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Short photoperiod influences energy intake and serum leptin level in Brandt's voles (*Microtus brandtii*)

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Abstract

Photoperiod cues play important roles in the regulation of seasonal variations in body mass (BM) and energy balance for many small mammals. The present study was designed to examine the effects of photoperiod acclimation on BM, energy intake, and serum leptin levels in Brandt's voles (*Microtus (Lasiopodomys) brandtii*). After 4 weeks of acclimation to either long (LD; light:dark, 16:8) or short (SD; 8:16) photoperiod, SD voles had lower BM, body fat mass, and dry mass of liver and kidneys, but higher digestible energy intake in comparison to LD voles. SD voles also showed a lower level of serum leptin than did LD voles. Furthermore, the level of serum leptin was correlated positively with body fat mass and negatively with gross energy intake. Together, these data suggest that Brandt's voles employ a strategy of minimizing body growth, increasing energy intake, and mobilizing fat deposition in response to cues associated with short photoperiod. Furthermore, leptin seems to be involved in the regulation of BM and energy balance mediated by photoperiod.
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Introduction

Animals have developed various physiological and behavioral strategies, such as changes in reproductive status, thermoregulation, thermogenic capacity, energy intake, digestive tract morphology, and body mass (BM), to deal with seasonal variations in the environment (Li and Wang, 2005; Rousseau et al., 2002, 2003; Wang and Wang, 1996, 2000; Wang et al., 2000, 2003a,b; Wunder, 1984). Seasonal changes in BM have been extensively studied, especially in small rodents in which BM changes are induced by variations of fat reserves resulting from changes of energy intake and/or expenditure (Bartness et al., 1989; Dark and Zucker, 1986; Klingenspor et al., 2000; Steinlechner and Heldmaier, 1982). In many species, photoperiod has been found to play important roles in mediating seasonal variations in BM or energy balance (Bartness and Wade, 1985; Bartness et al., 1989; Genin and Perret, 2000). For example, short photoperiod, independent of cold temperature or food availability, induces a decrease of BM in Djungarian and Siberian hamsters (*Phodopus sungorus*) (Heldmaier, 1989; Klingenspor et al., 2000; Mercer et al., 1997, 2000; Rousseau et al., 2002) and bushy-tailed gerbils (*Sekeetamys calurus*) (Haim, 1996). However, species-specific responses of energy intake to short photoperiod were found in those studies; energy intake decreased in hamsters and increased in gerbils. Interestingly, although collared lemmings (*Dicrostonys groenlandicus*) and gray mouse lemurs (*Microcebus murinus*) responded to short photoperiod by showing an increase in BM, a species-specific pattern of energy intake was also found, in which energy intake showed no changes in lemmings (Powell et al., 2002) but decreased in lemurs (Genin and Perret, 2000). Such species-specific changes in BM and energy intake involve interactions between a network of central and peripheral hormonal signaling systems (Kalra et al., 1999; Mercer and Tups, 2003).

Leptin is the product of the obese gene (*ob*) and is expressed and secreted exclusively by adipocytes (Zhang et al., 1994). Its role in the reproductive endocrine system, the regulation of food intake, and metabolism has been widely studied (Barash et al., 1996; Baskin et al., 1999, 2001; Cheung et al., 2001; Schwartz et al., 2000). Leptin is considered to be an adipostatic signal linking energy metabolism, regulating food intake, and providing prompt feedback to brain areas involved in regulation of energy balance (Ahima and Flier, 2000; Halaas et al., 1995; Klingenspor et al., 1996; Pelleymounter et al., 1995; Zhang et al., 1994). Normal mice show increases in *ob* mRNA expression and serum leptin concentrations with increased fat mass (Maffei et al., 1995). The positive correlation between serum leptin levels and fat mass has also been found in collared lemmings (Johnson et al., 2004), Djungarian hamsters (Klingenspor et al., 2000), and cold acclimated Mongolian gerbils (*Meriones unguiculatus*) (Li et al., 2004). Leptin's role in regulating energy balance makes it a likely candidate for involvement in endocrine regulation of seasonal changes in BM (Johnson et al., 2004). Seasonal fluctuations in serum leptin levels, energy intake, BM, or fat mass have been found in many seasonal acclimated rodents (Klingenspor et al., 1996, 2000; Li and Wang, 2005; Li et al., 2004). Exposure to short photoperiod decreased leptin gene expression in both white and brown adipose tissues in Djungarian hamsters, indicating involvement of leptin in photoperiod-mediated seasonal adaptations (Klingenspor et al., 1996).

