Energetic parameters in pregnant and lactating rat (*Lasiopodomys brandtii*) fed high- or low-fibre diets

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Abstract

The effect of diet quality (high-fibre (HF) or low-fibre (LF)) on energetic parameters in pregnant and lactating rats (Lasiopodomys brandtii) was examined. There was no significant difference ($p > 0.05$) in body mass of voles prior to dietary acclimation and during pregnancy. Energetic parameters (dry matter, gross energy, digestible energy intake and digestibility) as well as body mass of pups was not significantly ($p > 0.05$) affected by diet quality. Low fibre diet caused a decreased ($p < 0.05$) in feed and gross energy intake and increased ($p < 0.001$) digestible energy intake at mid lactation while digestibility was significantly increased at early lactation. Liver and kidney were significantly ($p < 0.05$) lighter in voles on low fibre diet. No significant difference was observed between diets for metabolic rate. These results revealed that rats can compensate for poor quality (HF) diet physiologically by increasing food intake and decreasing digestible energy intake and digestibility to keep reproductive performance unaffected. The most energetically demanding period of breeding cycle of rat was mid lactation.

Key words: Energetic parameters, High- and low-fiber diet, Lactating, Pregnant, Rat

Introduction

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

Brandt's vole, (*Lasiopodomys brandtii*),

also known as the steppe vole, is a species of rodent in the family Cricetidae. They feed mainly on grass (Li and Wang, 2007). Steppe voles are non-hibernating herbivores that inhabit mainly the grasslands of Inner Mongolia of China, Mongolia, and the Baikal region of Russia. These rats are found in Nei Mongol, Jilin, and Hebei provinces in north-east China, in Mongolia and southern Transbaikalia in Russia. Their habitat is dry and pastures and they are sometimes also found in lakeside meadows and river valleys. However, little or nothing is known about the energy intake and allocation in pregnant and lactating steppe voles fed different fibre levels. It is hypothesized that energy intake in pregnant and lactating rat can be increased by low fibre diet and that low

fibre diet will improve pregnancy and lactation performance of rat. The objective of this work was to examine the effect of fibre levels on reproductive performance, energy intake and oxygen consumption of rat.

Materials and Methods

Animals

Rats (90–120 days old) were the offspring of the voles trapped in Inner Mongolian Grasslands in May 1999 and raised in the Institute of Zoology, Chinese Academy of Sciences. This rat has a gestation length of 20–22 days and lactation length of 21–22 days. Pups start eating solid food from day 15 of lactation. Virgin voles were housed individually in plastic cages (30 cm × 15 cm × 20 cm) with sawdust and a little cotton as bedding. The voles were kept at 23 ± 1°C, under a photoperiod of 16:8-h light-dark cycles (lights on at 0400 h).

Experimental animals

Twenty four rats were used for data collection (twelve rats per treatment). The animals were given free access to either high-fibre diet or low-fibre diet. Nutrient composition of the two diets is presented in Table 1. Two weeks after diet acclimatisation, the females were paired with males (1 male per female) for two days to allow for mating after which the males were removed. The females were thereafter

monitored until parturition and during lactation. The body mass of the pups were also monitored. During the test, female voles were housed individually in stainless steel mesh metabolic cage (30 cm × 15 cm × 20 cm), in which food and water were provided *ad libitum*. Residual food and faeces were collected after a 3-day test, oven dried at 60°C to constant weight and separated manually. The caloric value of food and faeces were determined using Parr 1281 oxygen bomb calorimeter (Parr Instruments). The cages were washed while the sawdust and beddings were changed every 3 days.

Energy Intake

Energy intake was measured at day 6 intervals from the start of the experiment to the end of the experiment as described previously (Liu and Wang, 2007, Song and Wang, 2006). Gross energy intake (GEI) contents of food and faeces were measured by a Parr 1281 oxygen bomb calorimeter (Parr Instruments). Gross energy intake (GEI), digestible energy intake (DEI), metabolizable energy intake (MEI), and digestibility (%) were calculated according to the following equations (Liu *et al.* 2003):

$$\begin{aligned} \text{Dry matter intake (DMI, g d}^{-1}\text{)} \\ &= \text{food intake (g d}^{-1}\text{)} \\ &\times \text{dry matter content of food (\%);} \end{aligned}$$

