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Plasticity in the Physiological Energetics of Mongolian Gerbils Is Associated with Diet Quality

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ABSTRACT

Small mammals usually show physiological and behavioral adaptations to cope with seasonal changes in food quality and availability. To examine the adaptive strategy of small rodents responding to varying dietary quality, we acclimated Mongolian gerbils (*Meriones unguiculatus*) to a high-fiber diet (HF: 35.5% neutral detergent fiber [NDF] and 21.4% acid detergent fiber [ADF]) for 4 wk and then a relatively low-fiber diet (LF: standard rat chow, 12.8% NDF and 4.8% ADF) for another 4 wk. Body mass was stable over the course of acclimation, but food intake and the size and mass of the digestive tract increased significantly in HF gerbils. The HF diet induced a decrease in basal metabolic rate and nonshivering thermogenesis associated with a reduction in the uncoupling protein 1 content of brown adipose tissue. After 4 wk of subsequent feeding on the LF diet, body mass, energy intake, digestive tract morphology, and thermogenic capacity recovered to the baseline. Serum leptin level decreased in HF gerbils and increased in the gerbils then fed with the LF diet. Further, the change in serum leptin level was positively related to body fat mass and negatively related to food intake, suggesting that the decreased leptin level associated with lower body fat content might be a signal that an animal was in negative energy balance. Finally, our data indicated that energy intake, body composition, and organ morphological plasticity are the main strategies by which gerbils cope with variations in food quality. Change in serum leptin level is related to change in food intake in Mongolian gerbils.

Introduction

The efficiency of energy intake, processing, allocation, and expenditure is critical to survival and ecological success in vertebrates (Bozinovic 1992; Veloso and Bozinovic 1993). Food quality, availability, and digestibility can affect the rate of energy metabolism (McNab 1986; Bozinovic 1995). In general, small herbivorous mammals consume a variety of plant species and select plants of low fiber content when available (Degen et al. 2000). Nevertheless, during nutritional bottlenecks, many small mammals must consume low-quality, high-fiber food from necessity rather than from choice (Bozinovic 1995). When consuming high-fiber vegetation, some rodent species compensate for the low-quality diet by a combination of digestive mechanisms, including increased food intake—by enlarging the gastrointestinal tract (Bozinovic et al. 1997; Owl and Batzli 1998; Sassi et al. 2007)—and/or increasing gut turnover time (Karason and Diamond 1988; Pei et al. 2001a, 2001b).

Leptin, secreted mainly by adipocytes, is considered to be an adipostatic signal linking energy metabolism and food intake regulation (Zhang et al. 1994; Halaas et al. 1995; Pelleymounter et al. 1995). In several rodents, exogenous administration of leptin caused a dramatic decrease in food intake and loss in body weight (Halaas et al. 1995; Gullicksen et al. 2002; Mercer and Tups 2003). Thus, the role of leptin in the regulation of food intake makes it a likely candidate to be involved in the regulation of energy balance during compensation for high-fiber diet.

It has been suggested that mammals eating low-quality food might evolve lower rates of basal metabolism (BMRs; McNab 1986; Cruz-Neto and Bozinovic 2004). In nature, it might be beneficial to reduce energy expenditure when only poor-quality diets are available (Nussear et al. 1998). It has been hypothesized that small mammals lower their BMR to survive a high-fiber diet (low-quality food; Veloso and Bozinovic 1993; Cork 1994; Cruz-Neto and Bozinovic 2004; Silva et al. 2004). However, herbivorous degus (*Octodon degus*), Levant voles (*Microtus guentieri*), and deer mice (*Peromyscus maniculatus*) showed significantly lower BMRs after 190, 35, and 10 d of acclimation to low-quality food, respectively (Choshniak and Yahav 1987; Veloso and Bozinovic 1993; Koteja 1996, respectively). In addition, the field leaf-eared mouse (*Phyllotis darwini*) showed significant correlation between BMR and the proportion of dietary plants and seeds (Bozinovic et al. 2007), but *O. degus* did not show any difference in BMR when offered a high-fiber diet (Bozinovic 1995; Bozinovic et al. 1997). In the desert gerbil (*Meriones crassus*), diet quality did not affect BMR (Choshniak and Yahav 1987).

Nonshivering thermogenesis (NST) also plays an important

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role in energy metabolism in small mammals, especially those living in cold environments. In order to cope with seasonal changes in natural environment, nonhibernating rodents show seasonal changes in NST: higher in winter and lower in summer (Heldmaier et al. 1981; Wunder 1984; Wang et al. 2003; Li and Wang 2005a, 2005b). Brown adipose tissue (BAT) is the main site of NST (Ricquier and Bouillaud 2000). Uncoupling protein 1 (UCP1), a 32-kDa protein uniquely expressed in the inner membrane of BAT mitochondria, is considered to be the molecular basis of NST (Ricquier and Bouillaud 2000; Rial and González-Barroso 2001). The effects of several factors, including photoperiod and temperature, on NST and BAT UCP1 expression have been well studied (Heldmaier et al. 1981; Wunder 1984; Kageyama et al. 2003; Wang et al. 2003; Li and Wang 2005a, 2005b). However, few data about the effects of diet quality on NST and UCP1 are available. The role of NST in energy metabolism during compensation for a high-fiber diet is still not clear.

The study of phenotypic plasticity has become a central topic in evolutionary ecology (Nespolo et al. 2001). Through phenotypic plasticity, organisms are able to match environmental changes and to enhance their adaptability to various environmental conditions (Nespolo et al. 2001). Some studies have indicated that NST increases after cold exposure or under a short photoperiod in small mammals (Heldmaier and Buchberger 1985; Wang et al. 1999, 2003; Klingenspor 2003; Zhao and Wang 2005). Several rodent species decrease BMR to minimize energy expenditure in an environment of low-quality diet (Choshniak and Yahav 1987; Veloso and Bozinovic 1993; Koteja 1996) or change organ size and function (Karasov and Diamond 1988; Sabat and Bozinovic 2000; Nespolo et al. 2002). However, we are not aware of any studies relating the physiological plasticity of those variables in rodents fed a high-fiber diet and then a relatively low-fiber diet.

The Mongolian gerbil (*Meriones unguiculatus*) is a dominant small rodent species that inhabits mainly desert and semiarid regions of northern China. The climate is arid and characterized by a warm, dry summer (the average temperature in the warmest month is 18.8°C) and a cold winter (extreme temperatures below -40°C; Chen 1988; Wang et al. 2000). Thus, the species must experience great seasonal fluctuations in temperature, photoperiod, and food availability and quality. In summer, gerbils feed mainly on stems and leaves of plants, and during the autumn and winter, they feed mainly on plant and crop seeds (Zhang and Wang 1998). Our previous findings showed that Mongolian gerbils enlarged gut capacity and decreased digestibility in response to an increase in dietary fiber content (Pei et al. 2001a). It also has been shown that Mongolian gerbils have a wide thermal neutral zone (Wang et al. 2000, 2003) and wide seasonal variations in energy intake, BMR, and NST (Wang et al. 2003; Li and Wang 2005b).