Brandt's voles are typical steppe herbivores that mainly inhabit the Inner Mongolia grasslands of China, Mongolia, as well as the region of Beigaer Lake in Russia (Zhang and Wang, 1998). These animals show seasonal variations in basal metabolic rate (BMR), nonshivering thermogenesis (NST), and BM (Wang et al., 2003a). Furthermore, these animals show seasonal changes in energy intake, BM, body fat mass, and serum leptin levels independent of food availability, indicating potential roles for ambient temperature and photoperiod in the regulation of energy balance and BM (Li and Wang, 2005). The present study was designed to further investigate the role of photoperiod, independent of ambient temperature and food availability, on BM and energy intake and the potential underlying mechanisms in the Brandt's voles. We hypothesized that the cues associated with short photoperiod could influence BM, energy intake, and serum leptin levels in Brandt's voles.

Materials and methods

Subjects

Brandt's voles were obtained from a breeding colony started with animals that were initially trapped from Inner Mongolian grasslands. The breeding colony was maintained under 12L:12D (light:dark, lights on 08:00) photoperiod, and room temperature was kept at 23 ± 1°C. After weaning around 25 days of age, all voles were housed in single sex groups (3–4) in plastic cages (30 × 15 × 20 cm) that contained sawdust bedding. Food (rabbit pellets Beijing KeAo Feed Co.) and water were provided ad libitum. The macronutrient composition of the diet was 6.2% crude fat, 20.8% crude protein, 23.1% neutral detergent fiber, 12.5% acid detergent fiber, and 10.0% ash, and the caloric value

is 17.5 kJ/g. At 80–95 days of age, subjects were moved into individual cages for 2 weeks and then randomly assigned into one of two experimental groups that were acclimated either to short photoperiod (SD; 8L:16D with lights on at 08:00; 4 males and 4 females) or to long photoperiod (LD; 16L:8D with lights on at 04:00; 4 males and 4 females) for 4 weeks. Each subject's BM was monitored every week during the photoperiod acclimation.

Energy budget

Food intake was measured in metabolic cages (Liu et al., 2002, 2003; Song and Wang, 2001). Food was provided quantitatively. Food residues and feces were collected from each animal over the 3 days before the photoperiod acclimation began and over the last 3 days of each week during photoperiod acclimation (total 5 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 measured by an oxygen bomb calorimeter (Parr 1281, 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:

$$GEI \ (kJ \cdot d^{-1}) = dry \ matter \ intake \ (DMI) \ (g \cdot d^{-1}) \\ \times energy \ content \ of \ food \ (kJ \cdot g^{-1});$$

$$DEI \ (kJ \cdot d^{-1}) = GEI - (dry \ mass \ of \ feces \cdot (g \cdot d^{-1}) \\ \times energy \ content \ of \ feces \ (kJ \cdot g^{-1}));$$

$$Digestibility \ (\%) = DEI/GEI \times 100\%.$$

Serum leptin levels

All subjects were sacrificed by decapitation between 09:00 and 11:00 after 4 weeks of photoperiodic acclimation. Trunk blood was collected for leptin measurement. Serum was separated from each blood sample and stored at −75°C. Serum leptin concentrations were determined by radio-immunoassay (RIA) using the Linco ^{125}I Multi-species Kit (Cat. No. XL-85K, Linco Research Inc.) which has been validated previously for Brandt's voles (Li and Wang, 2005). 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.

