Effects of diet quality on energy budgets and thermogenesis in Brandt's voles

Zhi-Jun Zhao [a,b,c], De-Hua Wang [a,*]

[a] *State Key Laboratory of Integrated Management for Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China*
[b] *School of Agricultural Science, Liaocheng University, Liaocheng, Shandong, 252059, China*
[c] *Graduate School of the Chinese Academy of Sciences, Beijing 100039, China*

Abstract

Food quality and availability play an important role in an animal's life history. The aim of this study was to examine the effect of diet quality [high-fiber diet (HF) or low-fiber diet (LF)] on energy budgets and thermogenesis in Brandt's voles (*Lasiopodomys* (*Microtus*) *brandtii*). Dry matter intake and gross energy intake increased and digestibility decreased in HF voles compared with LF voles, while the digestible energy intake was similar for both HF and LF voles. Nonshivering thermogenesis (NST) decreased in HF voles, while LF voles kept stable; no significant differences were detected in basal metabolic rate (BMR), BAT uncoupling protein 1 (UCP1) content and the levels of serum thyroid hormones (T3 and T4) between HF and LF voles. Although there were no differences in body fat content and serum leptin concentrations between HF and LF voles, serum leptin concentrations in HF voles were reduced to nearly half as those seen in LF voles after 4-weeks acclimation. These results support the hypothesis that Brandt's voles can compensate the poor quality diet physiologically by the means of increasing food intake and decreasing thermogenesis.
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1. Introduction

The efficiency of energy intake and energy allocation is critical to the survival and ecological success for the mammals living in seasonal environments (Bozinovic, 1992; Veloso and Bozinovic, 1993). Many wild small mammals show seasonal variations in energy budgets (Bartness et al., 1989; Voltura, 1997; Li and Wang, 2005a,b) and must consume low-quality or high-fiber food from necessity rather than from choice during nutritional bottlenecks (Bozinovic, 1995). When fed high-fiber diet, small mammals could increase energy intake to compensate the low digestibility caused by high-fiber content in diet (Karasov and Diamond, 1988; Bozinovic et al., 1997; Owl and Batzli, 1998; Juana et al., 2006).

Further, animals fed poor quality diets will reduce the basal metabolic rate (BMR) (McNab, 1986; Veloso and Bozinovic, 1993; Cork, 1994; Silva et al., 2004) and thus can reduce the

energy expenditure, i.e. the hypothesis that small mammals lower BMR to survive on a high-fiber diet, such as degus (*Octodon degus*) (Veloso and Bozinovic, 1993) and Levant vole (*Microtus guenteri*). McNab (1986) also proposed that mammals eating low-quality food might evolve lower rate of basal metabolism. However, the desert gerbil (*Meriones crassus*) (Choshniak and Yahav, 1987) and leaf-eared mouse (*Phylotis darwini*) (Bozinovic and Novoa, 1997) did not show differences in metabolic rate when fed with different quality of diet.

Nonshivering thermogenesis (NST) is also one of the means of energy expenditures and important for survival in small mammals. Several small non-hibernating mammals show seasonal changes in NST which is higher in winter and lower in summer (Heldmaier et al., 1981; Wunder, 1984; Wang et al., 2003a; Li and Wang, 2005a,b). It has been shown that short photoperiod and cold can enhance the thermogenic capacity in many rodent species (Heldmaier et al., 1981; Wunder, 1984; Wang et al., 2003a; Li and Wang, 2005a,b). However, the role of low-quality food in NST regulation is still not clear.

Leptin, an important hormone secreted mainly from adipose tissue (Zhang et al., 1994), plays an important role in energy balance and body mass in seasonal small mammals (Klingenspor

* Corresponding author. Institute of Zoology, Chinese Academy of Sciences, 25 Beisihuan Xilu, Zhongguancun, Haidian, Beijing 100080, People's Republic of China. Tel.: +86 10 62613511; fax: +86 10 62565689.
E-mail address: wangdh@ioz.ac.cn (D.-H. Wang).

et al., 1996a, 2000; Li et al., 2004). Leptin can cause the decrease in food intake and loss in body weight (Halaas et al., 1995; Shannon and Jean-Michel, 2000) and was considered to be an adipostatic signal (Zhang et al., 1994; Halaas et al., 1995; Pelleymounter et al., 1995; Klingenspor et al., 1996a). Environmental factors, such as photoperiod and temperature, have been found to affect the circulating leptin concentrations in some small mammals (Klingenspor et al., 1996a, 2000; Li et al., 2004). Nevertheless, very little is known about the role of leptin in energy budgets in wild herbivorous small mammals exposed to high-fiber food.