The aim of this study was to examine the effects of fiber content on body mass, body composition, energy budget, BMR, NST, and the role of leptin and UCP1 in the regulation of energy intake and thermogenesis in Mongolian gerbils. We hypothesized that Mongolian gerbils can compensate for a high-

fiber diet by integrating changes in gut morphology, body composition, food intake, and thermogenesis. We predicted that when facing a high-fiber-content diet, Mongolian gerbils would increase gastrointestinal tract size and food intake but decrease BMR and NST. When restored to a low-fiber diet, the gerbils would reverse these changes. We also predicted that BAT, UCP1, and serum leptin are involved in the regulation of thermogenesis and food intake.

Material and Methods

Animals and Experimental Designs

Animals were male and female adult offspring of Mongolian gerbils captured in Inner Mongolian grasslands and were raised in the Institute of Zoology, Chinese Academy of Sciences. After weaning, gerbils were housed in single-sex groups (three to five) in plastic cages (30 cm × 15 cm × 20 cm), with sawdust as bedding. All the animals were maintained in a 12L:12D photoperiod at an ambient temperature of 23° ± 1°C. Food (standard rat chow; Beijing KeAo Feed) and water were provided ad lib. Gerbils were separated and housed individually for 3 wk before the start of experiments.

Experiment 1

To determine the effects of diets with differing fiber content on body mass, energy budgets, and thermogenesis, 20 gerbils were divided randomly into either a control group (LF group: five males and five females, fed with standard rat chow, a relatively low-fiber [LF] diet, for 8 wk) or an experimental group (HF-LF group: five males and five females, fed a high-fiber [HF] diet for 4 wk and then restored to the LF diet for another 4 wk). The compositions of the HF and LF diets are presented in Table 1. All animals had free access to food and water. Each subject's body mass was recorded every 3 d. Measurements of BMR, NST, and energy budgets were carried out before acclimation began (day 0) and again at 7-d intervals throughout the acclimation (a total of nine measurements).

Metabolic Trial. Metabolic rates were measured in a closed-circuit respirometer (Gorecki 1975; Wang et al. 2000). The metabolic chamber size was 3.6 L, and the temperature in the chamber was controlled to within ±0.5°C by a water bath.

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

	Low Fiber (Standard Rat Chow)	High Fiber
Crude fat (%)	7.0	3.9
Crude protein (%)	25.5	19.4
NDF (%)	12.8	35.5
ADF (%)	4.8	21.4
Ash (%)	9.0	10.5
Caloric value (kJ/g)	18.3	17.3

Note. NDF = neutral detergent fiber; ADF = acid detergent fiber.

Carbon dioxide and water in the metabolic chamber were absorbed with KOH and silica gel, respectively. BMR was quantified as the rate of oxygen consumption at $30^{\circ} \pm 0.5^{\circ}\text{C}$, which is within the thermoneutral zone of the gerbils (Wang et al. 2000, 2003). Briefly, animals were fasted for 3 h before being transferred into the metabolic chamber. After 1 h of adaptation to the chamber, metabolic measurement was conducted for another 1 h, during which oxygen consumption was read at 5-min intervals. BMR was calculated according to the two continuous, stable, minimum recordings. NST was measured as the maximum metabolic response to a mass-dependent subcutaneous injection of norepinephrine (Shanghai Harvest Pharmaceutical) on the next day (Heldmaier et al. 1982). BMR and NST were corrected to standard temperature and air pressure conditions and expressed as milliliters of $\text{O}_2 \text{ h}^{-1} \text{ g}^{-1}$. Gerbils were weighed before and after each trial. All measurements were made between 1000 and 1700 hours.

Energy Budgets. Food was allotted quantitatively, and food residues and feces were collected for each subject over the last 3 d of each week during the acclimation. After being oven-dried at 60°C to a constant mass, they were manually separated (Liu et al. 2002, 2003). Energy contents of dry matter and feces were measured by a Parr 1281 oxygen bomb calorimeter (Parr Instrument). Gross energy intake (GEI), digestible energy intake (DEI), and apparent digestibility of energy (hereafter referred to simply as digestibility) were then determined as follows: $\text{GEI} (\text{kJ d}^{-1}) = \text{dry-matter intake (DMI; g d}^{-1}) \times \text{gross energy (GE) content of food (kJ g}^{-1})$; $\text{DEI} (\text{kJ d}^{-1}) = \text{GEI} - (\text{mass of feces [g d}^{-1}] \times \text{GE content of feces [kJ g}^{-1}])$; $\text{digestibility} (\%) = (\text{DEI/GEI}) \times 100$ (Grodzinski and Wunder 1975; Liu et al. 2002, 2003).

Experiment 2

In experiment 1, we found that several variables in the HF-LF gerbils displayed significant plasticity in response to HF and LF diet acclimation. In experiment 2, we tested the changes in body composition and digestive tracts in the gerbils over the acclimation. We also tested the changes in serum leptin concentration and BAT UCP1 content. Fifty gerbils were divided randomly into five groups: control (no treatment), HF-W1 (offered the HF diet for 1 wk), HF-W4 (offered the HF diet for 4 wk), R-W1 (offered the HF diet for 4 wk and then restored to the LF diet for 1 wk), and R-W4 (offered the HF diet for 4 wk and then restored to the LF for 4 wk), with five males and five females in each group. The control and acclimated gerbils (five groups) were decapitated between 0900 and 1100 hours at the end of each acclimation.

Serum Leptin Levels. Trunk blood was collected, and serum was separated from each blood sample and stored in -70°C for leptin measurement. Serum leptin levels were determined by radio-immunoassay with a Linco 125I Multi-species Kit (XL-85K, Linco Research). The lower and upper limits of the assay

kit were 1 and 50 ng mL^{-1} and the inter- and intra-assay variations were $<3.6\%$ and 8.7% , respectively.

Measurements of Cytochrome c Oxidase (COX) and UCP1 Content. Interscapular BAT was removed and weighed immediately after trunk blood was collected. Mitochondrial protein was prepared as described in Zhao and Wang (2005). Total mitochondrial protein content was determined by the Folin phenol method (Lowry et al. 1951), with bovine serum albumin as the standard. The COX activity of BAT was measured polarographically with oxygen electrode units (Hansatech Instruments, England; Sundin et al. 1987). The UCP1 content of total mitochondrial protein was determined by western blotting as described in Zhao and Wang (2005), expressed as relative units, and quantified with Scion Image software.

Body Composition. After interscapular BAT was removed, we removed first the gastrointestinal tract (stomach, small intestine, large intestine, and cecum) and then the liver, heart, lungs, spleen, and kidneys. The size of the gastrointestinal tract was measured (to the nearest 0.1 cm). The fresh masses of gastrointestinal tract with and without content, organs, and remaining carcass were weighed (to the nearest 1 mg or 0.1 g). Then the gastrointestinal tract without content, all organs, and the carcass were oven-dried at 60°C for 10 d to a constant mass and weighed again to obtain the dry mass. Total body fat was extracted from the dried carcass by ether extraction in a Soxhlet apparatus.

