



Limits to sustainable energy budget during lactation in the striped hamster (*Cricetulus barabensis*) raising litters of different size

Zhi-Jun Zhao^{a,*}, Qing-Sheng Chi^b, Jing Cao^a

^a School of Agricultural Science, Liaocheng University, 1 Hunan Lu, Liaocheng, Shandong 252059, China

^b State Key Laboratory of Integrated Management for Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China

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ABSTRACT

A female animal appears to approach an upper limit to the rate of sustained energy intake/metabolic rate (SusEI/MR) during lactation. However, different species of animals may respond differently to the sustainable limit. Here, we measured energy budget during lactation in female striped hamsters raising litters of natural size (Con), and females whose litter size was manipulated during early lactation to support fewer or more pups (minus pups, MP or plus pups, PP). The striped hamsters significantly decreased their body mass and increased food intake from early to late lactation; and MP females had lower weight loss and food intake than the control and PP females. Litter size of the PP group decreased significantly over the period of lactation, and pups were weaned at a similar weight to that of the controls. MP females supported a significantly lower litter mass throughout lactation compared with the control and PP females, but during late lactation the pups from the MP group were significantly heavier. Resting metabolic rate (RMR) did not differ significantly between the three groups and the gross energy intake during peak lactation was $5.0\times$, $4.2\times$ and $5.0\times$ RMR for the control, MP and PP females, respectively. Female striped hamsters reached a plateau in food intake at around 14 g/d during peak lactation, which might signify a limit of SusEI at $5.0\times$ RMR. However, it was not possible to determine whether the limitation on SusEI was imposed centrally by the capacity of the gastrointestinal tract to process food, peripherally by the capacity of the mammary gland to produce milk, or by the capacity of animals to dissipate heat.

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1. Introduction

Lactation is the most energetically demanding period encountered by small mammals. Maternal energy requirement at peak lactation can approximate the maximum for sustained work (Kirkwood, 1983; Weiner, 1987, 1989; Peterson et al., 1990; Hammond and Diamond, 1992, 1997; Koteja, 1996; Rogowitz, 1996, 1998; Thompson and Nicoll, 1986; Speakman and Król, 2005; Speakman, 2008; Zhang and Wang, 2007; Zhang et al., 2009). In many situations, mothers appear to approach an upper limit or “ceiling” to their rate of sustained energy intake/metabolic rate (SusEI/MR) during lactation (Myers and Master, 1983; Kenagy et al., 1990; Hammond and Diamond, 1992, 1994, 1997; Rogowitz, 1996, 1998; Speakman and Król, 2005, 2010; Speakman, 2007). It has been reported in some mammal species that the factor limiting SusEI/MR may not be the capacity of the intestinal tract to take in, process and distribute energy (Hammond and Diamond, 1992, 1994; Speakman and Król, 2005, 2010; Zhang and Wang, 2007). The limits to SusEI/MR might also be set peripherally by

the capacity of the mammary gland to produce milk (peripheral limitation hypothesis) (Hammond and Diamond, 1992, 1994; Zhao and Cao, 2009a) or by the capacity of the animal to dissipate body heat generated as a by-product of processing food and producing milk (heat dissipation limitation hypothesis) (Król et al., 2003; Król and Speakman, 2003a,b; Speakman and Król, 2005, 2010). For example, MF1 mice lactating at 21 °C were not able to increase food intake to meet the increased energy demands imposed by raising larger litter sizes or to meet combined energy demands by lactation and concurrent pregnancy, but the asymptotic food intake in females lactating at cold temperatures did increase beyond that observed in normal lactating females (Johnson and Speakman, 2001; Johnson et al., 2001a,b,c; Król and Speakman, 2003a,b; Król et al., 2003; Speakman and Król, 2005, 2010). After exposure to high temperatures during lactation (35 °C), MF1 mice and Brandt's voles exhibited significant decreases in food intake and milk energy output during peak lactation (Król and Speakman, 2003a,b; Wu et al., 2009). Fur removal further increased both asymptotic food intake and reproductive output in MF1 females, supporting the “heat dissipation limitation hypothesis” (Król et al., 2007).

However, when Hammond et al. (1996) manipulated Swiss mice by surgically removing some mammary tissue they found that

* Corresponding author. Tel.: +86 635 8538232; fax: +86 635 8239963.

E-mail address: zhaozj73@yahoo.com.cn (Z.-J. Zhao).

mice manipulated in this way were unable to upregulate the milk production of the remaining tissue as would be predicted by the heat dissipation limit hypothesis (Hammond et al., 1996). Additionally, shaved female Swiss mice did not raise larger litter sizes or heavier litter masses (Zhao and Cao, 2009a). Milk production did not differ significantly between lactating cotton rats (*Sigmodon hispidus*) at 8 and 21 °C (Rogowitz, 1998). Brandt's voles lactating at cold temperatures increased their food intake during late lactation but raised lighter litter masses as compared to the animals lactating at room temperature (Zhang and Wang, 2007). These studies provide support for the “peripheral limitation hypothesis” instead of the “heat dissipation limitation hypothesis”. Thus, different limitations on SusEI/MR may exist in different animal species. Even within a species, the limits may be imposed by different factors depending on the litter size (Wu et al., 2009), but the reasons for these differences remain unknown.