Brandt's voles (*Lasiopodomys* (*Microtus*) *brandtii*) are typical steppe herbivores that mainly inhabit the Inner Mongolia grasslands of China, Mongolia, as well as the region of Baikal in Russia (Zhang and Wang, 1998). In Inner Mongolia the annual average temperature is −0.4 °C, the average temperature in the coldest month is −22.3 °C and in the warmest month is 18.8 °C, with extreme minimum temperatures below −40 °C (Chen, 1988; Wang et al., 2000). Brandt's voles feed primarily on stems and leaves of *Aneurolepdium chinense* and *Melissitus ruthenica* with relative low-fiber content (account for 40% and 29% in their diet, respectively) in summer, and mainly on the root of *Artemisia frigida* with relative high-fiber content (account for 50–90% in their food storage) and few invertebrates (less than 1% in storage even in the year of locust breaking out) in winter and early spring (Zhang and Wang, 1998). To survive the harsh environment, Brandt's voles showed seasonal variations in energy budgets, thermogenesis and body mass (Wang et al., 2003b; Li and Wang, 2005a). Short photoperiod and/or cold induced increases in energy intake, BMR and NST, and decreases in body mass, body fat mass and serum leptin levels (Li et al., 1995, 2001; Zhao and Wang, 2005, 2006). In contrast, little is known about the role of diet quality on morphology and physiology, especially on energy budgets and thermogenesis in Brandt's voles. The purpose of the present study was to test the hypothesis that small mammals, showing seasonal changes in body mass and thermogenesis, can compensate for the poor quality diet physiologically. We predicted that Brandt's voles, when exposed to high-fiber content diet, will increase food intake and decrease the digestibility and energy expenditure associated with BMR and NST to match their energy demands. Furthermore, the body mass, body fat content and serum leptin levels will be reduced as well.

2. Materials and methods

2.1. Subjects

Brandt's voles (*L.* (*Microtus*) *brandtii*) were obtained from our laboratory-breeding colony. This colony was originally trapped from Inner Mongolian grasslands in 1999. Food (standard rabbit pellet chow; Beijing KeAo Feed Co.) and water were provided *ad libitum* and temperature was constant at 23± 1 °C with a 12L:12D photoperiod (light:dark, lights on 0800). Voles were weaned at 25 days of age and then housed with same-sex siblings in plastic cages (30×15×20 cm) that contained fresh sawdust bedding. Adult voles (80–95 days of age) were singly housed at least two weeks before diet acclimation.

The experiments were carried out from November 2004 to March 2005.

2.2. Experiment 1

In order to determine the effects of high-fiber diet acclimation on body mass, BMR, NST, and energy budgets, 20 voles were randomly divided into one of two groups that were acclimated to either standard rabbit pellet chow (low-fiber group, 5 males and 5 females) or to high-fiber diet (high-fiber group, 5 males and 5 females) for 10 weeks. The compositions for the two kinds of diet were presented in Table 1. Body mass was recorded every three days, and BMR, NST and energy budgets were determined at the start (week 0) and at a week intervals during diet acclimation.

2.2.1. Energy intake

Food intake was measured in metabolic cages (Liu et al., 2003; Zhao and Wang, 2006). Food was provided quantitatively and food residues and feces were collected from each subject over the three days before the acclimation began and over the last three days of each week during diet acclimation (total 11 measurements), and separated after they were dried at 60 °C to constant mass (Liu et al., 2002, 2003). Energy contents of the food and feces were determined by a Parr 1281 oxygen bomb calorimeter (Parr Instrument, USA). Gross energy intake (GEI), digestible energy intake (DEI) and apparent digestibility of energy (hereafter referred to as digestibility) were calculated according to Grodzinski and Wunder (1975) and Liu et al. (2002, 2003), and as follows:

$$GEI\ (kJ/d) = dry\ matter\ intake\ (DMI)(g/d)$$
$$\times\ energy\ content\ of\ food\ (kJ/g);$$
$$DEI\ (kJ/d) = GEI - (dry\ mass\ of\ feces\ (g/d)$$
$$\times\ energy\ content\ of\ feces\ (kJ/g));$$
$$Digestibility(\%) = DEI/GEI \times 100\%.$$

2.2.2. Metabolic trial

We measured BMR and NST in a closed-circuit respirometer (Gorecki, 1975; Wang et al., 2000), as described by Zhao and Wang (2005). In brief, the metabolic chamber temperature was controlled within ±0.5 °C by a water bath. Water and carbon dioxide in the chamber were absorbed with silica gel and KOH, respectively. BMR was measured at the temperature of 30± 0.5 °C which is within the thermoneutral zone for this species (27.5–32.5 °C) (Wang et al., 2003b). All subjects were fasted

Table 1
Compositions of high- and low-fiber diet based on dry mass

	High-fiber diet (HF)	Low-fiber diet (LF)
Crude fat (%)	6.2	3.9
Crude protein (%)	20.8	19.4
NDF (%)	23.1	35.5
ADF (%)	12.5	21.4
Ash (%)	10.0	10.5
Caloric value (kJ/g)	17.5	17.3

Note: NDF, neutral detergent fiber; ADF, acid detergent fiber.

3 h before being put into the chamber. After 1 h stabilization in the metabolic chamber, oxygen consumption was measured for a further 1 h at 5-min intervals. Two continuous stable minimum recordings were taken to calculate BMR. Maximum NST was defined as the maximum metabolic response to norepinephrine (NE) (Heldmaier et al., 1982), and was determined following a mass-dependent subcutaneous injection of NE at 25 ± 1 °C. The dosage of NE (Shanghai Harvest Pharmaceutical Co. LTD) was calculated according to Heldmaier (Heldmaier, 1971). Oxygen consumption was recorded for 1 h at 5-min intervals, and two continuous stable maximal recordings were used to calculate maximum NST. All measurements were made between 1000 and 1700 h.

2.3. Experiment 2

Based on the results of changes in body mass, BMR, NST and energy budgets in Experiment 1, the second experiment was designed to examine the changes of body composition and digestive tracts in the course of high-fiber diet acclimation. We further tested the characteristics of circulating leptin and BAT UCP1 in the voles acclimated to high-fiber diet. 40 adult voles were randomly divided into four major groups of 10 each. Each group (5 males and 5 females) was performed by one of four treatments: 1) LF-4W, low-fiber diet for 4 weeks; 2) HF-4W, high-fiber diet for 4 weeks; 3) HF-7W, high-fiber diet for 7 weeks; and 4) HF-10W, high-fiber diet for 10 weeks. After 4, 7 and 10 weeks, the voles (total 4 groups) were sacrificed, respectively, by decapitation between 0900–1100 h.