Body composition

After trunk blood was collected, we first extracted the gastrointestinal tract (stomach, small intestine, large intestine, and cecum) and then the thyroid, heart, lungs, liver, pancreas, spleen, kidneys, and urinary bladder. The remaining carcass (including the brain), liver, heart, lungs, spleen, and kidneys each were weighed (to 0.1 g or 0.001 g) to determine wet mass, dried in an oven at 60°C for 10 days to a constant mass, and then weighed (to 0.1 g or 0.001 g) again to determine dry mass. Total body fat was extracted from the dried carcass by ether extraction in a Soxhlet apparatus.

Statistical analysis

Data were analyzed using the SPSS software package (10.0). Distributions of all variables were tested for normality using the Kolmogorov–Smirnov test. Group differences in BM at each time point were analyzed by a two-way analysis of variance (ANOVA) (photoperiod by sex). Group differences in energy parameters (DMI, GEI, DEI, and digestibility), organ wet and dry mass, body fat mass, and serum leptin levels were analyzed by a two-way analysis of covariance (ANCOVA) with BM as a covariate. Repeated one-way ANOVA or ANCOVA (with BM as a covariate) followed by Least-Significant Difference (LSD) post-hoc tests was also used to analyze changes of the BM and energy parameters over the course of photoperiod acclimation. Finally, Pearson's correlation was performed to determine the correlation between serum leptin levels and body fat mass or GEI. Statistical significance was determined at $P < 0.05$.

Results

There were no significant sex differences in any measured parameters in the present study. Therefore, data from males and females were combined.

Effects of photoperiod on BM and energy parameters

Prior to photoperiodic acclimation, there was no difference in BM between LD and SD voles ($F_{(1,12)} = 0.36$, $P > 0.05$) (Fig. 1). However, LD voles had a higher BM than SD voles on day 21 ($F_{(1,12)} = 9.801$, $P < 0.01$) and day 28 ($F_{(1,12)} = 41.523$, $P < 0.01$) of the acclimation (Fig. 1). These differences were largely due to a steady and significant increase in BM in LD voles ($F_{(4,28)} = 38.74$, $P < 0.01$; Fig. 1). The SD voles showed an increase in BM on day 14 of the acclimation ($F_{(4,28)} = 5.47$, $P < 0.01$) and thereafter maintained a relatively constant BM.

There were no significant differences in DMI ($F_{(1,11)} = 0.83$, $P > 0.05$; Fig. 2A), GEI ($F_{(1,11)} = 1.11$, $P > 0.05$; Fig. 2B), DEI ($F_{(1,11)} = 2.35$, $P > 0.05$; Fig. 2C), or digestibility ($F_{(1,11)} = 2.83$, $P > 0.05$; Fig. 2D) between LD and SD voles prior to acclimation. However, at the end of the acclimation (4 weeks), SD voles showed significant increases in DMI ($F_{(1,11)} = 7.79$, $P < 0.05$), GEI ($F_{(1,11)} = 7.77$, $P < 0.05$), and DEI ($F_{(1,11)} = 7.52$, $P < 0.05$) compared to LD voles (Fig. 2). No group difference was found in digestibility at this time point ($F_{(1,11)} = 3.90$, $P > 0.05$). There were no significant differences in these energy parameters over the course of acclimation within both LD voles (DMI, $F_{(4,24)} = 2.01$, $P > 0.05$; GEI, $F_{(4,24)} = 2.02$, $P > 0.05$; digestibility, $F_{(4,24)} = 0.83$, $P > 0.05$), and SD voles (DMI, $F_{(4,24)} = 0.30$, $P > 0.05$; GEI, $F_{(4,24)} = 0.30$, $P > 0.05$; DEI, $F_{(4,24)} = 0.33$, $P > 0.05$; digestibility, $F_{(4,24)} = 2.15$, $P > 0.05$), except for DEI in LD voles ($F_{(4,24)} = 3.42$, $P < 0.05$). Finally, the regression analysis indicated that, for SD voles, DMI ($r = 0.62$, $P < 0.01$), GEI ($r = 0.46$, $P < 0.01$), and DEI ($r = 0.61$, $P < 0.01$) increased significantly over the course of photoperiod acclimation. Such changes were not found either in digestibility for SD voles or for any of the above-mentioned measurements for LD voles.

