR. In the present study, voles on short days had shorter but heavier guts than those on long day. The decrease in gut length was not associated with a decrease in digestive efficiency, and so the increase in digestible energy intake may be due to an increase in nutrient transport numbers per unit mass of intestine. In this way, digestible energy intake can increase and BMR can be maintained stable. Li et al. [9] reported that short days could not induce an increase in BMR in early spring but could in autumn. Our study was carried out in April–May (spring) and we also found no effect of photoperiod on BMR in Brandt's voles.

4.4. Seasonal variations

The changes in organ masses of animals represent phenotypic plasticity that can be used to defend against environmental stresses. The changes we observed in heart, liver, kidneys, and gastrointestinal tract in Brandt's voles are direct responses to environmental stress. BMR variation in this study showed significant correlation with changes in metabolically active organs. In the field, organ sizes (D.H. Wang, unpublished data) and thermogenesis [5] of Brandt's voles also showed significant seasonal variations. Many similar seasonal variations in morphology have been found [44]. Seasonal variations in the length and dry mass of stomach, small intestine, cecum and colon were reported in *Ochotona curzoniae* [45] and *Microtus oeconomus* [46]. These adjustments in organ sizes may play an important role in BMR variation of small mammals in natural environments.

4.5. Assimilation capacity model

The positive correlations between BMR and dry masses of the four organs (heart, liver, kidneys and cecum) in the present study agreed with the findings of Daan et al. [13] on birds. Garland and Else [47] also observed a positive interspecific correlation between standard metabolic rate and liver and heart masses in lizards. The same intraspecific correlation is implicit in the observations that mice with high BMR have disproportionately large organs [14,15]. In our study, digestible energy intake was also related to the masses of stomach and kidneys. These data support the idea that sustained daily energy expenditure and BMR may be linked in a causal manner by the effects of sustained energy demands on the size of those organs that are expensive to maintain in the resting state [48,17,49].

According to the 'assimilation capacity model' of endothermy [17], natural selection acts in favor of increased routine locomotor activity. More active individuals should increase their daily energy expenditure (which must be balanced by digestible energy intake), and ingest more food, consequently the key organs (such as liver, heart, and kidneys) are stimulated to hypertrophy. These organs have high metabolic capacity and therefore can cause the increase in BMR. A high BMR will contribute to a further increase in the daily energy expenditure. Thus animals can self-reinforce BMR and daily energy expenditure again.

In summary, our results show that food intake is sensitive to environmental stress in Brandt's voles. Under conditions of low ambient temperature, low-quality diet and short photoperiod, food intake increased significantly. Increased food intake can directly stimulate increases in the masses of kidneys, liver, and gut, thus can increase digestible energy intake. Because these internal organs have high metabolic capacity, small variations in each organ can result in changes in metabolism at the organismal level. The correlation between daily energy expenditure and BMR is a key element for the 'assimilation capacity model' [17]. When removing the effects of body mass, temperature, photoperiod and diet quality, the correlation between BMR and digestible energy intake were significant and are consistent with the assimilation capacity model of endothermy.