2.3.1. Serum leptin levels and thyroid hormones

Trunk blood was collected. Serum was separated from each blood sample and stored at −75 °C for leptin and thyroid hormones measurement. Serum leptin levels were quantified by radio-immunoassay (RIA) using the Linco ^{125}I Multi-species Kit (Cat. No. XL-85K, Linco Research Inc.). The lower and upper limits of the assay kit were 1 and 50 ng/ml and the inter- and intra-assay variations were <3.6% and 8.7%, respectively.

Serum thyroid hormones (tri-iodothyronine, T_3 and thyroxine, T_4) were determined by radio-immunoassay using RIA kits

from China Institute of Atomic Energy. Intra- and inter-assay coefficients of variation were 2.4% and 8.8% for the T_3, and 4.3% and 7.6% for T_4, respectively.

2.3.2. Measurements of BAT cytochrome c oxidase (COX) activity and UCP1 content

After trunk blood was collected, scapular BAT was removed and weighted, mitochondrial protein was prepared as described in Wiesinger et al. (1989). Mitochondrial protein content was measured by the Folin phenol method (Lowry et al., 1951) with bovine serum albumin as standard. COX activity was determined polarographically with oxygen electrode units (Hansatech Instruments LTD., England) (Sundin et al., 1978).

Five µl BAT mitochondrial protein (20 µg per lane) was run on an SDS-polyacrylamide gel (3% stacking gel and 12.5% running gel), and then transferred to a nitrocellulose membrane (Hybond-C, Amersham Biosciences, UK). To check for the efficiency of protein transfer, gels and nitrocellulose membranes were stained after transferring with Coommassie brilliant blue and Ponceau red, respectively. After blocking against non-specific binding by 5% skim milk at 4 °C overnight, the membrane was incubated with a rabbit polyclonal anti-hamster UCP1 (1:5000), and goat anti-rabbit (1:5000) as the secondly antibody (Klingenspor et al., 1996b). The enhanced chemoluminescence kit (ECL, Amersham Biosciences) was used for detection. UCP1 content was expressed as relative units (RU) and quantified with Scion Image Software (Scion Corporation).

2.3.3. Carcass and body fat content

After scapular BAT was removed, we first extracted the gastrointestinal tract (stomach, small intestine, colon, and cecum), and then the heart, lung, pancreas, spleen, kidneys, and urinary bladder. Stomach, small intestine, colon, and cecum were weighed with and without content (to 1 mg), and its size was measured (to 0.1 cm), respectively. All organs and the remaining carcass were weighed (to 1 mg and 0.1 g, respectively) to determine wet mass, dried in an oven at 60 °C to a constant mass, and then weighted again (dry mass). Total body fat was extracted from the dried carcass by ether extraction in a Soxhlet apparatus.
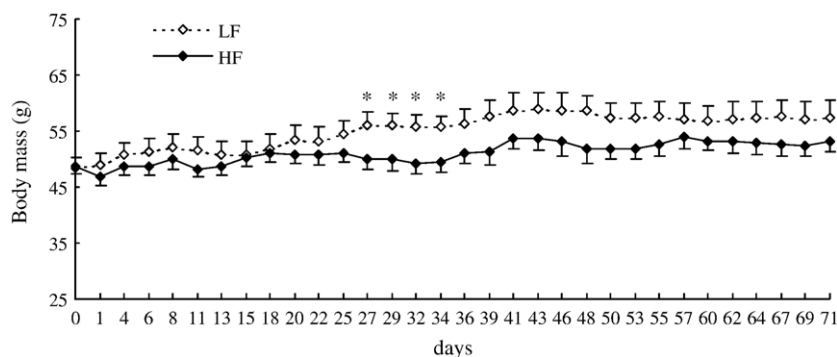