Limitations on SusEI during lactation may determine the maximum investment of mammals in their offspring (Johnson et al., 2001a). More energy allocation to offspring (in the form of milk) may increase the growth rate or decrease the mortality of dependent offspring, but at the same time may also increase weight loss in the mothers and maternal risk (Rogowitz, 1996, 1998). So, various trade-offs and conflicts may occur during lactation. Although females can increase their food intake and produce more milk with increasing litter size, this is generally insufficient to support the growth rates observed in small litters and, consequently, pups from larger litters have lower growth rates (Russell, 1980; Knight et al., 1986; Fiorotto et al., 1991; Rogowitz and McClure, 1995; Rogowitz, 1996, 1998; Johnson et al., 2001a). The trade-offs are also visible in female cotton rats, where the energy exported to pups in small litters increases during lactation, whereas the energy exported to pups in large litters is consistently low; hence, pups from large litter sizes are lighter compared with those from small litter sizes (Rogowitz, 1996, 1998). It is suggested that the potential trade-offs may vary depending on parental ability to increase energy intake from food and the investment in reproduction (Rogowitz, 1996, 1998). For instance, Swiss mice have an asymptotic food intake of 19 g/d during peak lactation and raise a maximum of 14 pups (Hammond and Diamond, 1992, 1994; Hammond et al., 1994, 1996; Zhao and Cao, 2009a), while for MF1 mice, the asymptotic food intake during peak lactation is 26 g/d, and the maximum litter size raised is 16 pups (Speakman and McQueenie, 1996; Johnson et al., 2001a), indicating that different animal species may respond differently to the sustainable limit. To what extent should the mother allocate her resources to offspring or conserve resources to meet maternal requirements? This decision may have important fitness consequences (Rogowitz, 1996, 1998).

The striped hamster (*Cricetulus barabensis*) is a major rodent in northern China and is also common in Russia, Mongolia, and Korea (Zhang and Wang, 1998). It has been shown that there are seasonal variations in population dynamics in wild hamsters and two peaks usually occur in April and August (Zhu and Qin, 1991). The reproductive period comprises 10 months (ranging from February to November), during which this species has two reproductive peaks in spring and autumn (Xing et al., 1991; Zhu and Qin, 1991; Dong et al., 1993; Hou et al., 1993; Jiang et al., 1994; Bao et al., 2001; Wang et al., 2003).

Regarding the different responses to the limitation of food intake and reproductive output, we aimed to investigate the factors limiting sustainable energy budget during lactation in striped hamsters raising litters of different sizes. For this purpose, we measured maternal body mass, food intake, litter size and mass in females raising natural litter sizes as well as smaller or larger litter sizes. Maternal resting metabolic rate during late lactation was also measured.

2. Materials and methods

2.1. Animals and experimental protocol

Striped hamsters were obtained from our laboratory-breeding colony (three generations in captivity), which was started with animals that were initially trapped from farmland at the center of Hebei province (115°13'E, 38°12'N), North China Plain. The animals were housed under a photoperiod of 12L:12D (lights on at 07:00) at a temperature of 23 ± 1 °C. Food (standard rodent chow; Beijing KeAo Feed Co., Beijing, China) 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. All animal procedures were approved by the Institutional Animal Care and Use Committee of the School of Agricultural Science, Liaocheng University.

Thirty-three virgin female hamsters aged 3.5–4 months were housed individually in plastic cages (29 cm × 18 cm × 16 cm) with fresh saw dust bedding. These females were paired with males for 11 days, after which time the males were removed. Following parturition (day 0 of lactation), 12 of the females were allowed to raise a natural litter size throughout lactation and termed the “control” females (Con, $n = 12$, total number of offspring = 58). The litter sizes of the remaining females were manipulated by cross-fostering starting on day 0. Two to three pups (average of 2.2) were removed from the females and therefore these females raised fewer offspring than they gave birth to; these mothers were termed “minus pups” (MP) females ($n = 10$, total number of offspring = 27). The females with additional pups (average of 2.5) raised more offspring and were termed “plus pups” (PP) females ($n = 11$, total number of offspring = 80). All pups were weaned on day 19 of lactation.

2.2. Body mass and food intake

Body mass and food intake of the females were measured from day 3 of lactation to peak lactation (day 19 of lactation). When separating the sawdust bedding of the lactating females we found the spillage of diet mixed with the bedding was less than 2%; thus it was considered negligible. The daily food intake was therefore calculated as the weight of food missing from the hopper every day (Johnson et al., 2001a,b,c; Zhao and Cao, 2009a). There was no significant difference in daily food intake between days 16–18 of lactation as determined by repeated measurements; the asymptotic food intake during peak lactation was therefore calculated as the mean daily food intake over this period. Litter size and mass were also measured throughout lactation on a daily basis. Energy content of the food was measured by an oxygen bomb calorimeter (Parr 1281; Parr Instruments, Moline, IL, USA). The asymptotic gross energy intake (GEI) was calculated according to the equation: $GEI (kJ/d) = \text{asymptotic food intake} \times \text{energy content of the food}$.

2.3. Resting metabolic rate

The resting metabolic rate (RMR) of the females was measured on day 19 of lactation using a closed-circuit respirometer as described previously (Gorecki, 1975; Wang et al., 2000; Zhao and Wang, 2006, 2007). The metabolic chamber size was 3.6 l. KOH and silica gel were used to absorb CO₂ and water in the metabolic chamber, respectively. The temperature in the chamber was set at 29 ± 0.5 °C (controlled by a water bath), which is within the thermal neutral zone of the striped hamster (which is 27–30 °C according to Song and Wang, 2003). The female was separated from the litter for 5 h prior to measurement. The animals were in the metabolic chambers for about 60 min to stabilize prior to RMR measurement. Oxygen consumption was recorded for 60 min at 5 min intervals.