Data Analysis. Statistical analysis was carried out with the SPSS software package. For experiment 1, group differences (two groups) in body mass and digestibility were analyzed by two-way ANOVA (diet \times sex), and group differences in BMR, NST, DMI, GEI, and DEI were analyzed by two-way ANCOVA, with body mass as covariate. In addition, differences in body mass, BMR, NST, and energy parameters over the course of acclimation were analyzed by repeated-measures one-way ANOVA, and significant differences were further evaluated with Tukey's HSD test. For experiment 2, group differences (five groups) in BAT COX activity and UCP1 content were analyzed by two-way ANOVA (diet \times sex), and group differences in body composition and serum leptin levels were analyzed by two-way ANCOVA, with body mass as the covariate, followed by Tukey's HSD test. Finally, Pearson's correlation was performed to determine the correlation between serum leptin levels and body fat mass. Statistical significance was taken at $P < 0.05$. All data were expressed as means \pm SEM.

Results

Experiment 1

There were no significant differences between the experimental and control groups in any variables before the study (body mass: $F_{1,16} = 0.081$, $P > 0.05$; BMR: $F_{1,15} = 1.142$, $P > 0.05$; NST: $F_{1,15} = 1.616$, $P > 0.05$; DMI: $F_{1,15} = 1.053$, $P > 0.05$; GEI: $F_{1,15} = 1.835$, $P > 0.05$; DEI: $F_{1,15} = 1.245$, $P > 0.05$; and di-

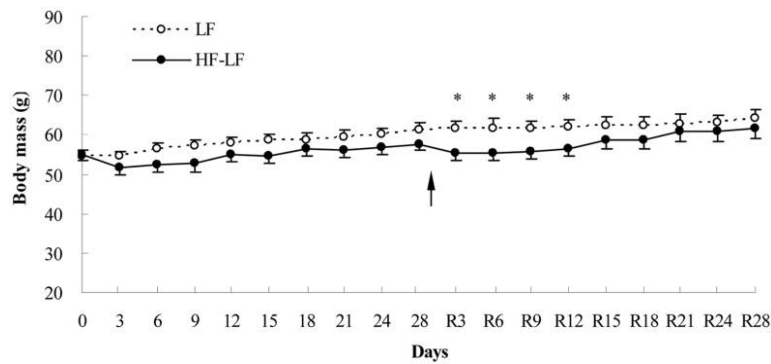


Figure 1. Changes in body mass in response to high-fiber (HF) diet acclimation and restoration of the low-fiber (LF) diet (standard rat chow) in Mongolian gerbils. *Dotted line*, LF-diet group; *solid line*, HF diet for 4 wk, followed by LF diet for another 4 wk. The arrow indicates the time point at which HF-LF gerbils began to be fed with the LF diet; the days thereafter are accordingly designated R1–R28. An asterisk indicates $P < 0.05$. Error bars represent 1 SEM.

gestibility: $F_{1,16} = 0.402$, $P > 0.05$). Furthermore, there were no differences between sexes for any parameters; therefore, data were pooled for statistical analysis.

Body Mass. Both LF and HF-LF gerbils maintained constant body mass, and the HF diet had no significant effects on body mass at any point before day 28 (day 28: $F_{1,16} = 2.030$, $P > 0.05$, Fig. 1). When gerbils were restored to the LF diet, their body mass decreased, and body mass was significantly lower in HF-LF gerbils than in LF gerbils (day R3 [i.e., day 3 of the restored LF diet]: $F_{1,16} = 8.499$, $P < 0.05$; day R12: $F_{1,16} = 5.406$, $P < 0.05$). However, after day R12, HF-LF gerbils increased their body mass, which reached a level similar to that for LF gerbils on day R15 (day R15: $F_{1,16} = 2.072$, $P > 0.05$) and thereafter (day R28: $F_{1,16} = 0.740$, $P > 0.05$; Fig. 1).

BMR and NST. Over the course of acclimation, LF gerbils exhibited a relatively constant BMR (repeated-measures one-way ANOVA: $F_{8,72} = 0.751$, $P > 0.05$; Fig. 2A). HF-LF gerbils, however, showed marked plasticity: BMR was significantly lower from day 14 until day 28 on the HF diet (day 14: $F_{1,15} = 6.768$, $P < 0.05$; day 28: $F_{1,15} = 5.611$, $P < 0.05$) and then increased sharply when the LF diet was restored (repeated-measures one-way ANOVA: $F_{8,72} = 3.345$, $P < 0.001$). No group differences were found on day R7 (day R7: $F_{1,15} = 1.503$, $P > 0.05$) and thereafter (day R28: $F_{1,15} = 0.097$, $P > 0.05$, Fig. 2A).

When HF-LF gerbils were offered the HF diet, their NST decreased sharply (repeated-measures one-way ANOVA: $F_{8,72} = 17.554$, $P < 0.001$), indicating that NST was affected significantly by the HF diet (Fig. 2B). Further, NST was significantly lower in HF-LF gerbils than in LF gerbils from day 7 ($F_{1,15} = 21.270$, $P < 0.001$) until day 28 (day 28: $F_{1,15} = 23.372$, $P < 0.001$). As HF-LF gerbils were restored to the LF diet, NST increased sharply and recovered to the levels for LF gerbils on day R7 (repeated-measures one-way ANOVA: $F_{8,72} = 17.554$, $P < 0.001$; day R7: $F_{1,15} = 4.432$, $P > 0.05$; day R28: $F_{1,15} = 1.159$, $P > 0.05$; Fig. 2B), indicating a marked regulation in plasticity as well. For LF gerbils, NST maintained a stable state

over the course of acclimation (repeated-measures one-way ANOVA: $F_{8,72} = 0.635$, $P > 0.05$; Fig. 2B).

Energy Parameters. The HF diet had significant effects on energy parameters. DMI and GEI increased sharply in HF-LF gerbils and were 97% and 113% higher, respectively, on day 14 than on day 0 (repeated-measures one-way ANOVA, DMI: $F_{8,72} = 65.513$, $P < 0.001$; GEI: $F_{8,72} = 68.680$, $P < 0.001$); they then maintained a relatively constant level (Fig. 3A, 3B). Further, both DMI and GEI were significantly higher in HF-LF than in LF gerbils (DMI, day 7: $F_{1,15} = 27.608$, $P < 0.001$; day 28:

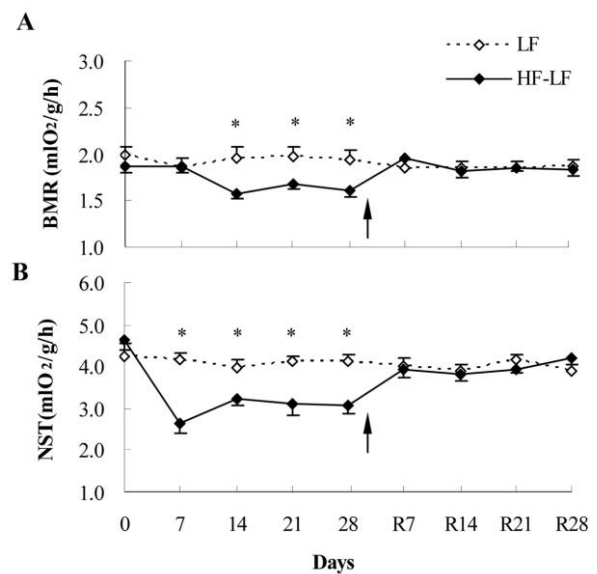


Figure 2. Changes in basal metabolic rate (BMR; A) and nonshivering thermogenesis (NST; B) in response to high-fiber (HF) diet acclimation and restoration of the low-fiber (LF) diet (standard rat chow) in Mongolian gerbils. *Dotted lines*, LF-diet group; *solid lines*, HF diet for 4 wk, followed by LF diet for another 4 wk. The arrow indicates the time point at which HF-LF gerbils began to be fed with the LF diet; the days thereafter are accordingly designated R1–R28. An asterisk indicates $P < 0.05$. Error bars represent 1 SEM.