Table 1. Nutrient composition of high- and low-fibre diet based on dry mass

Parameter (%)	High-fibre diet (HFD)	Low-fibre diet (LFD)
Crude fibre	12.36	3.54
Crude fat	3.94	5.44
Crude protein	16.64	21.04
Moisture	9.58	8.86
Ash	8.68	6.33
Ca	1.06	1.06
P	0.72	0.87
Caloric value (kJ/g)	19.70	17.58

$$\text{GEI (kJ}\cdot\text{d}^{-1}) = \frac{\text{dry matter intake (DMI) (g}\cdot\text{d}^{-1}) \times \text{gross energy content of food (kJ}\cdot\text{g}^{-1})}{1000}$$

$$\text{DEI (kJ}\cdot\text{d}^{-1}) = \frac{\text{GEI} - [\text{mass of feces (g}\cdot\text{d}^{-1}) \times \text{gross energy content of feces (kJ}\cdot\text{g}^{-1})]}{1000}$$

$$\text{Digestibility (\%)} = \frac{\text{DEI}}{\text{GEI}} \times 100\%$$

Metabolic trials

Resting metabolic rate (RMR) was measured on day 18 of lactation by using an established closed-circuit respirometer at $30\pm0.5^{\circ}\text{C}$ (within their thermal neutral zone) as described previously (Wang *et al.* 2000; Li and Wang 2005b). Briefly, the metabolic chamber volume was 3.6 L and the temperature inside the chamber was maintained by a water bath. KOH and silica gel were used to absorb carbon dioxide and water, respectively, in the metabolic chamber. The voles were weighed before and after each test. After 60 minutes stabilization in the chamber, oxygen consumption was recorded for another 60 minutes at 5 minutes intervals. Two stable consecutive lowest readings will be taken to calculate RMR and corrected to standard temperature and pressure (STP). All metabolic measurements were taken between 0900 and 1700 hours to minimize any effects of circadian rhythms.

Maternal Body Composition

After the 18 days of experiments, the dams were asphyxiated by CO_2 overdose between 09:00 h and 11:00 h. The interscapular BAT (IBAT) was immediately removed and dissected, weighed, and stored at -80°C until assayed. After interscapular BAT was removed, the visceral organs, including heart, lung, liver, kidneys, spleen, uterus

and gastrointestinal tract (stomach, small intestine, cecum, proximal colon and distal colon) were extracted and weighed (± 1 mg). The gastrointestinal tract was rinsed with saline to remove its contents and weighed. The body mass without visceral organs was defined as wet carcass mass.

Statistical analysis

All data were expressed as mean $\pm$ SE. Differences in parameters measured were determined by independent samples t-tests. Body mass variation was measured with repeated measurements followed by Tukey's HSD post-hoc to determine the daily variation. Data were analysed using the SPSS 2007 software package. Statistical significance was assumed at $P < 0.05$.

Results

Body mass of dams and pups

There were no differences in body mass prior to dietary acclimatisation, body mass of control (high fibre) and low fibre vole averaged (day 0, HF, 35.37 ± 1.13 ; LF, 35.93 ± 0.76 g; $F_{1,22} = 3.841$, $P > 0.05$ Fig.1). Generally, body mass of Vole dams fed high fibre diet were slightly higher than those on low fibre diet during pregnancy and lactation. Also, there was no significant effect of diet on body mass (BM, g) of rat throughout pregnancy and lactation, although body mass was slightly low in HF voles on day 21 (HF, 42.61 ± 2.36 ; LF, 42.65 ± 1.46 g; $F_{1,22} = 2.970$, $P > 0.05$) of pregnancy and day 15 (HF, 51.48 ± 2.37 ; LF, 52.23 ± 1.77 ; $F_{1,22} = 1.131$, $P > 0.05$) of lactation (Fig. 1). The body mass of high and low fibre lactating voles decreased as lactation advanced. Pups body mass of high and low fibre vole averaged (day 0, HF, 21.98 ± 1.67 ; LF, 18.23 ± 1.25 g; $F_{1,22} = 1.629$, $P > 0.05$). Also, pups body mass was not significantly affected by diet throughout lactation (Fig. 2). The

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Fig. 1. Changes in body mass responding to high-fibre diet (HF) and low fibre diet (LF) during 14 days of acclimatisation, 21 days pregnancy and 18 days lactation in Brandt's voles. High-fibre voles did not differ significantly during acclimatisation, pregnancy and lactation. Data are mean $\pm$ SE. $P>0.05$