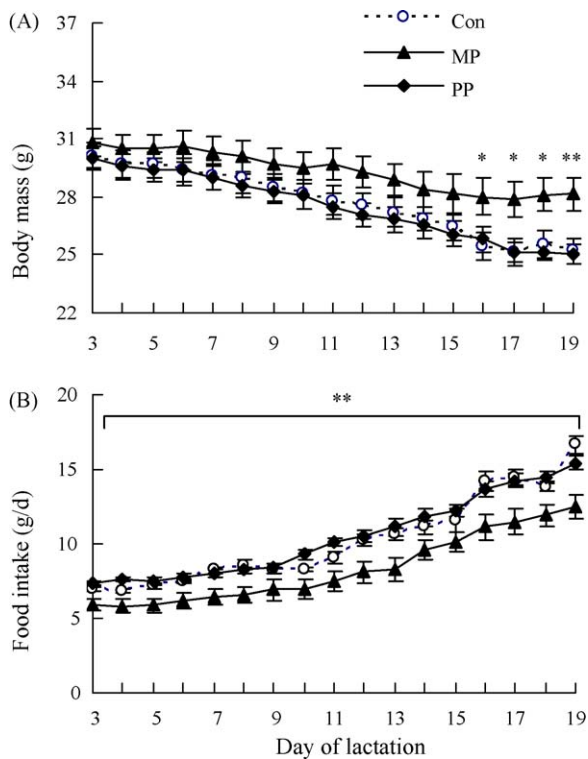


Fig. 1. (A) Maternal body mass and (B) food intake throughout lactation in striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. MP females had a significantly heavier body mass on days 16–19 and lower food intake throughout lactation compared with the control and PP females. Values are mean \pm SE. * $P < 0.05$; ** $P < 0.01$.

Two continuous stable minimum recordings were taken to calculate the RMR, which was then corrected to standard temperature and air pressure (STP) conditions. Oxygen consumption (ml O_2 /h) was converted to energy expenditure (kJ/d), using the equation of Weir (1 ml O_2 /h = 20.9 kJ/h; Weir, 1949; Speakman, 2000; Johnson et al., 2001a). All measurements were carried out between 09:00 and 14:00 h.

2.4. Statistics

Data were analyzed using SPSS 13.0. Repeated-measures analysis of variance (ANOVA) was used to determine the significance of changes in body mass, food intake, litter size and mass over time. The differences in body mass, food intake, litter size and mass on each day during lactation between the control, MP and PP groups were examined by one-way ANOVA, followed by Tukey's HSD post-hoc tests where appropriate. One-way ANOVA was also used to examine the group differences in GEI, RMR and GEI/RMR. Pearson's correlation was performed to examine the correlations between body mass, food intake, litter size, litter mass, GEI and RMR. Data were calculated as mean \pm SE. Statistical significance was determined at $P < 0.05$.

3. Results

3.1. Body mass

The maternal body mass decreased significantly throughout lactation. Body mass averaged 30.1 ± 0.7 g on day 3 of lactation and was 25.2 ± 0.6 g at weaning in the control females (decrease by 16.4%, $F_{16,176} = 68.96$, $P < 0.001$, Fig. 1A). Similarly, body mass averaged 30.8 ± 0.7 and 30.0 ± 0.6 g on day 3 and was 28.2 ± 0.9

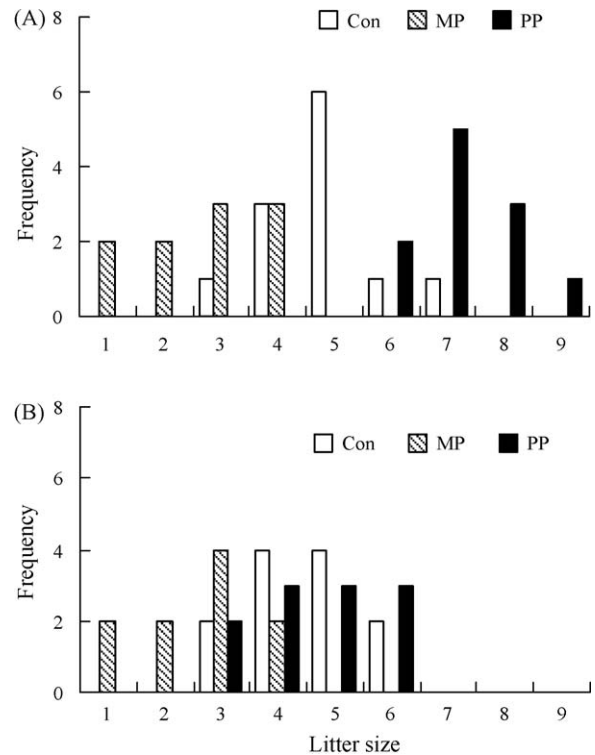


Fig. 2. Histogram of the litter sizes (A) on day 3 of lactation and (B) at weaning (day 19) in striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition.

and 25.0 ± 0.5 g at weaning in MP and PP females, respectively (MP, decrease by 8.7%, $F_{16,144} = 26.49$, $P < 0.001$; PP, decrease by 16.5%, $F_{16,160} = 94.59$, $P < 0.001$). There was no significant difference in body mass among the three groups on day 3 of lactation ($F_{2,32} = 0.44$, $P > 0.05$). On day 16 and thereafter, MP females had a heavier body mass than Con and PP females (d16, $F_{2,32} = 3.26$, $P < 0.05$, Fig. 1A).

3.2. Food intake

On day 3 of lactation, food intake averaged 7.0 ± 0.2 , 6.0 ± 0.4 and 7.4 ± 0.1 g/d in the Con, MP and PP females, respectively. MP females had a significantly lower food intake than the other two groups throughout lactation (d3, $F_{2,32} = 8.23$, $P < 0.01$; d19, $F_{2,32} = 11.81$, $P < 0.001$, Fig. 1B). PP females did not differ in food intake from control females over the period of lactation. During peak lactation, the asymptotic food intake (mean daily food intake between days 16 and 18) averaged 14.4 ± 0.4 , 11.5 ± 0.8 and 14.1 ± 0.4 g/d in Con, MP and PP females, respectively. Asymptotic food intake of MP females was lower by 20.3 and 18.6% than that of Con and PP females, respectively ($F_{2,32} = 8.56$, $P < 0.01$, Fig. 1B).