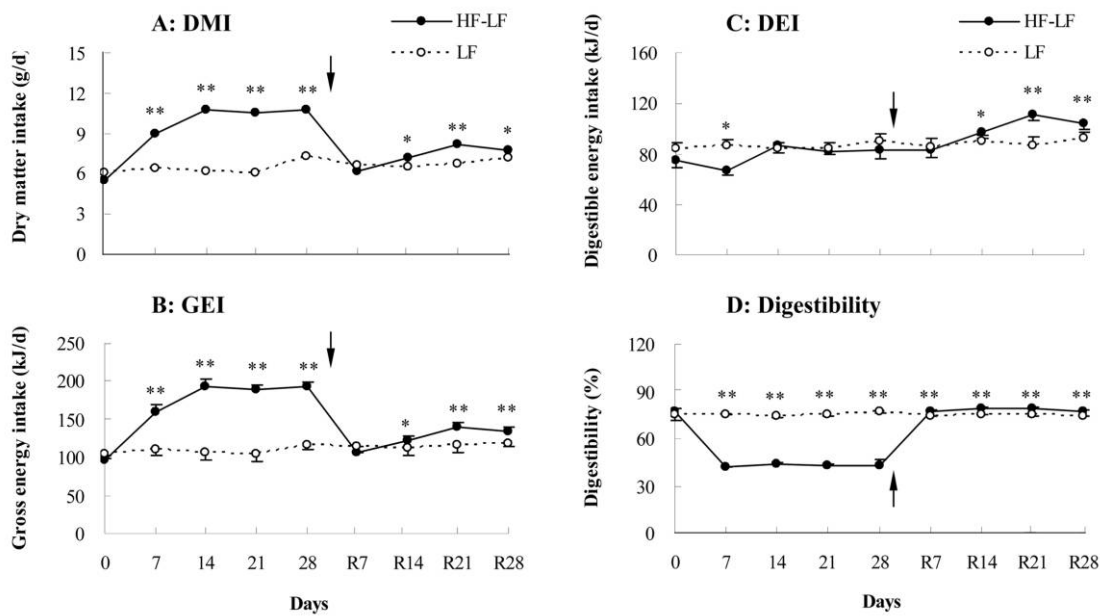


Figure 3. Changes in dry-matter intake (DMI; A), gross energy intake (GEI; B), digestible-energy intake (DEI; C), and digestibility (D) in response to high-fiber (HF) diet acclimation and restoration of the low-fiber (LF) diet (standard rat chow) in Mongolian gerbils. Dotted lines, LF-diet group; solid lines, HF diet for 4 wk, followed by LF diet for another 4 wk. The arrow indicates the time point at which HF-LF gerbils began to be fed with the LF diet; the days thereafter are accordingly designated R1–R28. A single asterisk indicates $P < 0.05$; a double asterisk indicates $P < 0.01$. Error bars represent 1 SEM.

$F_{1,15} = 116.895$, $P < 0.001$; GEI, day 7: $F_{1,15} = 34.140$, $P < 0.001$; day 28: $F_{1,15} = 155.740$, $P < 0.001$). After restoration of the LF diet, DMI and GEI decreased sharply and reverted to the levels of LF gerbils after day R7 (repeated-measures one-way ANOVA, DMI: $F_{8,72} = 65.513$, $P < 0.001$; GEI: $F_{8,72} = 68.680$, $P < 0.001$), and no group differences were found between HF and HF-LF gerbils on day R7 (DMI: $F_{1,15} = 0.778$, $P > 0.05$; GEI: $F_{1,15} = 0.758$, $P > 0.05$). However, DMI and GEI were still higher in HF-LF gerbils than in LF gerbils on day R14 (DMI: $F_{1,15} = 6.324$, $P < 0.05$; GEI: $F_{1,15} = 6.559$, $P < 0.05$) and thereafter (day 28, DMI: $F_{1,15} = 6.756$, $P < 0.05$; GEI: $F_{1,15} = 6.511$, $P < 0.05$; Fig. 3A, 3B).

In contrast to DMI and GEI, DEI decreased significantly and was lower in HF-LF gerbils than in LF gerbils on day 7 ($F_{1,15} = 7.896$, $P < 0.05$; Fig. 3C). No group differences, however, were found from day 14 ($F_{1,15} = 1.528$, $P > 0.05$) until day 28 ($F_{1,15} = 0.187$, $P > 0.05$). On restoration of the LF diet, DEI increased significantly until day R14 and remained at a high level thereafter, compared to day 0 (repeated-measures one-way ANOVA: $F_{8,72} = 7.373$, $P < 0.001$), and was significantly higher than that in LF gerbils from then until day R28 (day R14: $F_{1,15} = 8.915$, $P < 0.01$; day R28: $F_{1,15} = 10.585$, $P < 0.01$; Fig. 3C).

On the HF diet, gerbils' digestibility decreased sharply—46% lower on day 7 than on day 0—and then maintained a relatively stable level from day 7 until day 28. After restoration of the LF diet, however, digestibility increased markedly and then maintained a constant high level from day R7 onward (repeated-measures one-way ANOVA: $F_{8,72} = 211.998$, $P <$

0.001; Fig. 3D). Compared with that in LF gerbils, digestibility was significantly lower in HF-LF gerbils from day 7 until day 28 (day 7: $F_{1,16} = 3,735.869$, $P < 0.001$; day 28: $F_{1,16} = 109.531$, $P < 0.001$) and significantly higher on day R7 ($F_{1,16} = 12.136$, $P < 0.01$) and thereafter (day R28: $F_{1,16} = 17.238$, $P < 0.01$). LF gerbils maintained a stable digestibility over the course of acclimation (repeated-measures one-way ANOVA: $F_{8,72} = 0.470$, $P > 0.05$; Fig. 3D).

Experiment 2

Body Fat Mass and Serum Leptin Level. There were significant differences in body fat mass among the five groups ($F_{4,39} = 3.242$, $P < 0.05$; Fig. 4A), which was lower by 52% in HF-W1 gerbils than in controls but reached control levels in HF-W4 gerbils. Serum leptin levels also showed significant changes during acclimation ($F_{4,39} = 3.355$, $P < 0.05$; Fig. 4B). The change in serum leptin levels was consistent with the variations in body fat mass. The lowest leptin value, significantly lower than that in the controls, was also found in HF-W1 gerbils. The difference in leptin levels between the HF-W4 gerbils and the controls was not significant. Correlation analysis showed that serum leptin levels were positively correlated with body fat mass ($r = 0.432$, $P < 0.01$; Fig. 4C).

