ENERGY REQUIREMENTS DURING REPRODUCTION IN FEMALE BRANDT'S VOLES (*MICROTUS BRANDTII*)

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We compared energy intake of reproductive and nonreproductive female Brandt's voles (*Microtus brandtii*). Daily energy intake of pregnant voles was significantly higher than that of nonreproductive voles. Metabolizable energy intake increased after parturition and reached a maximum at the end of lactation (334.23 kJ/day), 323% of typical nonreproductive requirements. Moreover, pregnant females had significantly higher lipid mass than controls. During lactation lipid contents were lower than in controls. Over the course of lactation females decreased by 17.6% in body mass, suggesting that females have depleted their body reserve. Use of energy reserves and maximum metabolizable energy intake both were dependent on litter size. Our results indicate that Brandt's voles meet most of their energy demands for lactation by increasing food intake but also supplement that energy by using body reserves even before food intake is maximized.

Key words: body reserve, Brandt's vole, energy requirement, *Microtus brandtii*, reproduction

Energy requirements for reproduction by mammals can be satisfied through complete reliance on ingested energy, reliance on body reserve, or reliance on a combination of stored and ingested energy (Genoud and Vogel 1990; Kunkele 2000; Millar 1987). Generally, large mammals are considered "capital breeders," because they are thought to rely more on accumulated body reserves to satisfy the additional energy costs of reproduction (Festa-Bianchet et al. 1998; Jonsson 1997; Stearns 1992). However, most small mammals are "income breeders" and the energy demand for reproduction is obtained mainly from increased quantities of ingested food (Degen 1997; Gittleman and Thompson 1988). Most data on energy storage for reproduction are for large and intermediate-sized mammals (Bowen et al. 2001; Festa-Bianchet et al. 1998). Fewer studies focus on the use of body reserves in small mammals (Millar 1987). The aims of this

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study were to evaluate the total energy requirements of pregnant and lactating voles, to assess maximum metabolizable energy intake, and to determine the role of body reserve in reproduction in Brandt's vole (*Microtus brandtii*).

Brandt's vole is a typical steppe herbivore with the habit of storing grass for winter. It is distributed mainly in the Inner Mongolian grasslands in China, the Republic of Mongolia, as well as in the region of Beigaer Lake in Russia (Zhang and Wang 1998). Within their range, average annual temperature is 0–4°C and time suitable for reproduction is limited to March through August. Brandt's voles begin to reproduce before snow melts. Thus, voles can be somewhat energy-limited during reproduction, and increasing energy intake and using body reserves become more important.

MATERIALS AND METHODS

Experimental voles.—Brandt's voles were live-trapped in Inner Mongolian grasslands in

May 1999 and were maintained in the laboratory at the Institute of Zoology, the Chinese Academy of Sciences, under a light cycle of 12L:12D and a temperature of 23 ± 1°C. Voles were fed standard rabbit pellet chow (Beijing Ke Ao Feed Co., Beijing, People's Republic of China) and water ad libitum. For our experiments, 78 females were used during the breeding season of March–August 2000.

Females were separated from males at least 1 month before the experiment started to ensure their nonreproductive status. Control females were randomly chosen and other females were paired randomly with males in breeding boxes (47 by 35 by 20 cm). Paired animals were kept at constant temperature of 23 ± 1°C on a 16L:8D light cycle (lights on at 0700 h). Water and food were offered ad libitum. Females were identified as pregnant once a vaginal embolus was noticed or when the body mass increased dramatically over a 3–6-day period. Pregnant females were separated immediately from their mates and raised individually in stainless steel mesh metabolic cages (24 by 24 by 24 cm) with metal trays placed underneath to collect fecal pellets.

Energy intake.—Thirty-five females successfully raised litters. Five reproductive females were tested for food intake from day −18 to day 21 (date of parturition was regarded as day 0). Five nonreproductive females were monitored simultaneously as controls. Gestation in Brandt's vole is 18 days and the lactation period is 21 days. At day 15, young voles begin to eat some solid food, but it is poorly digested. Maternal milk is still their primary food. In our experiments, food boxes were attached to the cages at a height that young were unable to reach. During lactation, mothers and their offspring were held in the same box and provided with cotton as nesting material.