Fig. 2 Body mass of Brandt's voles pups whose mother's were fed high and low fibre diet. Data are mean $\pm$ SE. $P>0.05$

difference was not significant ($P>0.05$). The interaction between diet and time was not significant ($F_{23,456}=1.521$)

Dry matter intake during pregnancy

The DMI of Voles increased, on average, from 7.82 ± 0.75 g on day 6 of pregnancy to 10.15 ± 0.95 g on day 18 for high fibre diet and from 5.84 ± 0.51 g on day 6 of pregnancy to 8.78 ± 0.35 g on day 18 of pregnancy for rats on low fibre diet (Fig. 3). This intake was equivalent to a gross energy intake of 132.07 ± 12.75 kJ/day on day 6 of pregnancy to 171.64 ± 16.11 kJ/day on day 18 for rats on high fibre diet and 103.19 ± 9.10 kJ/day on day 6 to (155.09 ± 6.26) kJ/day on day 18 for rats on low fibre diet.

Energy intake during lactation

The daily feed intake increased, on average, from 11.38 ± 1.28 g on day 6 of lactation to 15.18 ± 2.23 g on day 18 in voles on high fibre diet and from 8.35 ± 1.31 g on day 6 of lactation to 12.97 ± 0.75 g on day 18 in voles on low fibre diet (Fig. 3). This intake was equivalent to a gross energy intake of 192.28 ± 28.42 kJ/day on day 0 of lactation to 256.56 ± 37.80 kJ/day on day 18 for the high fibre diet and 147.60 ± 16.20 kJ/day and on day 0 of lactation and 229.21 ± 13.21 kJ/day on day 18 in voles on low fibre diet. Dry matter intake and GEI in HF voles were significantly higher than LF voles at mid lactation (DMI $F_{1,10} = 0.011$, $P<0.05$, GEI $F_{1,10} = 10.55$, $P<0.05$). Feed and energy intake increased in voles on high fibre diet by 89% at mid lactation when compared with voles on low fibre diet. However, digestible energy intake and digestibility were significantly lower in HF voles at mid lactation (DEI, $F_{(1,10)}=77.628$; $P<0.001$) and (DIG, $F_{(1,10)}=4.38$, $P<0.05$) respectively.

Basal metabolic rate

Diet had no significant ($P>0.05$) effect on oxygen consumption of lactating voles. The average values were 191.48 ± 86.01 and

193.79 ± 80.97 ml/h/g for high and low fibre diet respectively (Table 2).

Body composition

There was no significant ($P>0.05$) effect of diet on body composition of lactating voles except for liver and kidney that were significantly higher in high fibre voles Table 2.

Discussion

The present study showed that there were no differences in body mass during acclimatisation, pregnancy and lactation. However, voles on high fibre diet had a slightly higher body mass as compared to voles on low fibre diet. A previous study on growing voles showed lower body mass in high-fibre compared to low-fibre voles (Zhao and Wang, 2007). Voles on high and low fibre diet showed a steady decrease in body mass. This is consistent with the report of Zhang and Wang, (2007). Higher body mass in voles on HF diet may be due to increased body fat mass. Low fibre diet stimulated increase in metabolic rate. Dry matter intake and GEI were higher in voles fed high fibre diet than voles fed low fibre. This implies that rat can physiologically regulate energy parameters and metabolic rate in response to changes in food quality.

The increase in dietary fibre intake from voles on high fibre diet can result in decreased in digestibility (Zhao and Wang, 2007), which was confirmed in this study. 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). Animals on lower calorie intake were able to enhance their digestive efficiency to extract more energy from digested food (Hambly and Speakman, 2005). For rat, the higher digestibility in low fibre diet group was likely to compensate for the decrease in

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Table 2: Body composition (g) and oxygen consumption (ml/h/g) of lactating Brandt's vole fed low and high fibre diet