3.3. Litter size

On day 3 of lactation, mean natural litter size was 4.8 ± 0.3 in the controls (range: 3–7, Fig. 2A). After litter size manipulation, MP females raised fewer offspring (2.7 ± 0.4 , range: 1–4) and PP females had larger litter sizes compared with control females (7.3 ± 0.3 , range: 6–9, $F_{2,32} = 51.67$, $P < 0.001$, Fig. 3A). The litter size in the controls averaged 4.5 ± 0.3 on day 8 and thereafter, which was 6.9% lower than that on day 3 of lactation ($F_{5,55} = 2.76$, $P < 0.05$) and the litter size in MP females averaged 2.6 ± 0.3 on day 4 until weaning, which did not differ from that on day 3

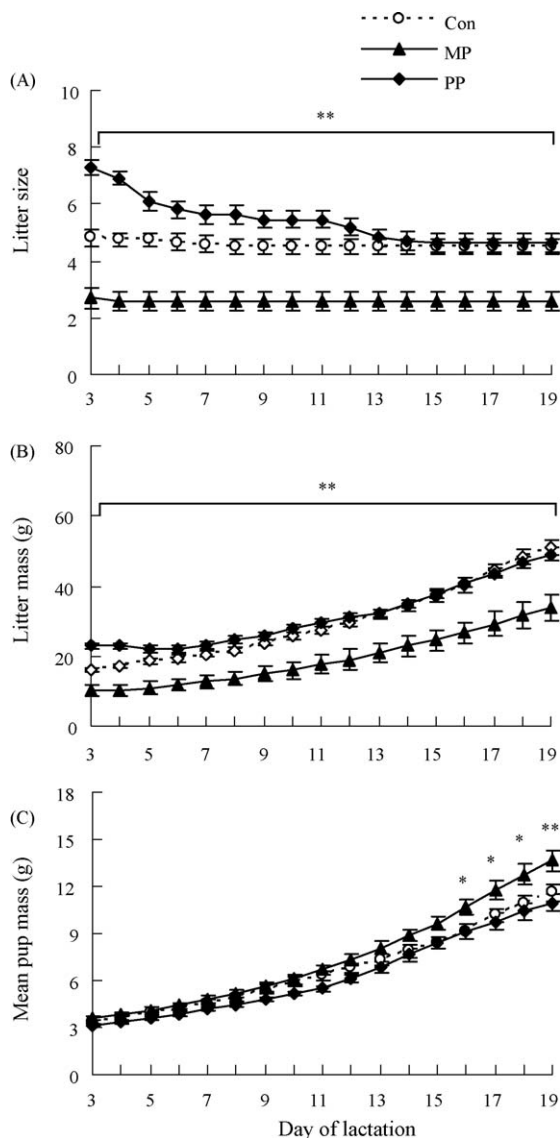


Fig. 3. (A) Litter size, (B) litter mass and (C) mean pup mass throughout lactation in striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. MP females raised significantly smaller litter sizes and lower litter mass throughout lactation than the control and PP females. The mean pup mass of MP females was significantly higher on day 16 and thereafter compared with controls and PP hamsters. Values are mean \pm SE. * $P < 0.05$; ** $P < 0.01$.

($F_{1,9} = 1.00$, $P > 0.05$). However, the mean litter size in PP females decreased significantly throughout lactation and was reduced to 4.6 ± 0.3 by day 15 of lactation, which was 36.2% lower than on day 3 ($F_{12,120} = 19.76$, $P < 0.001$). There was no difference in litter size on day 19 between Con and PP females (Tukey's post-hoc test, $P > 0.05$), whereas MP females raised fewer pups than the control females ($F_{2,32} = 11.94$, $P < 0.001$, Figs. 2B and 3A).

3.4. Litter mass

There were significant differences in litter mass on day 3 between the three groups. MP females had lower litter mass and PP females had heavier litter mass compared with the controls (Con, 16.0 ± 0.7 g; MP, 10.1 ± 1.5 ; PP, 22.9 ± 0.8 ; $F_{2,32} = 38.19$, $P < 0.001$, Fig. 3B). Litter mass increased significantly throughout lactation and pups were weaned at 50.9 ± 2.2 , 33.9 ± 3.8 and 49.0 ± 1.8 g in controls, MP and PP females, respectively

(Con, $F_{16,176} = 267.15$, $P < 0.001$; MP, $F_{16,144} = 92.18$, $P < 0.001$; PP, $F_{16,160} = 119.27$, $P < 0.001$). Litter mass at weaning in MP females was significantly lower than in the control group ($F_{2,32} = 12.00$, $P < 0.001$). However, PP females did not differ significantly in litter mass from the control females at weaning (Tukey's post-hoc test, $P > 0.05$).

3.5. Mean pup mass

There was no significant difference in mean pup mass between the three groups on day 3 (Con, 3.4 ± 0.1 g; MP, 3.6 ± 0.1 ; PP, 3.2 ± 0.1 ; $F_{2,32} = 3.94$, $P > 0.05$, Fig. 3C). The mean pup mass increased significantly over the period of lactation and at weaned was 11.6 ± 0.5 , 13.7 ± 0.7 and 10.9 ± 0.6 g in the controls, MP and PP females, respectively (Con, $F_{16,176} = 244.08$, $P < 0.001$; MP, $F_{16,144} = 124.47$, $P < 0.001$; PP, $F_{16,160} = 130.96$, $P < 0.001$). There was no significant difference in mean pup mass at weaning between the PP group and the controls (Tukey's post-hoc test, $P > 0.05$), whereas mean pup mass at weaning was 17.9% heavier in the MP females than in the control females ($F_{2,32} = 5.97$, $P < 0.01$, Fig. 3C).