Fig. 1. Changes of body mass in Brandt's voles responding to high (HF; high-fiber diet) and low-fiber diet (LF). From day 27 to 34, HF voles had significantly lower body mass compared to LF voles. Data are mean ± SE. *: $p < 0.05$.
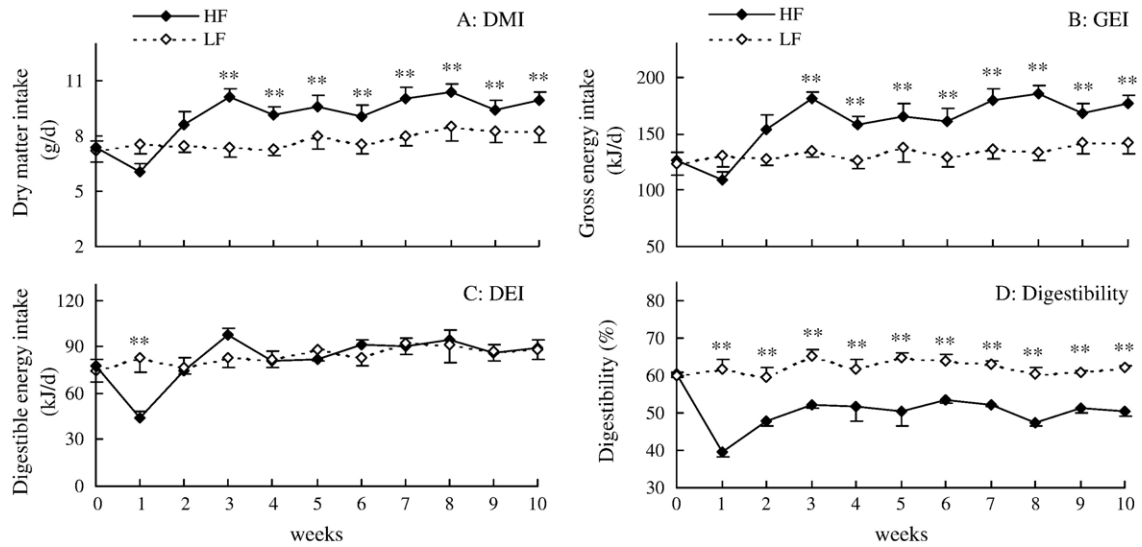
Fig. 2. Changes of dry matter intake (DMI; panel A), gross energy intake (GEI, panel B), digestible energy intake (DEI, panel C) and digestibility (panel, D) of Brandt's voles acclimated to high (HF; high-fiber diet) or low-fiber diet (LF). On week 3 and thereafter, HF voles had significantly higher DMI and GEI compared to LF voles. HF voles had significantly lower DEI than LF voles on week 1. Digestibility was significantly lower in HF voles than that in LF voles. Data are mean±SE. **: $p < 0.01$.

2.4. Statistical analysis

Data were analyzed by using the SPSS software package (10.0). Distributions of all variables were tested for normality using the Kolmogorov–Smirnov test. In Experiment 1, we use a two-way analysis (diet by sex) of variance (ANOVA) or co-variance (ANCOVA) with body mass as a covariance to evaluate the effects of diet and sex on body mass, energy parameters, BMR and NST at each time point. Further, Tukey's HSD post-hoc tests were also used to analyze changes of the variables above over the course of diet acclimation. In Experiment 2, BAT COX activity, UCP1 content and serum thyroid hormones, and organs wet and dry mass, body fat mass and serum leptin concentration were analyzed by a two-way ANOVA or ANCOVA (with carcass mass as a covariate), followed by Tukey's HSD post-hoc tests. Finally, Pearson's correlation was carried out to examine the correlation between body fat mass and serum leptin levels. Statistic significance was assumed at $p < 0.05$.

3. Results

There were no significant sex differences in all of the measured parameters, therefore data from male and female voles were combined.

3.1. Experiment 1

3.1.1. Body mass

There were no differences in body mass (BM, g) (day 0, HF, 48.6±1.3; LF, 48.4±2.0; $F_{(1,16)} = 0.015$, $p > 0.05$; Fig. 1) between LF and HF voles prior to dietary acclimation. However, HF voles only showed a statistically significant lower BM than LF voles from day 27 to day 34 (day 27, HF, 50.1±1.7; LF, 56.1±2.3; $F_{(1,16)} = 4.685$, $p < 0.05$), although BM was slightly low in HF voles to day 71. During the acclimation, BM in LF

voles increased before day 27 by 15.8% compared to the baseline measurement ($F_{(12, 108)} = 4.974$, $p < 0.05$) and thereafter kept relatively stable to day 71 ($F_{(18, 162)} = 0.863$, $p > 0.05$). For HF voles, BM showed significant differences in the course of acclimation ($F_{(31,279)} = 6.331$, $p < 0.01$), especially from day 0 to day 39 ($F_{(17, 153)} = 2.088$, $p < 0.01$; Fig. 1). The interaction between diet and time was significant ($F_{(31, 558)} = 1.505$, $p < 0.05$).

3.1.2. Energy intake

Prior to acclimation, DMI (g/d; Fig. 2A), GEI (kJ/d; Fig. 2B), DEI (kJ/d; Fig. 2C) and digestibility (%; Fig. 2D) were similar between LF and HF voles (week 0, DMI, $F_{(1, 15)} = 0.045$, $p > 0.05$; GEI, $F_{(1, 15)} = 0.045$, $p > 0.05$; DEI, $F_{(1, 15)} = 0.065$, $p >$
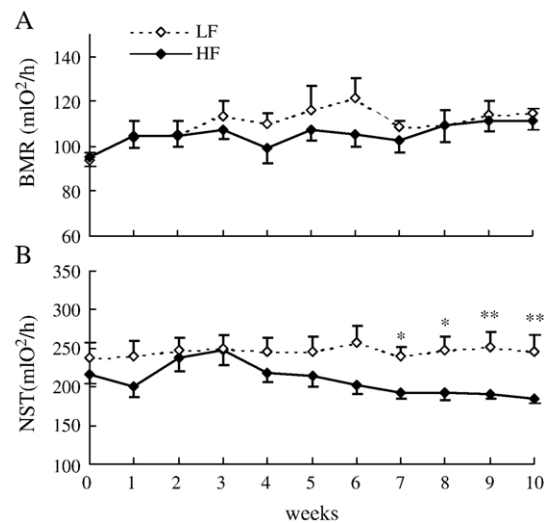

Fig. 3. Effects of diet on the basal metabolic rate (BMR) and nonshivering thermogenesis (NST)+ in Brandt's voles acclimated to high (HF; high-fiber diet) and low-fiber diet (LF). On week 7, HF voles had significantly lower NST compared to LF voles. Data are mean±SE. *: $p < 0.05$; **: $p < 0.01$.