Carcass and Organs. HF and LF diet acclimation had significant effects on dry masses of carcass, heart, and spleen (Table 2). The lowest dry carcass mass was found in HF-W1 gerbils; it was higher in HF-W4 gerbils and reached the control levels in

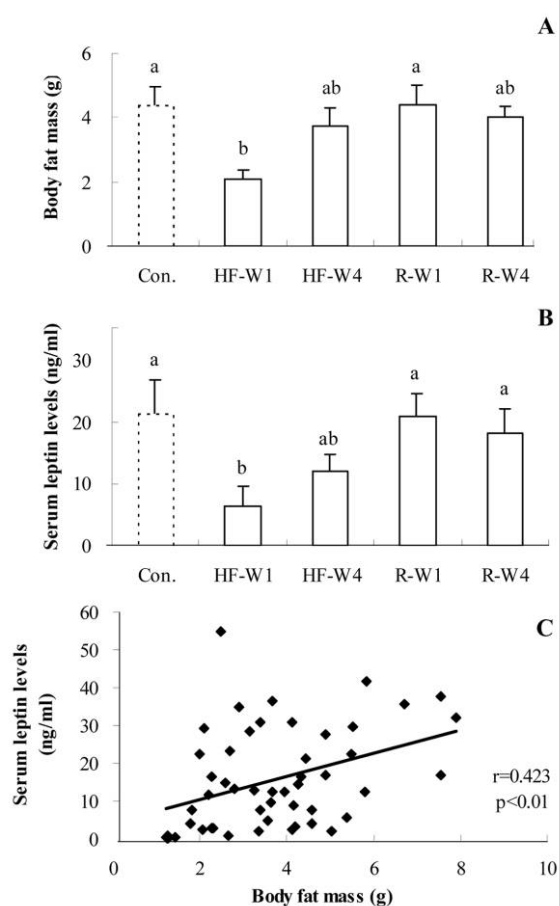


Figure 4. Changes in body fat mass (A), serum leptin level (B), and the correlation between body fat mass and serum leptin (C) in response to high-fiber (HF) diet acclimation and restoration of the low-fiber (LF) diet (standard rat chow) in Mongolian gerbils. Con.: control group; HF-W1, HF-W4: HF diet for 1 and 4 wk, respectively; R-W1, R-W4: HF diet acclimation for 4 wk, followed by restoration of the LF diet for 1 and 4 wk, respectively. Different letters above bars indicate significant differences ($P < 0.05$). Error bars represent 1 SEM.

R-W1 and R-W4 gerbils ($F_{4,39} = 4.658$, $P < 0.01$). Dry heart mass was lowest in HF-W4 gerbils and reached control levels after restoration of the LF diet ($F_{4,39} = 4.271$, $P < 0.01$). In addition, dry spleen mass was lowest in HF-W1 gerbils and reached control levels in R-W4 gerbils ($F_{4,39} = 3.299$, $P < 0.05$). There were no significant differences in dry masses of liver, lung, and kidneys among groups (liver: $F_{4,39} = 1.463$, $P > 0.05$; lung: $F_{4,39} = 1.728$, $P > 0.05$; kidneys: $F_{4,39} = 1.428$, $P > 0.05$; Table 2).

Digestive Tract. The digestive tract showed significant changes, indicating a marked influence of HF-LF diet acclimation. First, wet and dry masses of stomach were significantly higher in the HF-W4 gerbils than in the controls but reverted to control levels after restoration of the LF diet for 4 wk (stomach wet mass: $F_{4,39} = 11.029$, $P < 0.001$; stomach dry mass: $F_{4,39} = 3.921$, $P < 0.05$; Table 3). Second, the mass of small intestine contents was higher in HF gerbils and lower in R-W1 and R-

W4 gerbils than in control gerbils ($F_{4,39} = 15.231$, $P < 0.001$). The HF diet also showed a significant effect on content mass and wet and dry masses of the large intestine, which were highest in the HF-W4 gerbils and sharply lower (control levels) after 4 wk of LF diet acclimation (i.e., R-W4 gerbils; content mass of large intestine: $F_{4,39} = 25.398$, $P < 0.001$; wet mass: $F_{4,39} = 22.136$, $P < 0.001$; dry mass: $F_{4,39} = 13.555$, $P < 0.001$). Finally, the size, content mass, and wet and dry masses of the cecum showed significant differences: higher in HF gerbils and at the control level in R-W1 and R-W4 gerbils (cecum size: $F_{4,39} = 8.821$, $P < 0.001$; wet mass: $F_{4,39} = 24.726$, $P < 0.001$; dry mass: $F_{4,39} = 21.177$, $P < 0.001$; $F_{4,39} = 9.695$, $P < 0.001$). Similarly, the size, content mass, and wet and dry masses of the total digestive tract were higher in HF gerbils and lower in the gerbils restored to an LF diet, indicating marked plasticity changes over the course of HF-LF diet acclimation (size of total digestive tract: $F_{4,39} = 3.065$, $P < 0.05$; content mass: $F_{4,39} = 26.384$, $P < 0.001$; wet mass: $F_{4,39} = 7.441$, $P < 0.001$; dry mass: $F_{4,39} = 4.463$, $P < 0.01$; Table 3).

BAT COX Activity and UCP1 Content. We did not detect group differences in BAT COX activity ($F_{4,40} = 1.013$, $P > 0.05$; Fig. 5A). BAT UCP1 content, however, differed significantly among groups: lower in HF-W1 and HF-W4 gerbils and at control levels in R-W1 and R-W4 gerbils ($F_{4,40} = 8.737$, $P < 0.001$; Fig. 5B). Further, the Pearson analysis showed a positive correlation between UCP1 content and serum leptin levels ($r = 0.362$, $P = 0.01$; Fig. 5C).

Discussion

This study indicated that body mass, body composition, digestive tract morphology, energy intake, BMR, and NST showed strong plasticity in Mongolian gerbils acclimated to the HF-LF diet, suggesting that gerbils can change physiological functions integratively to cope with changes in diet quality.