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References

[1] Rosenmann M, Morrison P, Feist D. Seasonal changes in the metabolic capacity of red-backed voles. Physiol Zool 1975;48:303–10.
[2] Wunder BA. Hormonal mechanisms. In: Underwood LS, Tieszen LL, Callahan AB, Folk GE, editors. Comparative mechanisms of cold adaptations. New York: Academic Press; 1979. p. 141–58.
[3] Wang DH, Wang ZW. Seasonal variations in thermogenesis and energy requirements of plateau pika *Ochotona curzoniae* and root vole *Microtus oeconomus*. Acta Theriol 1996;41:225–36.
[4] Bao WD, Wang DH, Wang ZW. Metabolism in four rodent species from Ordos arid environment in Inner Mongolia, China. Folia Zool 2002;51 (suppl 1):3–7.
[5] Wang DH, Wang ZW, Wang YS, Yang JC. Seasonal changes of thermogenesis in Mongolian gerbils (*Meriones unguiculatus*) and Brandt's voles (*Microtus brandti*). Comp Biochem Physiol, Part A 2003;134 (Supplement 1):S96.
[6] Lynch GR. Seasonal changes in thermogenesis, organ weights, and body composition in the white-footed mouse, *Peromyscus leucopus*. Oecologia 1973;13:363–76.
[7] Heldmaier G, Steinlechner S, Rafael J, Visiansky P. Photoperiodic control and effects of melatonin on non-shivering thermogenesis and brown adipose tissue. Science 1981;212:917–9.
[8] Wunder BA. Strategies for, and environmental cueing mechanisms of, seasonal changes in thermoregulatory parameters of small mammals. In: Merritt JF, editor. Winter ecology of small mammalsSpecial Publication Carnegie Museum of Natural History, Pittsburgh; 1984. p. 165–72.