Maternal body mass was not correlated with litter size (Con, $R^2 = 0.07$, $P > 0.05$; MP, $R^2 = 0.16$, $P > 0.05$; PP, $R^2 = 0.04$, $P > 0.05$, Fig. 4A). Litter size was positively correlated with litter mass in the controls ($R^2 = 0.60$, $P < 0.01$), MP females ($R^2 = 0.89$, $P < 0.01$) and the PP females ($R^2 = 0.75$, $P < 0.01$, Fig. 4B), but negatively correlated with mean pup mass for the three groups (Con, $R^2 = 0.53$, $P < 0.01$; MP, $R^2 = 0.61$, $P < 0.01$; PP, $R^2 = 0.81$, $P < 0.01$, Fig. 4C). Maternal body mass loss throughout lactation was positively correlated with litter mass in MP and PP females (MP, $R^2 = 0.67$, $P < 0.01$; PP, $R^2 = 0.56$, $P < 0.01$, Fig. 5A), but not in the controls ($R^2 = 0.01$, $P > 0.05$). Litter mass was correlated with asymptotic food intake in the three groups (Con, $R^2 = 0.48$, $P < 0.05$; MP, $R^2 = 0.87$, $P < 0.01$; PP, $R^2 = 0.45$, $P < 0.05$, Fig. 5B). There were also significant correlations between body mass loss and asymptotic food intake and the growth of litters (litter mass gain between days 3 and 19) in the MP and PP groups, but not in the control group (Fig. 6).

3.6. GEI/RMR

There was a significant difference in asymptotic GEI (mean daily gross energy intake) from day 16 to 19 between the three groups; MP females had lower GEI compared with the control and PP females (Con, 253.7 ± 6.7 kJ/d; MP, 202.5 ± 13.9 kJ/d; PP, 248.9 ± 7.4 kJ/d; $F_{2,32} = 8.56$, $P < 0.01$, Fig. 7A). RMR at weaning averaged 51.9 ± 2.4 , 49.3 ± 1.9 and 51.7 ± 3.4 kJ/d in controls, MP and PP females, respectively. Neither MP nor PP females differed in RMR from the controls ($F_{2,32} = 0.29$, $P > 0.05$, Fig. 7B). The SusEI during lactation was therefore $5.0 \times$ RMR, $4.2 \times$ RMR and $5.0 \times$ RMR for the controls, MP and PP females, respectively ($F_{2,32} = 2.70$, $P = 0.08$, Fig. 7C). RMR was positively correlated with GEI in the controls ($R^2 = 0.58$, $P < 0.01$), but not in the MP ($P > 0.05$) and PP females ($P = 0.08$, Fig. 8A). RMR was also correlated with litter mass for the control females ($R^2 = 0.55$, $P < 0.01$, Fig. 8B). There was no correlation between RMR and litter mass in MP ($P > 0.05$) and PP females ($P > 0.05$).

4. Discussion

The striped hamsters significantly decreased their body mass and increased food intake from early to late lactation, by which time the females raising small litter sizes (MP group) had lower weight loss and food intake than the females raising natural and large litters sizes (control and PP group, respectively). Litter size of the PP group decreased significantly over the period of lactation, and was at weaning similar to that of controls. Presumably the reduction in litter size was due to the fact that the females could not cope with

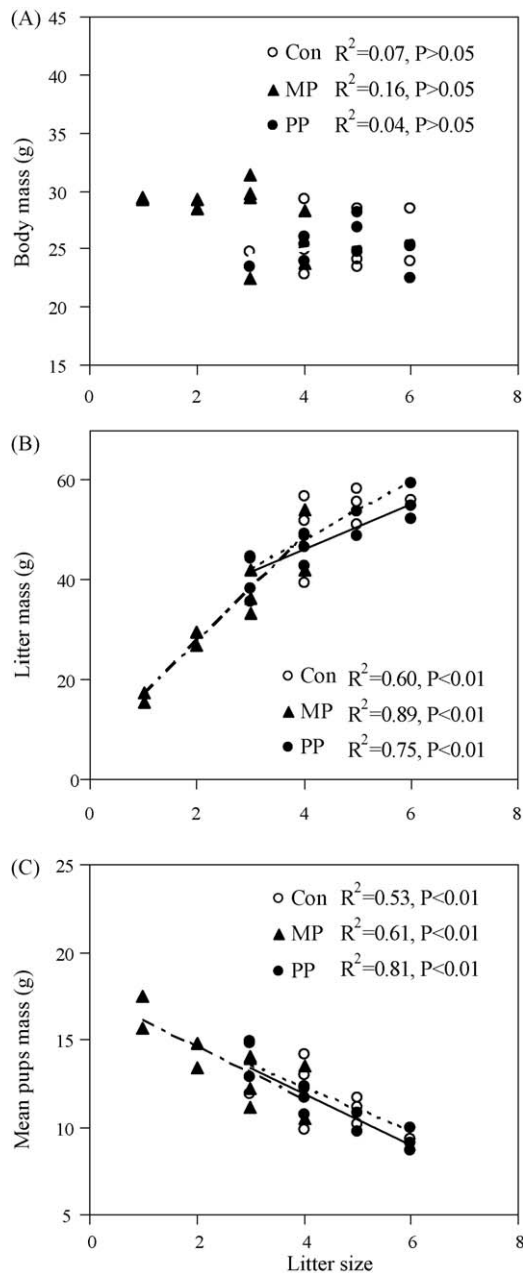


Fig. 4. Correlations between litter size and (A) maternal body mass, (B) litter mass and (C) mean pup mass at weaning in striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. Values are plotted.

the demands of the enlarged litter, supporting the assumption that their asymptotic intake is limited. MP females had a significantly lower litter mass throughout lactation compared with the control and PP females, but during late lactation, the pups from the MP group were significantly heavier. RMR did not differ between the three groups, but GEI during peak lactation was significantly lower in MP females. Finally, GEI was $5.0 \times \text{RMR}$, $4.2 \times \text{RMR}$ and $5.0 \times \text{RMR}$ for the control, MP and PP females, respectively.