Effects of photoperiod on body composition, body fat mass, and serum leptin levels

After 4 weeks of photoperiodic acclimation, SD and LD voles differed significantly on several measured parameters (Table 1). For example, LD voles showed higher values in BM, wet carcass mass ($F_{(1,11)} = 4.89$, $P < 0.05$), dry carcass mass ($F_{(1,11)} = 27.17$, $P < 0.01$), body fat mass ($F_{(1,11)} = 28.59$, $P < 0.01$), dry mass of liver ($F_{(1,11)} = 31.41$, $P < 0.01$), and kidneys ($F_{(1,11)} = 22.54$, $P < 0.01$) than did SD voles. LD voles also had a higher level of serum leptin ($F_{(1,11)} = 13.43$, $P < 0.01$) compared to SD voles. Finally, serum leptin levels were positively correlated with body fat mass ($r = 0.59$, $P < 0.05$) (Fig. 3A) and negatively correlated with GEI ($r = -0.58$, $P < 0.05$) (Fig. 3B).

Discussion

Changes of BM and energy balance responding to photoperiod

Seasonal fluctuation in BM is an important adaptive strategy for many small mammals and might be induced by seasonal changes of a variety of environmental factors, including food availability, temperature, or photoperiod (Bartness and Wade, 1985; Gottreich et al., 2000; Li and Wang, 2005). Data from our present study showed that, following 4 weeks of photoperiodic acclimation, SD voles had lower BM than did LD voles. These data are consistent with previous findings showing that changes in photoperiod altered BM in several rodent species including Siberian hamsters (Bartness et al., 1989), collared lemmings (Powell et al., 2002), meadow voles (*Microtus pennsylvanicus*) (Dark and Zucker, 1986), prairie voles (*Microtus ochrogaster*) (Kriegsfeld and Nelson, 1996), and root voles (*Microtus oeconomus*) (Wang et al., 1999). The time course data for BM illustrated two interesting points. First, LD, but not SD, voles showed a steady and significant increase in BM during the acclimation. Brandt's voles usually maintain a constant BM or even show a slight decrease in BM during winter conditions (Li and Wang, 2005). Our data indicate that short photoperiod alone is at least partially responsible for the lack of normal increases in BM in SD voles. Second, LD and SD voles did not differ in their BM until the third week of the acclimation, suggesting that 3 weeks are probably a critical period for short photoperiod to exert significant impacts on BM.

Seasonal changes in energy balance are considered to be a critical factor contributing to the maintenance of appropriate BM, which are affected by long or short photoperiod in several mammals (Haim, 1996; Klingenspor et al., 1996; Powell et al., 2002). Our data showed that the SD voles had higher DMI, GEI, and DEI than did LD voles after 4 weeks of photoperiodic acclimation, suggesting that, despite the lack of increase in BM, SD voles had increased energy intake. Photoperiod has been found to have species-specific effects on BM and energy balance. For example, Djungarian and Siberian hamsters
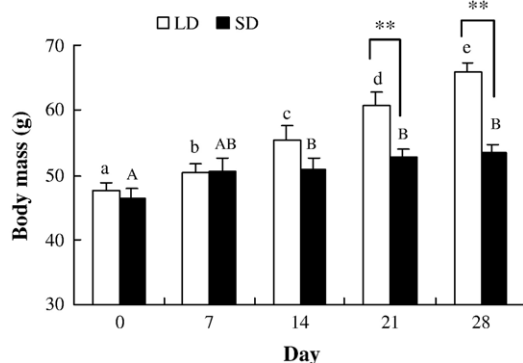