Table 2
Mitochondrial protein (MP) content, cytochrome *c* oxidase (COX) activity and uncoupling protein 1 (UCP1) content of brown adipose tissue (BAT), and T3 and T4 concentrations in Brandt's voles fed high-fiber diet (HF) or low-fiber diet (LF) (mean±SE)

	LF-W4	HF-W4	HF-W7	HF-W10	F	*p*
BAT mass (g)	0.221±0.017	0.146±0.010	0.181±0.015	0.156±0.011	3.021	ns
MP content						
(mg/g tissue)	5.02±0.61	4.56±0.41	4.77±0.43	5.22±0.40	0.381	ns
(mg in whole tissue)	1.15±0.19	0.68±0.10	0.84±0.08	0.82±0.09	2.507	ns
COX activity						
(nmol/min/mg Mt protein)	101.16±17.43	67.95±9.27	62.00±6.82	89.42±5.67	2.861	0.05
(nmol/min/g tissue)	440.50±63.08	312.83±49.08	286.97±35.86	449.28±16.82	2.507	ns
(nmol/min in whole tissue)	97.59±17.64[a]	46.88±9.06[b]	50.78±5.88[b]	70.02±5.56[ab]	3.585	<0.01
UCP1 (relative unit)	1.00±0.08	0.80±0.05	0.84±0.11	0.75±0.05	1.843	ns
Serum T_3 (ng/mL)	1.11±0.05	0.89±0.13	0.77±0.08	0.83±0.11	2.283	ns
Serum T_4 (ng/mL)	24.74±4.60	20.17±3.25	15.29±2.05	19.52±2.86	1.358	ns

Note. LF-W4, low-fiber diet for 4 weeks; HF-W4, W7 and W10, high-fiber diet for 4, 7 and 10 weeks respectively. Different letters in the same row indicate significant differences ($p<0.05$) in measurements among the LF-W4, HF-W4, HF-W7 and HF-W10 groups.

0.05; Digestibility, $F_{(1, 15)}=0.202$, $p>0.05$). DMI and GEI in HF voles decreased slightly in the first week and then increased markedly. After 3 weeks, DMI and GEI in HF voles were significantly higher than LF voles and was kept thereafter (week 3, DMI, $F_{(1, 15)}=14.449$, $p<0.01$; GEI, $F_{(1, 15)}=25.910$, $p<0.01$). DEI decreased in HF voles which was lower than LF voles in the first week (week 1, $F_{(1, 15)}=6.944$, $p<0.01$), and then increased to the level of LF voles at week 2 and were kept to the end of acclimation (week 2, $F_{(1, 15)}=0.011$, $p>0.05$). There was a significant effect of high-fiber diet on digestibility. Digestibility decreased by 34.4% in HF voles in the first week which was lower than that in LF voles (week 1, $F_{(1, 15)}=91.809$,

$p<0.001$), then slightly increased but still lower than LF voles in week 2 and thereafter (week 2, $F_{(1, 15)}=17.055$, $p<0.001$; Fig. 2D). The interactions of diet and time were significant for energetic parameters (DMI, $F_{(10, 170)}=3.194$, $p<0.01$; GEI, $F_{(10, 170)}=3.170$, $p<0.01$; DEI, $F_{(10, 170)}=2.756$, $p<0.05$; digestibility, $F_{(10, 180)}=4.311$, $p<0.001$).

3.1.3. BMR and NST

There were no differences in BMR and NST before the dietary acclimation between LF and HF voles (week 0, BMR, $F_{(1, 15)}=0.152$, $p>0.05$; NST, $F_{(1, 15)}=1.042$, $p>0.05$; Fig. 3A). BMR did not show any difference between LF and HF voles throughout the

Table 3
Morphometrics of digestive tract in Brandt's voles fed high-fiber diet (HF) or low-fiber diet (LF) (mean±SE)

	LF-W4	HF-W4	HF-W7	HF-W10	*F*	*p*
Stomach						
Size (cm)	2.2±0.2	2.1±0.2	2.4±0.1	2.1±0.1	1.025	ns
Mass with content (mg)	1069.8±172.3	1074.6±185.6	1430.9±196.7	953.6±88.3	1.623	ns
Wet mass (mg)	333.1±12.0	355.4±12.2	366.2±11.0	372.3±10.9	1.304	ns
Dry mass (mg)	72.6±2.9	68.7±4.0	76.5±2.2	79.8±3.2	2.282	ns
Small intestine						
Size (cm)	27.3±0.9	26.8±0.8	25.5±0.6	26.7±1.0	0.662	ns
Mass with content (mg)	1919.6±69.5	1746.4±106.9	1939.1±76.0	1839.9±130.9	0.644	ns
Wet mass (mg)	634.2±24.9	571.3±50.0	635.6±42.7	570.7±32.0	0.565	ns
Dry mass (mg)	129.1±11.1	97.5±6.3	131.2±9.9	103.9±7.3	1.983	ns
Colon						
Size (cm)	22.0±0.7	23.6±0.8	23.0±0.5	23.0±0.7	0.316	ns
Mass with content (mg)	780.9±42.7[b]	1232.4±81.4[a]	1014.9±47.3[a]	1138.6±65.4[ab]	5.513	<0.001
Wet mass (mg)	385.6±17.0	471.8±46.7	464.0±50.5	402.5±15.7	0.620	ns
Dry mass (mg)	71.4±4.0	94.4±18.4	71.8±5.3	72.2±5.8	0.763	ns
Cecum						
Size (cm)	13.6±0.4	14.8±0.5	14.8±0.5	14.2±0.4	0.743	ns
Mass with content (mg)	3204.4±349.1[b]	5539.1±396.8[a]	4794.5±250.5[a]	4796.5±247.3[a]	3.936	<0.01
Wet mass (mg)	560.8±22.8	637.8±51.9	645.1±37.6	598.7±52.1	1.674	ns
Dry mass (mg)	88.8±5.7	93.9±7.6	109.5±9.3	86.1±4.9	2.489	ns
Total digestive tract						
Size (cm)	65.0±1.8	67.2±2.0	65.6±1.1	66.0±1.7	0.282	ns
Mass with content (mg)	6974.7±475.2[b]	9592.5±669.8[a]	9179.4±446.2[a]	8729.0±355.0[ab]	2.070	<0.05
Wet mass (mg)	1913.7±46.4	2036.3±111.2	2110.9±75.6	1944.0±83.8	0.835	ns
Dry mass (mg)	361.9±18.6	354.5±19.6	389.0±18.5	339.0±10.1	1.466	ns