Body Mass, Body Composition, and Digestive Tract

Mongolian gerbils have shown seasonal changes in body mass in both natural environments and outdoor enclosures (Li and Wang 2005b; Zhang and Wang 2006, 2007). Several environmental factors, including temperature, photoperiod, and food availability and quality, have been implicated in the seasonal regulation of body mass. Diet quality has been found to affect body mass changes in collared lemmings (*Dicrostonyx groenlandicus*) and long-term-acclimated degus but not in fat sand rats (*Psammomys obesus*) and short-term-acclimated degus (Nagy and Negus 1993; Bozinovic et al. 1997; Degen et al. 2000; Veloso and Bozinovic 2000). Our data show that body mass did not change in the gerbils acclimated to an HF diet. After restoration of the LF diet, however, body mass first decreased and then increased to the control levels. It is interesting that body composition (fat, carcass, heart, and spleen masses) decreased significantly in gerbils fed an HF diet and increased on restoration of the LF diet, suggesting that Mongolian gerbils

Table 2: Mass of carcass and organs in Mongolian gerbils offered the high-fiber diet and then fed the low-fiber diet (standard rat chow)

	Control	HF-W1	HF-W4	R-W1	R-W4	P
Sample	10	10	10	10	10	
Body mass (g)	56.7 ± 2.3	52.9 ± 2.3	58.4 ± 2.3	56.0 ± 2.3	60.7 ± 2.3	NS
Wet carcass mass (g)	43.0 ± 1.7 ^A	35.3 ± 1.4 ^B	40.2 ± 2.0 ^B	42.1 ± 1.8 ^A	45.3 ± 1.8 ^A	.001
Dry carcass mass (g)	16.0 ± .8 ^A	12.7 ± .8 ^{BC}	14.4 ± .8 ^C	16.4 ± .8 ^A	16.2 ± .7 ^{AB}	.001
Wet mass (mg):						
BAT	136.1 ± 13.8 ^A	77.8 ± 8.0 ^B	114 ± 12.4 ^B	95.9 ± 3.2 ^B	106.9 ± 6.5 ^B	.01
Liver	2,004.6 ± 120.5	1,688.4 ± 75.1	2,137.5 ± 140.2	1,981.4 ± 95.7	2,366.5 ± 130.8	NS
Heart	275.2 ± 17.6 ^A	228.9 ± 10.9 ^{BC}	222.6 ± 10.9 ^C	261.1 ± 12.2 ^{AB}	288.6 ± 13.4 ^B	.01
Lung	425.1 ± 38.8 ^B	444.5 ± 33.0 ^B	492.2 ± 64.1 ^B	421.8 ± 26.0 ^B	685.3 ± 59.1 ^A	.01
Spleen	49.9 ± 7.6 ^A	24.1 ± 2.5 ^B	37.6 ± 3.1 ^{AB}	36.4 ± 3.3 ^{AB}	51.8 ± 6.3 ^A	.05
Kidneys	569.6 ± 28.2	537.2 ± 11.4	563.2 ± 19.0	551.3 ± 22.3	590.6 ± 24.2	NS
Dry mass (mg):						
Liver	639.9 ± 48.5	563.0 ± 37.6	595.6 ± 43.1	639.0 ± 30.8	644.8 ± 39.9	NS
Heart	65.7 ± 4.4 ^A	54.5 ± 2.7 ^{AB}	49.3 ± 2.4 ^B	61.8 ± 2.6 ^{AB}	67.4 ± 5.7 ^A	.01
Lung	100.4 ± 8.4	111.0 ± 11.1	106.7 ± 13.5	101.1 ± 7.6	140.4 ± 13.7	NS
Spleen	12.3 ± 1.8 ^A	6.1 ± .7 ^B	9.1 ± .9 ^{BC}	9.1 ± .8 ^{AB}	12.6 ± 1.7 ^A	.05
Kidneys	144.5 ± 6.8	136.6 ± 3.6	135.1 ± 5.4	139.0 ± 5.5	144.7 ± 8.1	NS

Note. Values are expressed as absolute mean ± SEM. HF-W1, HF-W4: high-fiber diet acclimation for 1 and 4 wk, respectively; R-W1, R-W4: high-fiber diet acclimation for 4 wk, followed by restoration of the standard rat diet (low fiber) for 1 and 4 wk, respectively. In each row, different letters indicate significant differences ($P < 0.05$). BAT = brown adipose tissue; NS = not significant.

may compensate for the HF (low-quality) diet by both decreasing energy demand, to maintain a lower carcass mass, and mobilizing the energy depot associated with lower body fat (Zhao and Wang 2007).

In addition to body composition changes, digestive tract morphology showed changes in some rodent species when different diets were offered (Gross et al. 1985; Hammond and Wunder 1991; Nagy and Negus 1993; Derting and Hornung 2003; Zhao and Wang 2007). Our results show that digestive tract size, especially in the large intestine and cecum, increased in the gerbils fed an HF diet and decreased after restoration of the LF diet. Further, the contents of the small and large intestines and cecum increased in mass in HF gerbils and decreased in HF-LF individuals, suggesting that the gerbils could eat more when only an HF diet was available. It seems that changes in digestive tract morphology can contribute greatly to changes in body mass. The data presented here confirm the findings that small mammals fed an HF diet had large gut mass (Gross et al. 1985; Hammond and Wunder 1991; Nagy and Negus 1993). Our results indicate that gerbils adapt to diets of differing fiber content mainly by phenotypic plasticity in digestive tract morphology. Similarly, such gut morphological plasticity in response to different-quality diets occurs not only in small mammals (Sibly 1981; Gross et al. 1985; Hammond and Wunder 1991; Wunder 1992; Nagy and Negus 1993; Derting and Hornung 2003) but also in some bird species, including European starlings (*Sturnus vulgaris*; Geluso and Hayes 1999), indicating the generality of phenotypic plasticity in digestive tract morphology. Finally, the results regarding the effect of different-quality diets on digestive tract morphology are strong evidence for a core prediction of digestion theory, namely, that the con-

sumption of diets with high content of indigestible material determines an increase in gut dimensions (Sibly 1981).

Energy Intake and Serum Leptin Level

The changes in food intake in response to diets with different fiber contents resulted in changes in digestive tract size and mass in the Mongolian gerbils. Several small mammals, such as degus, collared lemmings, and prairie voles (*Microtus ochrogaster*), were able to compensate for an HF diet by a combination of digestive mechanisms that include increased gut size and relatively longer digesta retention time and therefore increased nutrient uptake by the gut (Gross et al. 1985; Nagy and Negus 1993; Bozinovic 1995). Our data show clearly that in the gerbils offered the HF diet, DMI and GEI increased significantly and digestibility decreased sharply, whereas DEI maintained a relatively stable level. After restoration of the LF diet, the gerbils showed an increase in digestibility and DEI but decreases in DMI and GEI, suggesting that they were able to compensate for the HF diet by regulation of both food intake and digestibility.

Leptin has been implicated as one of the peripheral signals in regulation of body fat reserves and energy intake in mammals (Zhang et al. 1994; Halaas et al. 1995; Pellemounter et al. 1995; Friedman and Halaas 1998). Our data show that body fat mass decreased in the gerbils offered the HF diet for 1 wk, suggesting that gerbils compensated for the lower DEI by mobilizing the body fat reserve. Further, contrary to the changes in DMI, serum leptin levels were positively correlated with body fat mass and decreased (by 70.5% compared with controls) in the gerbils fed the HF diet for 1 wk, indicating that lowering

Table 3: Changes in digestive tract in Mongolian gerbils offered the high-fiber diet and then fed the low-fiber diet (standard rat chow)