Body traits	High-fibre N=12	Low-fibre N=12	P value	F _(1,22)
Body mass	46.88 ± 1.94	46.31 ± 1.49	ns	0.65
Oxygen (BMR)	191.48 ± 86.01	193.79 ± 80.97	ns	0.58
BAT1	0.07 ± 0.01	0.06 ± 0.01	ns	0.06
BAT2	0.07 ± 0.01	0.06 ± 0.01	ns	0.41
Liver	2.46 ± 0.18 ^a	2.35 ± 0.88 ^b	(p<0.05)	5.83
Heart	0.22 ± 0.01	0.22 ± 0.01	ns	2.40
Lungs	0.34 ± 0.02	0.36 ± 0.02	ns	1.80
Kidney	0.56 ± 0.04 ^a	0.50 ± 0.01 ^b	(p<0.05)	5.78
Spleen	0.04 ± 0.01	0.04 ± 0.01	ns	0.09
Stomach	0.39 ± 0.02	0.36 ± 0.02	ns	0.17
Small Intestine	0.75 ± 0.07	0.86 ± 0.05	ns	2.03
Caecum	0.61 ± 0.04	0.68 ± 0.05	ns	0.26
Colon	0.51 ± 0.04	0.64 ± 0.13	ns	0.47
Gonad	0.12 ± 0.01	0.12 ± 0.01	ns	0.15
Mammary gland	1.01 ± 0.15	0.91 ± 0.12	ns	0.49
Carcass	26.98 ± 1.01	25.29 ± 0.86	ns	0.10

gross energy intake (Peacock and Speakman, 2010). Together, these results indicated that high quality food associated with high digestibility might contribute to increased metabolic rate. When fed high-fibre diet, small mammals could increase energy intake to compensate for low digestibility caused by high fibre content in diet. The increase in DMI and GEI and decreased in DIG in Voles fed high fibre diet as compared with Voles on low fibre diet is in agreement with Zhao and Wang (2007). Energy demands increase with the process of reproduction; therefore, the maintenance of proper body mass is essential to the survival and breeding in small mammals. The higher energy demands during reproduction were mainly met by increased energy intake with a few exceptions such as some bats (McLean and Speakman, 1999). In the present and previous studies, voles on low fibre diet recorded higher digestibility than those on high fibre diet thus corroborating Zhao and

Wang (2007). These data suggest that the female voles increased energy intake to meet the high energy demand for fetus development and milk production.

Lactation is a state characterized by negative energy balance in the lactating female, due to the profound energy drain resulting from milk production (Li *et al.*, 1998). Generally, rat increased energy intake during lactation, that is, they rely mainly on increased energy intake and reduce digestibility to meet the high energy demands of reproduction (Mattingly and McClure, 1982; Millar, 1987). The increase in energy demand during lactation is usually met by increased food intake in small mammals (Bartness, 1997; Johnstone and Higuchi, 2001; Speakman and Król, 2005), such as cotton rats (*Sigmodon hispidus*) (Randolph *et al.*, 1977), northern grasshopper mice (*Onychomys leucogaster*) (Sikes, 1995), laboratory mice (*Mus musculus*) (Johnson *et al.*, 2001), and rat (Liu *et al.*, 2003). The high digestibility

associated with low fibre implies that low fibre diet reduces the work of enzymes and the requirement for large surface area for absorption of nutrient. However, different results can be found under natural conditions, for example large-littered species mobilized relatively more energy reserves during lactation and had a lower probability of encountering an energy shortage than the small-littered species (Millar, 1987; Zhang and Wang, 2008).

It has been known that changes in basal metabolic rate (BMR), one of the major component of total energy expenditure are important in the regulation of energy budgets and body mass in many small mammals in response to environmental fluctuations including temperature, photoperiod or food (Peacock and Speakman, 2010). In this study, significant effect of diet on BMR was not observed, although, it has been previously reported that poor quality food could decrease BMR (Zhao and Wang, 2007, Veloso and Bozivonia, 1993).

In the current study, voles on high fibre diet had increased liver and kidney weights suggesting an adaptive mechanism to cope with the high feed intake associated with voles on high fibre. The increase in mass especially the enlargement of liver has been known to contribute to dam's increased energy expenditure for maintenance (Zhang and Wang, 2008). Liver is the site of cytochrome c oxidase (COX) activity which is associated with thermogenesis (Zhang and Wang, 2008).

Conclusion

There were no significant differences in body mass of dams and pups fed high and low fibre diet. Dry matter and gross energy intake were significantly higher in voles on high fibre diet as compared to voles on low fibre diet at mid lactation only while

digestible energy intake and digestibility were significantly lower in high fibre fed voles at mid lactation. Visceral organs such as liver and kidney were significantly higher in voles on high fibre diet. Therefore, voles on high fibre level can compensate the poor quality diet physiologically by increasing food intake and decreasing basal metabolic rate. This result suggests that voles adjusts body mass, energy parameters and basal metabolic rate to meet the high demands of pregnancy and lactation and mid-lactation is the most energetically demanding period of the breeding cycle.

Recommendation

Diet of high quality and quantity should be fed to voles particularly at mid-lactation.

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