During lactation, the most energetically demanding period encountered by small mammals, mothers require energy to meet both maternal and offspring requirements (Rogowitz, 1996; Hammond and Diamond, 1997; Johnson et al., 2001a,b,c; Speakman and Król, 2005, 2010; Speakman, 2007). In the current study, body mass of the female striped hamsters decreased over the period of lactation, suggesting that fat storage mobilization or

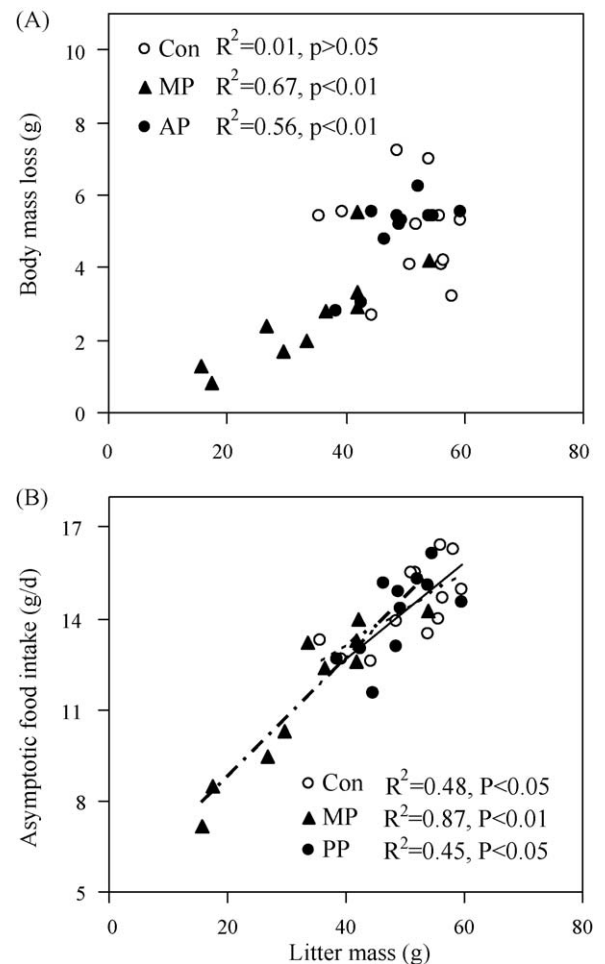


Fig. 5. Correlations between litter mass and (A) maternal body mass loss and (B) asymptotic food intake in lactating striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. Values are plotted.

even catabolism of maternal tissue likely occurred, which could have provided additional energy to their offspring. The weight loss (body mass difference between days 3 and 19 of lactation) was 4.9, 2.7 and 5.0 g for Con, MP and PP groups, respectively. Since 1 g adipose tissue contains about 0.8 g lipid (39 kJ/g) and thus contains 31.2 kJ energy (Forbes, 1987; Speakman et al., 2002), if it was assumed that all the mass loss of the female was fat, 153, 84 and 156 kJ energy would be mobilized in Con, MP and PP hamsters, respectively. On average, the accumulative energy intake of Con, MP and PP females during lactation (days 3–19) was 3196, 2561 and 3271 kJ, respectively (the accumulative food intake between days 3 and 19 (g) \times energy content of the diet (kJ/g)). Thus, the contribution of the weight loss to the total energy budget would be 4.8, 3.3 and 4.8%, respectively. Consistent with this finding, female Djungarian hamsters (*Phodopus sungorus*; Weiner, 1987), cotton rats (*Sigmodon hispidus*; Rogowitz, 1996) and Brandt's voles (*Lasiopodomys brandtii*; Zhang and Wang, 2007) also showed a significant weight loss during lactation. Grey seals (*Halichoerus grypus*) rely completely on stored energy to fuel lactation and fast throughout periods of high energy demand or low energy availability (Mellish et al., 1999; Sparling et al., 2006). In contrast, Swiss mice had a stable body mass over the period of lactation (Zhao and Cao, 2009a). MF1 mice increased their body mass by 17% from early to late lactation (Johnson et al., 2001c). These results suggest that different animal species might show different responses in body mass to meet energy demands during lactation.