Fig. 1. Changes of body mass in Brandt's voles responding to either long (LD; light:dark, 16:8) or short photoperiod (SD; 8:16). On day 21 and thereafter, LD voles had significantly heavier body weight compared to SD voles. Data are mean ± SE. **$P < 0.01$. Different letters (a, b, c, d, or e) above broken bars indicate significant differences ($P < 0.05$) in measurements within the LD group during the course of acclimation, and different letters (A or B) above solid bars indicate significant differences ($P < 0.05$) within the SD group.
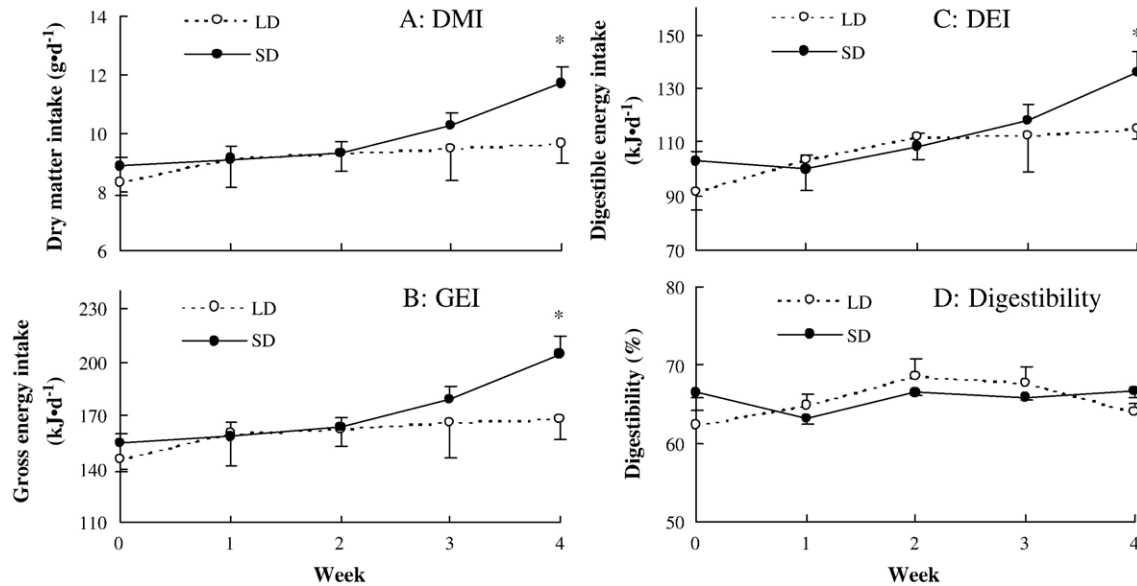
Fig. 2. The effects of photoperiod on the dry matter intake (DMI; A), gross energy intake (GEI, B), digestible energy intake (DEI, C), and digestibility (D) in Brandt's voles acclimated to either long (LD; light:dark, 16:8) or short photoperiod (SD; 8:16). After 4 weeks acclimation, SD voles had significantly higher levels of DMI, GEI, and DEI, compared to LD voles. There was no significant group difference in digestibility. Data are mean ± SE. *$P < 0.05$.

decrease their BM under short photoperiod, which results from a decrease in energy intake and an increase in energy expenditure (Heldmaier, 1989; Klingenspor et al., 2000; Mercer et al., 1997; 2000; Rousseau et al., 2002). On the other hand, collared lemmings (Powell et al., 2002) increase BM under short photoperiod most likely due to decreases in some aspects of energy expenditure rather than increases in energy intake (Krol et al., 2005; Nagy and Negus, 1993). The lower BM and higher energy intake in SD voles than that in LD voles in the present study suggest that the former may have an elevated energy expenditure. This notion is indeed supported by previous

studies (Zhao and Wang, 2005). Seasonal changes in thermogenesis have been found in field-captured Brandt's voles as well as in their breeding colony in outdoor enclosure (Wang et al., 2003a; Li and Wang, 2005). Furthermore, SD voles could increase both basal metabolism and nonshivering thermogenetic capacity, compared to LD voles (Zhao and Wang, 2005). It should be pointed out that Brandt's voles do not hibernate or enter torpor and thus must face high cost of thermoregulation during winter seasons. It is likely that this species has evolved an adaptive strategy not only to increase energy intake for elevated basal metabolism and thermogenesis demands during