[9] Li QF, Huang CX, Liu XT. Effects of photoperiod and temperature on thermogenesis in Brandt's voles (*Microtus brandti*). Acta Zool Sinica 1995;41:362–9.
[10] Wang DH, Sun RY, Wang ZW, Liu JS. Effects of temperature and photoperiod on thermogenesis in plateau pikas (*Ochotona curzoniae*) and root voles (*Microtus oeconomus*). J Comp Physiol B 1999;169:77–83.
[11] Veloso C, Bozinovic F. Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology 1993;74:2003–10.
[12] Geluso K, Hayes JP. Effects of dietary quality on basal metabolic rate and internal morphology of European starlings (*Sturnus vulgaris*). Physiol Zool 1999;72:189–97.
[13] Daan S, Masman D, Groenewold A. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am J Physiol 1990;259:R333–40.
[14] Konarzewski M, Diamond J. Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 1995;49:1239–48.
[15] Selman C, Lumsden S, Bunger L, Hill W, Speakman JR. Resting metabolic rate and morphology in mice (*Mus musculus*) selected for high and low food intake. J Exp Biol 2001;204:777–84.
[16] William JB, Tieleman BI. Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperature. J Exp Biol 2000;203:3153–9.
[17] Koteja P. Energy assimilation, parental care and the evolution of endothermy. Proc R Soc B 2000;267:479–84.
[18] Ricklefs RE, Konarreski M, Daan S. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. Am Nat 1996;147:1047–71.
[19] Koteja P, Swallow JG, Carter PA, Garland Jr T. Energy cost of wheel running in house mice: implications for coadaptation of locomotion and energy budgets. Physiol Biochem Zool 1999;72:238–49.
[20] Goering HK, Van Soest PJ. Forage fiber analysis. U.S. Dept. Agric. Handb., vol. 379; 1970. 20 pp.
[21] Van Soest PJ, Robertson JB, Lewis BA. Methods of dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. J Dairy Sci 1991;74:3583–97.
[22] Freehling MD, Moore J. A comparison of two techniques for measuring gut length. J Wildl Manage 1987;51:101–8.
[23] SPSS. SPSS. Beijing: Publishing House of Electronics Industry; 1988.
[24] Hammond KA, Kristan DM. Responses to lactation and cold exposure by deer mice (*Peromyscus maniculatus*). Physiol Biochem Zool 2000;73: 547–56.
[25] Krebs HA. Body size and tissue respiration. Biochim Biophys Acta 1950;4:249–69.
[26] Gross JE, Wang Z, Wunder BA. Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ocbrogaster*. J Mammal 1985;66:661–7.
[27] Bozinovic F, Novoa FF, Sabat P. Feeding and digesting fiber and tannins by an herbivorous rodent *Octodon degus* (Rodentia: Caviomorpha). Comp Biochem Physiol A 1997;118:625–30.
[28] Pei YX, Wang DH, Hume ID. Selective digesta retention and coprophagy in Brandt's vole (*Microtus brandti*). J Comp Physiol B 2001;171:457–64.
[29] Nagy TR, Negus NC. Energy acquisition and allocation in male collared lemmings (*Dicrostonyx groenlandicus*): effects of photoperiod, temperature, and diet quality. Physiol Zool 1993;69:555–9.
[30] Sibly RM. Strategies in digestion and defecation. In: Townsend CR, Calow P, editors. Physiological ecology. Blackwell: Oxford; 1981. p. 109–39.
[31] Hammond KA, Wunder BA. The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. Physiol Zool 1991;64:541–67.
[32] Karasov WH, Diamond JM. Adaptive regulation of sugar and amino acid transport by vertebrate intestine. Am J Physiol 1983;245:G443–62.
[33] McNab BK. The influence of food habits on the energetics of eutherian mammals. Ecol Monogr 1986;56:1–19.
[34] Cork SJ. Digestive constraints on dietary scope in small and moderately-small mammals: how much do we really understand? In: Chivers D, Langer P, editors. The digestive system in mammals: food, form and function. Cambridge: Cambridge University Press; 1994. p. 337–69.
[35] Bozinovic F. Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. J Mammal 1995;76:627–37.
[36] Choshniak I, Yahav S. Can desert rodents better utilize low quality roughage than their non-desert kindred. J Arid Environ 1987;12:241–6.
[37] Koteja P. Limits to the energy budget in a rodent, *Peromyscus maniculatus,* does gut capacity set the limit? Physiol Zool 1996;69:994–1020.
[38] Veloso C, Bozinovic F. Interplay between acclimation time and diet quality on basal metabolic rate in females of degus *Octodon degus* (Rodentia: Octodontidae). J Zool Lond 2000;252:531–3.
[39] Polly B, Henk V, Serge D. Effect of photoperiod on body mass, daily energy intake and energy expenditure in young rats. Physiol Behav 1997;62: 913–9.
[40] Gunduz B, Stetson MH. Effects of photoperiod, pinealectomy, and melatonin implants on testicular development in juvenile Siberian hamsters (*Phodopus sungorus*). Biol Reprod 1994;51:1181–7.
[41] Knopper LD, Boily P. The energy budget of captive Siberian hamsters, *Phodopus sungorus*, exposed to photoperiod changes: mass loss is caused by a voluntary decrease in food intake. Physiol Biochem Zool 2000;73:517–22.
[42] Dark J, Zucker I. Short photoperiods reduced winter energy requirements of the meadow vole. *Microtus pennsylvanicus*. Physiol Behav 1983;31: 699–702.
[43] Zhao ZJ, Wang DH. Short photoperiod influences energy intake and serum leptin level in Brandt's voles (*Microtus brandtii*). Horm Behav 2006;49: 463–9.
[44] Bozinovic F, Novoa FF, Veloso C. Seasonal changes in energy expenditure and digestive tract of *Abrothrix andinus* in the Andes range. Physiol Zool 1990;63:1216–31.
[45] Wang DH, Wang ZW. Seasonal variations in digestive tract morphology in plateau pikas (*Ochotona curzoniae*) on the Qinghai–Tibetan Plateau. Acta Zool Sinica 2001;47:495–501.
[46] Wang DH, Wang ZW, Sun RY. Seasonal variations in digestive tract morphology in root voles. Acta Theriol Sinica 1995;15:53–9.
[47] Garland Jr T, Else PL. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. Am J Physiol 1987;252: R439–49.
[48] Hammond KA, Diamond JM. Maximal sustained energy budgets in humans and animals. Nature 1997;386:457–62.
[49] Speakman JR, Johnson MS. Relationships between resting metabolic rate and morphology in lactating mice: what tissues are the major contributors to resting metabolism? In: Heldmaier G, Klingenspor M, editors. Life in the cold. Berlin: Springer-Verlag; 2000. p. 479–86.