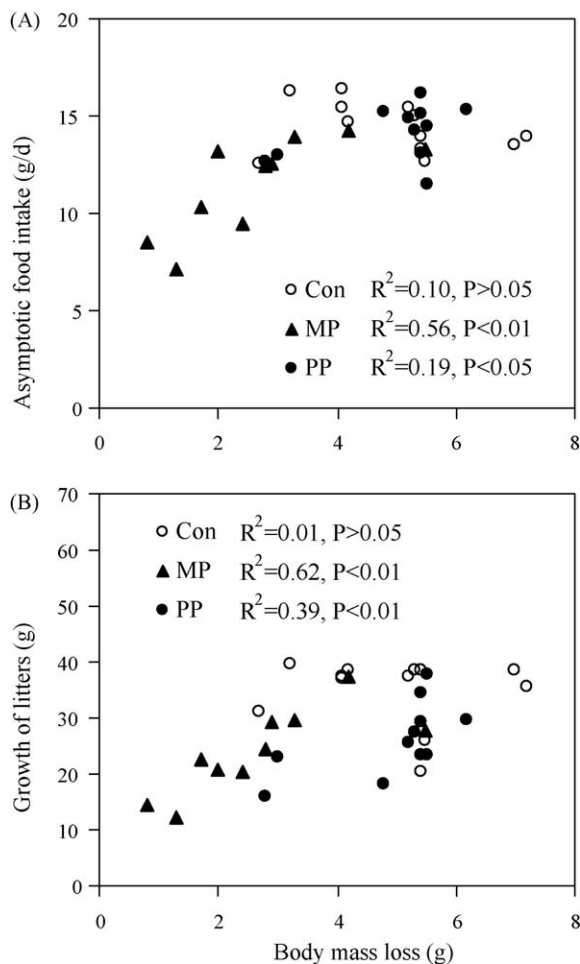


Fig. 6. Correlations between the maternal body mass loss and (A) asymptotic food intake and (B) growth of litters (litter mass gain between day 3 and 19) in lactating striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. Values are plotted.

Among the striped hamsters, PP females raising larger litters on day 3 had a similar weight loss to controls, but MP females supporting the pups of smaller litter sizes had a lower weight loss than control females. The energy allocation to offspring would definitely benefit the pups' growth and reduce the mortality of dependent pups, but at same time would also increase the mother's weight loss and hence the maternal risk (Rogowitz, 1996). Likely, there is a trade-off in energy allocation between maternal maintenance and growth of offspring (Rogowitz, 1996). For the striped hamsters rais-

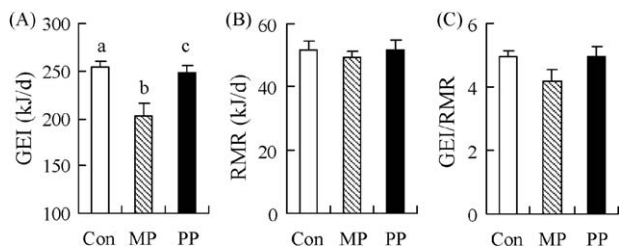


Fig. 7. (A) Gross energy intake (GEI), (B) resting metabolic rate (RMR) and (C) GEI/RMR in lactating striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. MP females had significantly lower GEI compared with control and PP females. Different superscript letters indicate significant differences between groups. Values are mean \pm SE.

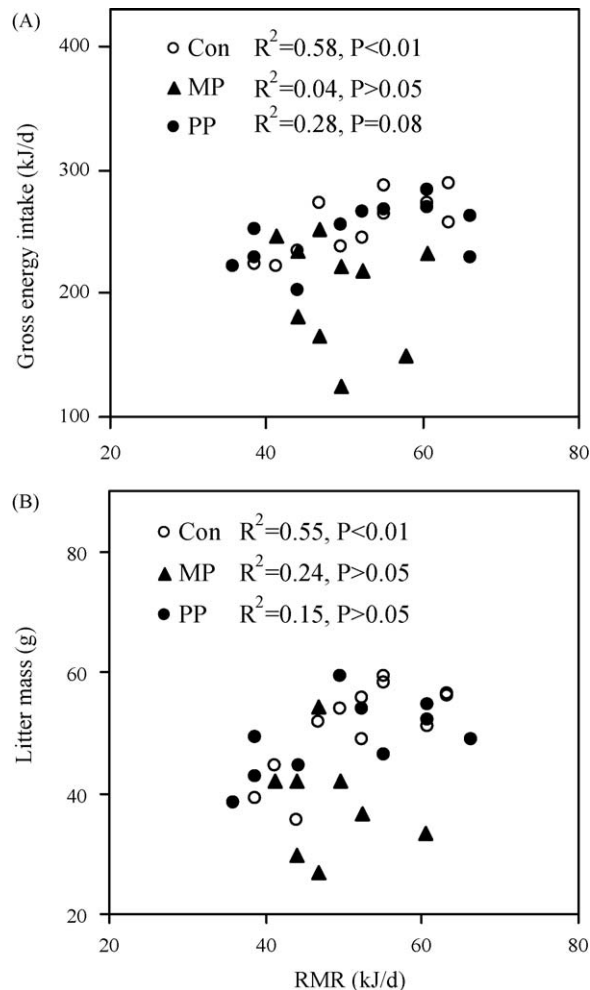


Fig. 8. Correlation between resting metabolic rate (RMR) and (A) gross energy intake (GEI) and (B) litter mass in lactating striped hamsters. Con, females raising natural litters; MP, females raising litters minus 2–3 pups following parturition; PP, females raising litters plus 2–3 pups following parturition. Values are plotted.

ing natural litter sizes and even those supporting the pups of larger litter sizes manipulated at early lactation, the 16% decrease in body mass throughout lactation (weaning at 25 g) might be the limit on weight loss.

Previous research on Swiss mice, MF1 mice and Brandt's voles suggested that there was no limitation to the capacity of their gastrointestinal tract to process ingested food and make its nutrients available for use. This allowed the animals to compensate for high energetic demands during lactation at nearly no maternal cost (Hammond and Diamond, 1992, 1997; Hammond et al., 1994, 1996; Hammond and Kristan, 2000; Johnson et al., 2001a,b,c; Speakman et al., 2001; Król and Speakman, 2003a,b; Speakman and Król, 2005, 2010; Speakman, 2007; Zhang and Wang, 2007; Zhao and Cao, 2009a). In the current study, food intake of striped hamsters increased greatly during lactation, but still did not completely compensate for the energy exported as milk to maintain offspring because weight loss occurred over the period of high energetic demands. So, for the hamsters supporting a natural litter size, the asymptotic food intake was likely constrained at 14 g/d, which is lower than the 19 g/d of Swiss mice (Hammond and Diamond, 1992, 1997; Hammond et al., 1994, 1996) and 23 g/d of MF1 mice at first lactation (Johnson et al., 2001a,b,c; Speakman et al., 2001; Speakman and Król, 2005, 2010). Consistent with Swiss mice and MF1 mice, when litter size was decreased, MP female hamsters decreased their food intake during peak lactation in relation to