Animals were weighed at the beginning and end of each interval. Food intake and fecal output were measured from onset of pregnancy to weaning. Food samples and feces were collected (between 1600 and 1800 h daily) individually and oven-dried to constant mass at 60°C. Food given to the voles was weighed and its dry mass was calculated from water content of samples. Young animals were euthanized at different times during lactation and used to determine the total body caloric content. The caloric contents of food, bodies of young, and feces were mea-

sured with a Parr 1281 Oxygen Bomb Calorimeter (Parr Instrument Company, Moline, Illinois) according to manufacturer's instructions.

Energy parameters were calculated using the following equations:

Ingested energy (kJ/day)

= (dry food ingested[g]/day)

× (kJ/g dry food)   (1)

Digested energy (kJ/day)

= (ingested energy[kJ]/day)

− ([dry feces{g}/day]

× [kJ/g dry feces])   (2)

Metabolizable energy intake (kJ/day)

= (digested energy[kJ]/day)

− (urine energy[kJ]/day), or

0.98(digested energy[kJ]/day)   (3)

Urinary energy loss was not measured and was assumed to be 2% of the digested energy (Drozdz 1975; Grodzinski and Wunder 1975).

Digestibility (%)

= (digested energy/ingested energy)

× 100   (4)

Net production (kJ/day)

= (dry litter mass gain[g]/day)

× (kJ/g dry mass of young)   (5)

Maternal body reserve (kJ/day)

= (dry maternal mass gain[g]/day)

× (kJ/g dry maternal body)   (6)

Total energy requirement (kJ/day)

= (metabolizable energy intake[kJ]/day)

± maternal body reserve(kJ)/day   (7)

Body lipid measurement.—Thirty eight adult voles (7 controls, 10 pregnant, 11 lactating, and 10 that were weaning young) were euthanized to measure body lipid content. Lactating females were euthanized at 12–15 days. Digestive tract, heart, lung, liver, spleen, kidney, embryos, and brown adipose tissue were removed from each carcass. White adipose tissue around the gut and

embryos was not removed. We weighed these eviscerated carcasses (= net fresh body mass), oven-dried each to constant mass at 60°C, and reweighed them (= net dry body mass). Dry carcasses were then ground in a mill. Lipid content of a 1- or 2-g dry subsample was measured by ether extraction in a Sohxlet fat extractor (Millar 1987). All samples were extracted for 7–10 h, oven-dried, and reweighed. Mass loss between pre-extraction and postextraction represents lipid content. Caloric content of each carcass was measured by bomb calorimeter as described previously.

Data analysis.—Percentages were transformed via the arcsine transformation. We regarded the period from day −18 to day 0 as pregnancy and from day 0 to day 21 as lactation. Differences in parameters between reproductive (pregnancy and lactation) and nonreproductive females were analyzed using independent sample t-tests. Differences in body mass during reproduction were analyzed with repeated-measures analysis of variance (ANOVA). The least significant difference (LSD) test was used for multiple comparisons. Because of differences in body mass, we analyzed ingested energy, digested energy, metabolizable energy intake, and digestibility with 1-way analysis of covariance (ANCOVA) with body mass as a covariate for pregnant, lactating, and nonreproductive females. We also used 1-way ANCOVA to test differences in net fresh body mass, net dry body mass, lipid content, body water content, and caloric values among pregnant, lactating, weaning, and nonreproductive females using body mass as a covariate. Bivariate correlation was used to analyze the influence of litter size on maximal metabolizable energy intake, maternal body mass, and change in maternal body mass.

For all statistical tests, differences with $P \leq 0.05$ were considered to be statistically significant. All values are presented as means ± *SE*. Statistical analyses were conducted using SPSS version 10.0 software (Lu 2000).