Note. LF-W4, low-fiber diet for 4 weeks; HF-W4, W7 and W10, high-fiber diet for 4, 7 and 10 weeks respectively. Different letters in the same row indicate significant differences ($p<0.05$) in measurements among the LF-W4, HF-W4, HF-W7 and HF-W10 groups.

acclimation (week 10, BMR, $F_{(1, 15)}=0.814$, $p>0.05$). However, NST decreased slightly in HF voles in week 1 and was significantly lower than LF voles on week 7, and were kept thereafter (week 7, $F_{(1, 15)}=9.213$, $p<0.001$; Fig. 3B). No significant interaction of diet and time were detected for BMR and NST (BMR, $F_{(10, 170)}=0.566$, $p>0.05$; NST, $F_{(10, 170)}=1.186$, $p>0.05$).

3.2. Experiment 2

3.2.1. BAT COX activity and UCP1 content

There were no significant differences in BAT mass (g) and mitochondrial protein content (mg/g) among the LF-W4 voles and HF-W4, W7 and W10 voles (Table 2). BAT COX activity (nmol/min in whole tissue) was lower in the HF-W4 and HF-W7 voles than that in LF-W4 voles (Table 2). BAT UCP1 content tended to decrease after feeding the high-fiber diet (by 25% after 10-weeks) and the changes were not statistically significant (Table 2).

3.2.2. Serum thyroid hormones

Serum thyroid hormone concentrations were not affected significantly by high-fiber diet acclimation in the voles. No differences in serum T_3 and T_4 concentrations were found among the LF voles and the voles followed by the high-fiber diet treatment (Table 2).

3.2.3. Digestive tracts

Dry mass of stomach was higher in HF-W7 and HF-W10 voles than LF-W4 voles and the size, mass with content and wet mass of stomach were similar between HF and LF voles. There were no significant differences in size, mass with content, wet and dry mass of small intestine. Mass with content of colon was greater in HF than LF voles, and was nearly 60% higher in HF-W4 voles compared to LF-W4 voles. Mass with content of cecum was significantly affected by high-fiber diet acclimation and was higher by 73% in HF-W4 voles than LF-W4 voles. Mass with content of total digestive tracts was greater in HF than LF voles (Table 3).

3.2.4. Body compositions and serum leptin concentrations

Wet and dry mass of carcass was lower in HF voles than LF voles ($p<0.01$). Body fat mass (g) was lower by 41% in HF-W4 voles than LF-W4 voles. Similar to body fat mass, serum leptin concentrations in HF-W4 voles were reduced to nearly half than that seen in LF-W4 voles. However, there were no significant differences in body fat mass and content (%), and serum leptin concentrations among the four groups (Table 4). Furthermore, serum leptin concentrations were positively correlated with body fat mass ($r=0.628$, $p<0.001$). Wet and dry organ mass did not show significant changes by diet treatment except for wet mass of lungs (Table 4).

4. Discussion

The present study showed that Brandt's voles can physiologically regulate the energy budgets and thermogenesis in response to the changes in food quality. DMI and GEI increased in HF voles and digestibility was reduced while digestible

Table 4
Body mass, body fat content, organ mass and serum leptin concentrations in Brandt's voles fed high-fiber diet (HF) or low-fiber diet (LF) (mean±SE)