	Control	HF-W1	HF-W4	R-W1	R-W4	P
Stomach:						
Size (cm)	3.3 ± .1	3.1 ± .1	3.5 ± .1	3.4 ± .1	3.5 ± .1	NS
Content mass (mg)	1,876.6 ± 188.3	1,479.5 ± 73.0	2,056.3 ± 275.3	1,976.0 ± 242.9	2,226.4 ± 257.0	NS
Wet mass (mg)	497.7 ± 15.2 ^C	484.8 ± 12.9 ^C	648.4 ± 25.3 ^A	584.0 ± 29.2 ^B	535.2 ± 19.3 ^C	.001
Dry mass (mg)	117.1 ± 3.5 ^B	108.1 ± 2.8 ^B	133.0 ± 5.4 ^A	131.7 ± 6.2 ^A	128.1 ± 5.9 ^{AB}	.05
Small intestine:						
Size (cm)	37.4 ± .7	37.0 ± .8	39.8 ± .9	39.2 ± .8	38.7 ± 1.0	NS
Content mass (mg)	2,673.4 ± 155.5 ^{BC}	3,429.4 ± 184.6 ^A	3,557.6 ± 141.8 ^A	2,403.8 ± 111.9 ^C	3,097.1 ± 164.0 ^B	.001
Wet mass (mg)	1,069.3 ± 49.9	896.1 ± 63.9	983.0 ± 50.7	1,086.3 ± 102.5	1,091.9 ± 58.4	NS
Dry mass (mg)	171.3 ± 16.6 ^{AB}	205.6 ± 20.8 ^A	146.6 ± 7.1 ^B	215.5 ± 19.6 ^A	199.7 ± 11.2 ^A	.05
Large intestine:						
Size (cm)	17.3 ± .4	16.8 ± .4	18.6 ± 1.4	16.3 ± .4	16.9 ± .5	NS
Content mass (mg)	1,201.2 ± 93.2 ^C	2,011.7 ± 152.2 ^B	2,573.7 ± 222.7 ^A	1,096.1 ± 64.0 ^C	1,182.8 ± 56.6 ^C	.001
Wet mass (mg)	408.8 ± 23.2 ^D	574.2 ± 46.7 ^B	786.5 ± 51.7 ^A	513.6 ± 17.2 ^{BC}	469.1 ± 28.9 ^{CD}	.001
Dry mass (mg)	77.4 ± 5.9 ^D	91.2 ± 7.2 ^{BC}	132.7 ± 10.7 ^A	107.9 ± 4.4 ^B	90.1 ± 4.9 ^{CD}	.001
Cecum:						
Size (cm)	5.5 ± .1 ^B	6.2 ± .1 ^A	6.6 ± .2 ^A	5.6 ± .2 ^B	5.7 ± .2 ^B	.001
Content mass (mg)	1,387.0 ± 62.3 ^B	3,531.7 ± 404.6 ^A	3,846.6 ± 358.5 ^A	1,635.2 ± 90.5 ^B	1,653.2 ± 115.4 ^B	.001
Wet mass (mg)	292.8 ± 22.1 ^C	495.6 ± 32.6 ^A	547.1 ± 36.4 ^A	410.5 ± 27.5 ^B	319.6 ± 13.7 ^C	.001
Dry mass (mg)	51.8 ± 4.3 ^B	70.3 ± 4.5 ^A	82.1 ± 5.9 ^A	76.5 ± 4.8 ^A	59.8 ± 4.1 ^B	.001
Total digestive tract:						
Size (cm)	63.5 ± 1.1 ^B	63.0 ± 1.1 ^{AB}	68.5 ± 2.0 ^A	64.4 ± 1.2 ^{AB}	64.1 ± 1.6 ^B	.05
Content mass (mg)	7,016.7 ± 383.9 ^B	10,452.3 ± 578.7 ^A	12,034.0 ± 769.2 ^A	7,111.1 ± 429.2 ^B	8,018.0 ± 481.6 ^B	.001
Wet mass (mg)	2,274.4 ± 59.4 ^C	2,450.7 ± 133.6 ^{BC}	2,965.0 ± 122.8 ^A	2,594.4 ± 146.5 ^B	2,415.7 ± 87.4 ^C	.001
Dry mass (mg)	417.6 ± 21.6 ^C	475.2 ± 27.8 ^{AB}	494.4 ± 21.6 ^{AB}	531.6 ± 27.8 ^A	477.6 ± 19.2 ^{BC}	.01

Note. Values are expressed as absolute mean ± SEM. HF-W1, HF-W4: high-fiber diet acclimation for 1 and 4 wk, respectively; R-W1, R-W4: high-fiber diet acclimation for 4 wk, followed by restoration to the standard rat diet (low fiber) for 1 and 4 wk, respectively. In each row, different letters indicate significant differences ($P < 0.05$). NS = not significant.

the leptin level reduced control of food intake. The lower DEI of HF gerbils shortly after feeding on the HF diet suggested that low leptin levels might be a signal of an animal in negative energy balance (Flier 1998; Li and Wang 2005a; Zhao and Wang 2005). After restoration of the LF diet, the gerbils increased serum leptin levels with the decrease in DMI, indicating that raising the leptin level increased control of food intake. Together, our data indicate that reversible changes in serum leptin levels played an important role in regulating the adaptive changes in energy intake in the gerbils fed different-quality diets.

BMR

Animals cope with low-quality food not only by changing digestive tract morphology to get more energy from food but also by regulating metabolism to reduce energy demands (McNab 1986; Cruz-Neto and Bozinovic 2004; Silva et al. 2004). Our data show that the gerbils decreased basal metabolism after consuming an HF diet for 2 wk, supporting the hypothesis that small mammals can lower their energy expenditure to survive on a poor-quality diet (Choshniak and Yahav 1987; Veloso and Bozinovic 1993, 2000; Cork 1994; Koteja 1996; Cruz-Neto and

Bozinovic 2004; Silva et al. 2004). In addition, MF1 mice are able to decrease energy expenditure associated with reductions in the time spent in “general activity” when these were insufficient to offset the lower digestible-energy content of food during lactation (Speakman et al. 2001). Similarly, Hambly and Speakman (2005) found that MF1 mice were able to recruit several compensatory mechanisms to maintain stable body mass on a restricted diet at 80% of their ad lib. intake by adjusting their energy expenditure. They also found that, among the components of energy expenditure, resting metabolic rate accounted for 22.3% and activity for 75.5% of the compensation for reduced energy intake (Hambly and Speakman 2005). It was obvious that the gerbils could reduce energy expenditure, as well as decreasing BMR, when consuming a lower-quality diet (high fiber content). Finally, a lower BMR might enhance digestion by retaining digesta in the digestive tract and extracting more energy and nutrients (Veloso and Bozinovic 1993, 2000). Interestingly, BMR recovered after restoration of the LF diet, suggesting that reversible changes in BMR are one of the ways gerbils adapt to differences in dietary quality.