Table 1

Wet and dry carcass mass, body fat mass and content, serum leptin levels, and wet and dry organ mass in Brandt's voles acclimated to either long photoperiod (LD, light:dark, 16:8 h) or short photoperiod (SD, light:dark, 8:16 h)

|	LD		SD		P
	Female	Male	Female	Male	(treatment)
Body mass (g)	64.6 ± 2.4	69.9 ± 3.7	54.4 ± 1.7	55.8 ± 2.5	<0.01
Wet carcass mass (g)	44.3 ± 2.8	51.1 ± 3.7	38.4 ± 1.2	42.3 ± 3.8	<0.05
Dry carcass mass (g)	20.1 ± 0.6	20.3 ± 1.6	14.8 ± 1.6	12.9 ± 0.4	<0.01
Body fat mass (g)	10.07 ± 0.56	10.63 ± 1.36	5.25 ± 0.79	5.31 ± 0.60	<0.01
Body fat content (%)	50.26 ± 2.38	51.76 ± 2.87	41.97 ± 5.57	41.04 ± 3.52	<0.05
Serum leptin levels (ng ml^{-1})	25.16 ± 5.56	27.16 ± 6.66	8.56 ± 2.59	9.52 ± 1.47	<0.01
Organ wet mass (g)					
Liver	3.107 ± 0.185	2.811 ± 0.173	2.063 ± 0.198	1.959 ± 0.143	<0.01
Heart	0.398 ± 0.016	0.310 ± 0.018	0.244 ± 0.022	0.282 ± 0.040	<0.01
Lung	0.436 ± 0.020	0.454 ± 0.047	0.292 ± 0.036	0.436 ± 0.101	ns
Spleen	0.064 ± 0.019	0.050 ± 0.007	0.049 ± 0.013	0.054 ± 0.006	ns
Kidneys	0.664 ± 0.024	0.616 ± 0.026	0.532 ± 0.053	0.503 ± 0.038	<0.01
Organ dry mass (g)					
Liver	1.467 ± 0.192	1.257 ± 0.166	0.679 ± 0.043	0.707 ± 0.074	<0.01
Heart	0.079 ± 0.016	0.072 ± 0.005	0.055 ± 0.005	0.065 ± 0.011	<0.09
Lung	0.454 ± 0.047	0.091 ± 0.003	0.436 ± 0.101	0.072 ± 0.008	ns
Spleen	0.014 ± 0.004	0.014 ± 0.002	0.025 ± 0.013	0.014 ± 0.001	ns
Kidneys	0.198 ± 0.003	0.176 ± 0.009	0.143 ± 0.011	0.140 ± 0.012	<0.01

Data are mean ± SE.
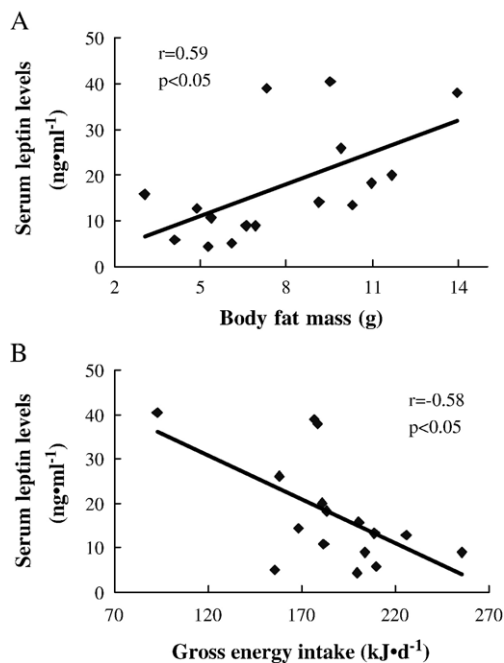
Fig. 3. Correlation of serum leptin levels with body fat mass (A) or gross energy intake (B) in Brandt's voles acclimated to either long (LD; light:dark, 16:8) or short photoperiod (SD; 8:16). Serum leptin levels were positively correlated with body fat mass ($r = 0.59$, $P < 0.05$) and negatively correlated with gross energy intake ($r = -0.58$, $P < 0.05$).

winter conditions but also to minimize energy requirements on maintenance of BM. Our data suggest that cues associated with SD acclimation, independent of ambient temperature and food availability, play important roles in regulating BM and energy intake in Brandt's voles.