	LF-W4	HF-W4	HF-W7	HF-W10	F	p
Sample size	10	10	10	10		
Body mass (g)	59.3±2.1[a]	46.9±2.1[b]	50.7±2.1[b]	51.8±1.9[ab]	6.511	<0.05
Carcass mass (g)						
Wet	46.0±2.0[a]	31.9±1.8[b]	36.8±1.6[b]	35.8±1.7[b]	11.367	<0.001
Dry	19.5±0.8[a]	12.4±1.1[b]	15.9±0.7[ab]	14.4±1.0[b]	10.078	<0.001
Body fat content						
g	8.7±0.5	5.1±0.9	7.4±0.5	6.3±0.7	1.001	ns
%	19.1±1.4	15.4±2.1	20.3±1.4	17.2±1.6	1.216	ns
Serum leptin levels (ng/ml)	3.13±0.44	1.80±0.12	2.05±0.24	2.00±0.24	1.587	ns
Organ wet mass (mg)						
Liver						
Wet	2101.1±140.9	1794.1±116.9	1964.2±127.0	1795.4±67.5	0.609	ns
Dry	750.6±86.2	729.4±62.8	624.0±46.1	571.3±31.3	2.862	ns
Heart						
Wet	251.5±8.4	194.1±8.4	212.9±9.0	211.9±6.5	2.165	ns
Dry	63.5±2.3	48.1±2.4	55.6±2.7	53.1±1.7	2.166	ns
Lung						
Wet	296.1±17.2[ab]	255.0±19.1[b]	275.3±18.0[ab]	353.0±31.3[a]	3.470	<0.05
Dry	83.3±9.5	72.9±13.4	86.4±11.0	96.8±14.9	0.629	ns
Spleen						
Wet	40.9±4.9	37.5±4.5	30.7±1.8	38.5±3.9	1.000	ns
Dry	10.9±1.7	10.4±1.1	10.9±1.0	8.8±1.1	0.564	ns
Kidneys						
Wet	413.4±67.9	463.5±22.3	487.8±28.7	462.3±16.4	0.779	ns
Dry	113.8±18.6	122.0±6.4	135.2±8.8	128.6±4.9	0.831	ns

Note. LF-W4, low-fiber diet for 4 weeks; HF-W4, W7 and W10, high-fiber diet for 4, 7 and 10 weeks respectively. Different letters in the same row indicate significant differences ($p<0.05$) in measurements among the LF-W4, HF-W4, HF-W7 and HF-W10 groups.

energy intake kept stable. Although both body fat mass and serum leptin levels tended to decrease, they didn't reach to the significant level. NST was lower in HF than LF voles and, however, no differences were detected in UCP1 content and serum thyroid hormones levels, BMR and the inner organs.

4.1. Energy intake and digestive tract morphology

The present results showed that dry matter intake and gross energy intake were slightly decreased and digestibility showed marked reduction in Brandt's voles and thus cause the digestible energy intake decrease in the first week. The increase in dietary fiber content can result in the decrease in food preference and digestibility (Hume et al., 1993). Most small herbivorous mammals prefer to select plants with low-fiber content (Degen et al., 2000). Degus, a herbivorous rodent, also showed pronounced preferences for low-fiber food (Bozinovic, 1995).

However, animals must consume low-quality (high-fiber) food from necessity rather than from choice when only poor quality diets are available (Bozinovic, 1995). Some rodents could compensate for the low digestibility associated with the high-fiber diet by increasing the food intake when low-fiber food was not available, such as degus (Bozinovic, 1995; Bozinovic et al., 1997), water voles (Arvicola terrestris) (Woodall, 1989), prairie voles (Microtus ochrogaster) (Voltura and Wunder, 1998) and collared lemmings (Dicrostonys groenlandicus) (Nagy and Negus, 1993). Cork and Foley (1991) pointed out that mammals with diminished digestibility and increased digesta transit time may compensate with high food intake. In other words, food with poor nutritional contents had to be consumed in higher amounts to meet the normal and/or higher physiological requirements (Cork and Foley, 1991; Veloso and Bozinovic, 1993).

Mass of total digestive tract with content was significantly increased in HF voles, suggesting that high-fiber diet increased the volume of the digestive tract (Demment and Van Soest, 1985), similar with that in Degus and collared lemmings (Nagy and Negus, 1993; Bozinovic, 1995). Several small mammals can respond to diet quality by changing the gut morphology (Gross et al., 1985; Hammond and Wunder, 1991; Bozinovic, 1995; Sabat et al., 1999), thus may be allowed to meet with the changes in food intake (Sibly, 1981; Hammond and Wunder, 1991). Brandt's voles can compensate the high-fiber diet by increasing the volume of digestive tract as a consequence of the increases in food intake and, thus can increase the turnover time of digesta. In short, no decrease in digestible energy intake in HF voles might result from the increases in the volume of the digestive tract and thus the turnover time of digesta, associated with the increases in food intake (Pei et al., 2001a,b).

4.2. Body mass, body composition and serum leptin levels

Body mass in the HF voles was lower in week 4 and 7 than LF voles in week 4. HF voles also showed lower carcass mass compared to the LF voles after 4 weeks acclimation. Body fat content kept relatively stable for LF voles and the HF voles after dietary acclimation. Similarly, both body mass and fat-free mass

were decreased and body fat mass and body fat content showed no changes in growing prairie voles fed on high-fiber diet (Voltura and Wunder, 1998). These results suggested that voles would increase energy intake and reduce energy requirement for maintenance, rather than mobilize lipid deposition when faced poor food quality (Voltura and Wunder, 1998).