In nature, it should be beneficial to decrease energy expenditure for BMR when only a low-quality diet is available. The

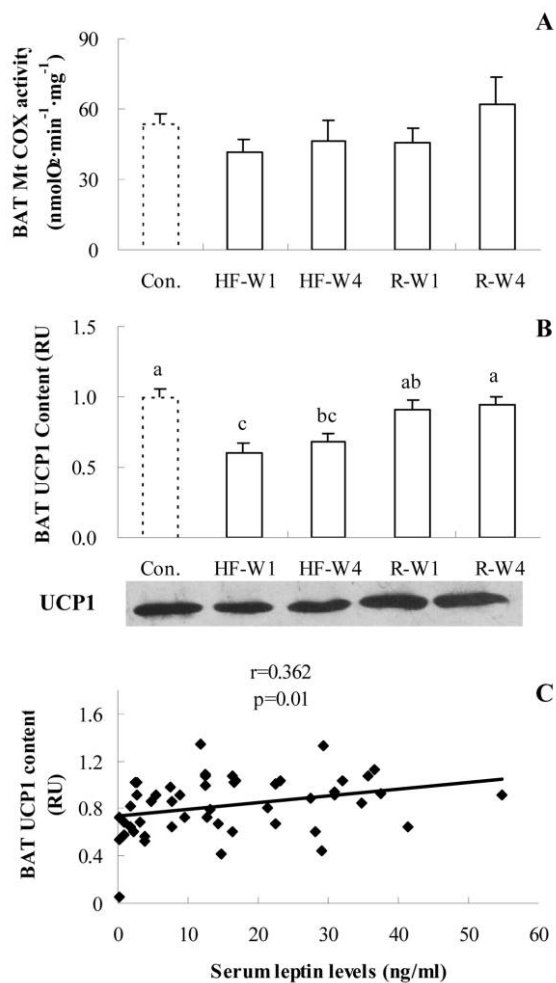


Figure 5. Changes in mitochondrial cytochrome *c* oxidase (Mt COX) activity (A) and uncoupling protein 1 (UCP1) content (B) in brown adipose tissue (BAT) and the correlation between UCP1 and serum leptin levels (C) in response to high-fiber (HF) diet acclimation and restoration of the low-fiber (LF) diet (standard rat chow) in Mongolian gerbils. *Con.*: control group; *HF-W1*, *HF-W4*: HF diet for 1 and 4 wk, respectively; *R-W1*, *R-W4*: HF diet acclimation for 4 wk, followed by restoration of the LF diet for 1 and 4 wk, respectively. Different letters above bars indicate significant differences ($P < 0.05$). Error bars represent 1 SEM.

increase in gut size and/or digestive function in response to poor-quality diet, however, might result in a higher metabolic rate (Nussey et al. 1998). In addition, many previous inter- and intraspecies studies have shown diverse effects of low-quality diets on basal or resting metabolism, not only in rodent species and birds but also in ectothermal species, including chuckwallas (*Sauromalus obesus*) and Steller sea lions (*Eumetopias jubatus*; Veloso and Bozinovic 1993, 2000; Koteja 1996; Nussey et al. 1998; Geluso and Hayes 1999; Rosen and Trites 1999; Cruz-Neto and Bozinovic 2004; Silva et al. 2004; Bozinovic et al. 2007). Thus, the generality of basal and/or resting metabolism changes in response to different-quality diets and the evolutionary relationships between metabolic rate and diet

are far from clear. Cruz-Neto and Bozinovic (2004) suggested that further studies should focus on alternative mechanisms shaping the interaction between diet and BMR, such as enzymatic plasticity, and the effects of diet quality on other components of energy budgets, such as sustainable metabolic and maximum thermogenic rates (Cruz-Neto and Bozinovic 2004).

NST and UCP1

NST, like BMR, is also one of the means of energy expenditure in small mammals, especially in species in cold environments (Heldmaier et al. 1981; Wunder 1984; Wang et al. 2003). Several environmental factors, including photoperiod, temperature, and food availability, can affect NST capacity (Heldmaier et al. 1981; Wunder 1984; Kageyama et al. 2003; Wang et al. 2003; Li and Wang 2005a, 2005b). Our data showed that NST was affected by the HF diet in gerbils: NST decreased by 43%, compared with the baseline, after 1 wk of consuming the HF diet. This suggests that the gerbils could reduce the energy expenditure associated with NST to compensate for the low digestibility and assimilated energy of the HF diet. Under the conditions of similar DEI for HF-LF and LF gerbils from day 14 until day 28, the lower heat production of the HF-LF gerbils did not result in positive energy balance because more energy might have been demanded by the physiological process of food digestion and absorption related to the less digestible HF diet. Similarly, fiber digestion provided 32% of maintenance requirements and 110% of BMR requirements in the fat sand rat, a diurnal gerbillid rodent, indicating higher energy cost on the digestive process (Degen et al. 2000). After restoration of the LF diet, the gerbils enhanced their thermogenic capacity and recovered to control levels of NST, indicating that adjustments in energy expenditure associated with thermogenesis might be one of the adaptive means by which small mammals respond to diets with different fiber contents (Zhao and Wang 2007).

Generally, the elevation of BAT UCP1 expression was consistent with the increase in NST capacity (Demas et al. 2002; Zhao and Wang 2005, 2007). Similarly, our data show that BAT UCP1 expression was downregulated in gerbils after they were offered the HF diet and recovered to control levels after restoration of the LF diet (Zhao and Wang 2007). In addition, the role of leptin in thermogenic regulation seems to be complicated and is still not clear, and the relationship between UCP1 and leptin has been found to be complex (Scarpace et al. 1997; Bing et al. 1998; Abelenda et al. 2003; Li and Wang 2005b). When acclimated to different-quality diets, Mongolian gerbils showed positive correlations between serum leptin levels and UCP1 content, indicating a potential role for leptin in changes in BAT UCP1 expression. This suggests that leptin might regulate the energy expenditure associated with thermogenesis by altering BAT UCP1 expression.

Mongolian gerbils show significant seasonal variations in body mass, energy intake, and thermogenesis to survive in a changing environment. Body mass, body fat mass, and serum leptin levels are higher in summer than in winter, and DMI,

GEI, BMR, NST, and BAT UCP1 expression are lower in summer than in winter (Wang et al. 2000, 2003; Li and Wang 2005b). There are seasonal changes in food habits for gerbils that feed mainly on stems and leaves of plants (relatively low dietary quality) in summer and on plant and crop seeds (relatively high dietary quality) in late fall, winter, and early spring (Zhang and Wang 1998). Our data showed that the gerbils were able to compensate for low dietary quality (high fiber content) by a combination of digestive mechanisms (including increased digestive tract size, mass, and canal capacity, increased food intake and decreased digestibility), metabolic mechanisms (including reduced basal metabolism and thermogenesis), and neuroendocrine mechanisms associated with leptin. Finally, such large, reversible changes in studied phenotypic traits were mainly due to the differing fiber content of the two diets (22.7% and 16.6% difference in neutral detergent fiber and acid detergent fiber content, respectively) but also might be partly due to differing fat and protein content (2.1% and 6.1% difference in fat and protein content, respectively). In addition to diet quality, some natural environmental factors, including food availability and predictability as well as photoperiod and temperature, do have effects on seasonal energy budget changes in gerbils (Wang et al. 2000, 2003; Li and Wang 2005b; Zhao and Wang 2006; Z.-Q. Zhang and D.-H. Wang, unpublished observations). Our data indicate that variation in food quality is at least one of the main factors inducing energetics, body composition, and organ morphological plasticity.

In summary, our findings support our predictions that Mongolian gerbils can compensate for the HF diet by increasing the size and volume of their gastrointestinal tract and food intake and by decreasing thermogenesis. After restoration of the LF diet, gerbils can recover their body mass, body composition, thermogenic capacity, and serum leptin levels. Serum leptin level was related to the changes in food intake in gerbils.

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