the extent of reduction in litter size (Hammond and Diamond, 1992, 1997; Hammond et al., 1994, 1996; Johnson et al., 2001a,b,c; Speakman et al., 2001; Speakman and Król, 2005, 2010). When litter size was increased, females also had an asymptotic food intake of 14 g/d, similar to that of the females raising natural litter size, suggesting that they did not increase their food intake beyond 14 g/d to match the new litter size. As the energy demands of the pups increased notably during lactation, the food consumption of the females continued to increase even after a reduction in the number of pups. Thus, for female striped hamsters, a limitation on sustained food intake at first lactation is likely 14 g/d.

When given additional pups to raise (up to 9 pups on day 3 of lactation), the female hamsters cannibalized some of the pups throughout the first 13 days of lactation, thus decreasing litter size, and during peak lactation raised litter sizes similar to those of the females supporting natural litter sizes. The pups of PP females were weaned at the same body weight as those from the control females. Similarly, house mice (*Mus domesticus*) forced to run a pre-set number of revolutions during lactation to obtain a pellet of food cannibalized offspring throughout the first 12 days of lactation. Thus, as litter size decreased, surviving pups attained similar body weight to the pups of control females (Perrigo, 1987). However, forced running deer mice (*Peromyscus maniculatus*) exhibited a rigid “all-or-nothing” reproductive strategy in which they extended lactation well beyond the normal weaning age (Perrigo, 1987; Speakman and Król, 2005). When female Swiss mice and MF1 mice were given additional pups, the mass of the weaned pups also declined (Hammond and Diamond, 1992, 1994; Johnson et al., 2001a; Speakman and Król, 2005, 2010). Johnson et al. (2001a,b,c) suggested that two possible explanations might be involved in this failure to support large litter sizes. The first explanation was that the mammary glands were not working at their limit, but were responding to the suckling stimulus. As female mice have only 10 teats, whenever the litter was suckling all the teats were occupied and the females would receive the same stimulus from a litter of 10 as they would from a litter of more than 10 (Johnson et al., 2001a). Thus, the females supporting larger litter sizes might export the same energy in milk as the females raising a litter of 10. However, this may not be the case for striped hamsters, as the maximal litter size raised by females was up to 9 on early lactation but only 6 during peak lactation, which is fewer in number than the 8 teats of hamsters. The second explanation was that the mammary glands were working at their limit and were not capable of producing more milk to support large litter sizes manipulated during early lactation (Johnson et al., 2001a). In contrast to deer mice, Swiss mice and MF1 mice, with a limitation on mammary glands the female hamsters reduced litter size during early and middle lactation and supported a pup mass similar to that of the females raising natural litter sizes, which would decrease mortality of dependent offspring. Thus, the current study showed that striped hamsters exhibited a different reproductive strategy from the laboratory mice.

It has been widely confirmed that female animals increase their RMR during peak lactation (Garton et al., 1994; Speakman and McQueenie, 1996; Johnson et al., 2001b; Zhang and Wang, 2007). In the current study, female hamsters during late lactation also showed a higher RMR compared with that of non-lactating individuals as reported by Zhao and Cao (2009b). The RMR during late lactation was correlated with asymptotic food intake and litter mass in the females supporting natural litter size. This suggests that animals with higher RMR may have a greater capacity for absorbing energy and, therefore, be able to devote more energy to reproduction (Thompson, 1992; Johnson et al., 2001b). It also suggests that maximal capacity for daily energy expenditure is regulated by the level of RMR, as RMR reflects the energy demands of sustaining the visceral organs that are responsible for most of the energy flux observed as daily energy expenditure and hence food intake

(Drent and Daan, 1980; Weiner, 1987, 1989, 1992; Peterson et al., 1990; Król et al., 2003). However, no link between RMR and asymptotic food intake or litter mass was found in the females supporting manipulated litters, which indicates that the flexibility of RMR does not match the manipulation of litter size. Also, there was no significant correlation between RMR and reproductive output in female MF1 mice (Johnson et al., 2001b; Król et al., 2003), HSD/ICR mice (Hayes et al., 1992), deer mice (Earle and Lavigne, 1990) and hispid cotton rats (Derting and McClure, 1989). These results suggest that the response in the link between maternal RMR and life-history traits varies between animal species, but the causes remain unclear. Additionally, the current study indicates that a limit might exist in SusEI at $5.0 \times$ RMR for either the females raising natural litter size or those supporting large litter sizes manipulated in early lactation. This might constitute an upper boundary for energy exported to offspring, which would lead to the cannibalization and consequent decrease in litter size in the females supporting additional pups. However, in terms of the present data, we were not able to determine whether the limitation on SusEI was imposed centrally by the capacity of the gastrointestinal tract to process food, peripherally by the capacity of the mammary gland to produce milk, or by the capacity of the animals to dissipate heat.

In summary, the food intake of female striped hamsters at first lactation reached a plateau at around 14 g/d during peak lactation. When litter sizes were manipulated in early lactation, females raising fewer pups decreased their food intake, whereas females supporting more pups did not further increase food intake. This suggests that a limit might exist in SusEI at $5.0 \times$ RMR. Further work will be necessary to establish whether the central limitation hypothesis, the peripheral limitation hypothesis or the heat dissipation limit hypothesis is apt to explain the constraint on SusEI for this species.

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