Leptin is mainly produced and secreted by white adipose tissue (Zhang et al., 1994; Trayhurn et al., 1999). It has been reported that leptin, as an adipostatic signal, regulate food intake and energy metabolism in several mammal species even human (Zhang et al., 1994; Halaas et al., 1995; Pelleymounter et al., 1995; Klingenspor et al., 1996a; Baskin et al., 1999; Schwartz et al., 2000; Shannon and Jean-Michel, 2000; Wauters et al., 2000; Baskin et al., 2001). The present data showed that high-fiber diet did not affect serum leptin levels, whereas the changes of serum leptin levels were similar to the changes of body fat mass, and contrary to energy intake. Several small mammals including collared lemmings (Johnson et al., 2004), Siberian hamsters (Phodopus sungorus) (Klingenspor et al., 2000), cold acclimated Mongolian gerbils (Meriones unguiculatus) (Li et al., 2004) also show the correlations between body fat mass and serum leptin levels. Brandt's voles show seasonal variations in serum leptin levels, associated with the changes in body mass and fat mass, and energy intake (Li and Wang, 2005a). Photoperiod and temperature can influence the circulating leptin concentrations in several rodent species (Klingenspor et al., 1996a,b, 2000; Li et al., 2004). Short photoperiod decreased leptin expression and increased sensitivity in adipose tissue in Siberian hamster (Klingenspor et al., 1996a). When exposed to cold temperature, rat and mice increased the food intake, decreased body mass and fat mass, and serum leptin levels (Bing et al., 1998; Abelenda et al., 2003). Low leptin levels might be a hungry signal associated with increased energy intake when animals were in a negative energy balance (Flier, 1998; Li and Wang, 2005a,b). However, dissociation of leptin secretion and adiposity happened during the prehibernatory phase in the little brown bat (Myotis lucifugus) (Kronfeld-Schor et al., 2000a). Decreased leptin levels might be a metabolic signal to launch hibernation during the fattening period of prehibernation (Kronfeld-Schor et al., 2000a). The role of leptin in the energy budgets in Brandt's voles acclimated to low-quality diet is still not clear and need to be further investigated.

4.3. BMR and NST

Mammals eating low-quality food might evolve lower BMR (McNab, 1986). Cork (1994) hypothesized that small mammals lower their BMR to survive on a high-fiber diet (Veloso and Bozinovic, 1993; Cork, 1994; Silva et al., 2004). It has been reported that poor food quality decreased BMR in degus and Levant vole, which supported Cork's hypothesis (Veloso and Bozinovic, 1993; Cork, 1994). Contrary to that, we did not observe any effects of low-quality diet on BMR in Brandt's voles in the present study. Similar results were found in desert gerbil (Choshniak and Yahav, 1987) and leaf-eared mouse (Bozinovic and Novoa, 1997). It has been found BMR was significantly related to the some vital organ including heart,

liver, kidneys and digestive tract (Nespolo et al., 2002; Song and Wang, 2006). Our data showed that high-fiber diet had a negligible effect on size of digestive tract and vital organs. The fact of no significant variation in BMR could be explained by the relatively constant vital organs in the voles acclimated to high-fiber diet.

Contrary to BMR, food quality influenced the capacity of NST in Brandt's voles. NST decreased in the voles fed high-fiber diet after 7-week acclimation. Variations of photoperiod, temperature and/or food availability can induce the changes of thermogenic capacity in some small mammals (Heldmaier et al., 1981; Wunder, 1984; André et al., 1998; Wang et al., 2003b; Li and Wang, 2005a,b). Based on the present data, it suggests that changes in NST will contribute to the energy budgets when voles faced poor diet.

4.4. BAT COX activity, UCP1 content and levels of serum thyroid hormones

Brown adipose tissue (BAT) is the main site of NST (Ricquier and Bouillaud, 2000). COX (complex IV), the terminal enzyme in oxidative phosphorylation in the mitochondria, is involved in mitochondrial energy metabolism (Kadenbach et al., 2000). The uncoupling protein 1 (UCP1), a 32 kDa protein uniquely expressed in the inner membrane of BAT mitochondria, uncouples oxidative metabolism from ATP synthesis, which is considered to be an adaptation of mammalian tissues to nonshivering heat production (Ricquier and Bouillaud, 2000; Rial and Gonzalez-Barroso, 2001). It has been reported that variations in NST was associated with changes of BAT COX activity and/or UCP1 content in several small mammals (Heldmaier et al., 1981; Wunder, 1984; Li and Wang, 2005a,b; Zhao and Wang, 2005, 2006). Cold induces the enhancement in nonshivering thermogenic capacity, together with the increase in BAT UCP1 expression in Brandt's voles, Djungarian hamsters (*P. sungorus*) and Mongolian gerbils (Klingenspor et al., 1999b; Li et al., 2001; Klingenspor, 2003). Furthermore, thyroid hormones can increase thermogenesis by decreasing the metabolic efficiency. Higher serum thyroid hormones levels may contribute to the increase in thermogenic capacity in some small mammals (Li et al., 2001; Tomasi and Mitchell, 1996; Zhao and Wang, 2005). However, the present data showed that only COX activity for whole BAT was affected by high-fiber diet, which consist with the changes in NST. BAT COX activity per mg mitochondrial protein or per g BAT tissue, UCP1 content, and serum T_3 and T_4 levels were kept relatively stable. The inconsistent response of NST capacity with UCP1 was also found in golden spiny mice (*Acomys russatus*) (Kronfeld-Schor et al., 2000b). Brandt's voles showed similar changes of these parameters with NST when they were exposed to cold or short photoperiod (Li et al., 2001; Li and Wang, 2005a; Zhao and Wang, 2005). Thus, it seems that the decrease in NST plays a role to reduce the energy expenditure in the voles faced poor food quality.

In natural seasonal environment, Brandt's voles showed seasonal fluctuations in energy budgets, body mass and thermogenesis to cope with the variations in temperature, photoperiod and food quality. Our data indicated that low-quality food, independent of temperature and photoperiod, increased the food intake and decreased digestibility, wet carcass mass, NST in Brandt's voles, suggesting that herbivorous rodent species could compensate for poor quality diet by increasing food intake associated with the increased volume of the digesta (Bozinovic et al., 1997) and turnover time (Karasov and Diamond, 1988), and also by the decrease in NST.

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