Changes of body composition responding to photoperiod

Decreased BM in Siberian hamsters under short photoperiod is generally accompanied by decreases of body fat mass (Klingenspor et al., 1996). Similarly, our results showed that SD voles had lower body fat mass than did LD voles after 4 weeks of photoperiodic acclimation. These data indicate that SD voles likely had greater energy mobilization than did LD voles, although we cannot exclude a possibility that the two also differed in energy deposition. Furthermore, SD voles had significantly lower dry masses of carcass (45.3%), liver (97.1%), and kidneys (32.6%) in comparison to that of LD voles, suggesting that the former minimized energy expenditure for maintenance by reducing the sizes of body components. Therefore, the significantly increased energy intake in SD voles did not contribute to larger BM and body components but might mainly contribute to the significantly increased energy expenditure for basal metabolism and nonshivering thermogenesis.

Changes of serum leptin levels responding to photoperiod

Leptin, expressed and secreted exclusively by adipocytes, is involved in the endocrine regulation of seasonal changes in BM

(Johnson et al., 2004; Zhang et al., 1994). Our data showed that LD voles had higher serum leptin levels than did SD voles with increased body fat mass after 4 weeks of photoperiodic acclimation, and there was a significant positive correlation between body fat mass and serum leptin levels. A previous study has found that Brandt's voles showed seasonal variations in BM and body fat mass associated with significant seasonal changes in circulating leptin levels (Li and Wang, 2005), similar to that for Siberian hamsters (Rousseau et al., 2002). Furthermore, the seasonally acclimatized Brandt's voles also showed a significant positive correlation between BM or body fat mass and serum leptin levels (Li and Wang, 2005). It has been demonstrated that seasonal changes in circulating leptin levels are partially attributable to changes in photoperiod. For example, short photoperiod causes a decrease of plasma leptin levels and down-regulation of mRNA for leptin gene in Siberian hamsters (Horton et al., 2000; Klingenspor et al., 1996; Mercer et al., 2000). Similar to hamsters, SD voles showed lower serum leptin levels compared to LD voles. Although we did not examine the leptin mRNA of adipose tissues, data from the present study provide evidence to support our hypothesis that seasonal changes of BM and body fat mass, partly driven by photoperiod, might be mediated by leptin.

SD voles showed decreased serum leptin levels with increased energy intake compared to LD voles. However, there was also a species-specific change in serum leptin levels in response to photoperiod. Short photoperiod induced decreased serum leptin levels with decreased energy intake in Siberian hamsters (Klingenspor et al., 1996) and increased serum leptin levels with increased energy intake in collared lemmings (Johnson et al., 2004). Furthermore, the present data showed a significant negative correlation between serum leptin levels and GEI in Brandt's voles, which also has been found in their breeding colony in an outdoor enclosure without specific diet availability and quality (Li and Wang, 2005). Furthermore, these voles increased expenditure for basal metabolism and nonshivering thermogenesis under short photoperiod (Zhao and Wang, 2005), suggesting that leptin might be a starvation signal when the SD voles were in a negative energy balance (Flier, 1998; Li and Wang, 2005). To maintain energy balance, SD voles increased energy intake in response to a hunger signal via leptin to meet the increased energy expenditure for thermogenesis. It also suggested that leptin involved changes of energy balance induced by photoperiod.

Conclusion

Seasonal changes in BM, energy balance, and thermogenesis are an important strategy for Brandt's voles for coping with remarkable seasonal environmental variation (Li and Wang, 2005; Wang et al., 2003a). Our data show that SD voles have higher GEI and lower BM and serum leptin levels compared to LD voles. Furthermore, a positive correlation between serum leptin levels and body fat mass and a negative correlation between serum leptin levels and GEI were found in the voles. Short photoperiod increased energy intake and decreased BM or body fat mass and serum leptin levels independent of cold

temperature and food availability. It suggests that seasonal changes in energy balance, BM, and body fat mass were partly driven by photoperiod in the voles. By responding to a hunger signal associated with leptin, SD voles increased energy intake to meet the increased energy expenditure for thermogenesis. Our data also suggest that leptin might be involved in photoperiod-mediated seasonal variations of energy balance and BM in Brandt's voles.

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