RESULTS

Body mass.—Body mass differed significantly during reproduction (repeated-measures ANOVA, $F = 18.132$, $d.f. = 13, 52$, $P < 0.001$, Table 1). At parturition mean maternal body mass was 36.9% higher than mean body mass of nonreproductive voles

($t = −3.766$, $d.f. = 8$, $P = 0.005$). Mean body mass of lactating females was significantly heavier than that of nonreproductive females ($t = −4.002$, $d.f. = 8$, $P = 0.004$). Maternal body mass was stable for days 0–9 of lactation, then declined from day 9 (61.8 ± 2.2g) to day 21 (51.5 ± 2.7g). Mean mass loss from parturition to weaning was 9.4 ± 1.04g ($n = 35$).

Energy requirements during pregnancy.—Means of ingested energy, digested energy, and metabolizable energy intake during pregnancy were significantly higher than those of nonreproductive voles by 22.9%, 25.5%, and 25.8%, respectively (ingested energy: $t = 2.169$, $d.f. = 43$, $P = 0.036$; digested energy: $t = 2.240$, $d.f. = 43$, $P = 0.030$; and metabolizable energy intake: $t = 2.263$, $d.f. = 43$, $P = 0.029$, Table 1). Pregnant animals reached peak ingested energy at day −15 (164.33 ± 15.03 kJ/day; Table 1). Thereafter, gestating females decreased ingested energy until the day of parturition (Table 1). A similar trend was found for digested energy and metabolizable energy intake. Digestibility did not differ significantly between pregnant and nonreproductive voles ($t = 0.056$, $d.f. = 43$, $P = 0.956$).

Energy requirements during lactation.—Energy requirements during lactation were significantly higher than those of nonreproductive control voles and pregnant voles (ANCOVA, ingested energy: $F = 14.033$, $d.f. = 2, 81$, $P < 0.001$; digested energy: $F = 15.926$, $d.f. = 2, 81$, $P < 0.001$; metabolizable energy intake: $F = 15.962$, $d.f. = 2, 81$, $P < 0.001$; Fig. 1). At parturition the metabolizable energy intake was 66.67 ± 4.68 kJ/day, significantly lower than in nonreproducing females (77.79 ± 3.92 kJ/day; $P < 0.01$, Table 1). Ingested energy, digested energy, and metabolizable energy intake of voles continuously increased during lactation (Table 1) and were significantly higher than at any other stages. Maximum metabolizable energy intake was reached at the day 21 (334.23 ± 28.65 kJ/day), 3.23 times metabolizable energy intake of non-

TABLE 1.—Body mass, ingested energy, digested energy, metabolizable energy intake, and digestibility of gestating (days −18 to 0), lactating (days 0 to 18), and nonreproductive control Brandt's voles.

| Day	Body mass (g)		Ingested energy (kJ/day)		Digested energy (kJ/day)		Metabolizable energy intake (kJ/day)		Digestibility (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gestation[a]										
−18 to −15	59.3	1.9	145.23	12.33	96.47	8.99	94.54	8.81	66.34	2.29
−15 to −12	63.1	2.0	164.33	15.03	110.68	10.44	108.47	10.24	67.30	1.43
−12 to −9	67.3	2.4	163.34	21.01	107.56	15.41	105.41	15.11	65.51	1.40
−9 to −6	73.5	2.7	162.34	26.03	110.23	17.69	108.03	17.34	67.56	1.97
−6 to −3	83.6	3.8	151.46	26.18	107.37	19.21	105.22	18.82	70.91	2.38
−3 to 0	64.5	3.9	118.46	24.78	75.94	17.34	74.42	16.99	59.69	6.11
Mean of total gestation period	68.5	1.8	150.86	8.56	101.38	6.14	99.35	6.01	66.22	1.30
Lactation										
0 to 2	61.8	3.6	95.30	8.13	68.03	4.77	66.67	4.68	71.80	1.43
2 to 4	60.2	3.0	158.26	23.58	112.02	21.17	109.78	20.75	68.90	4.01
4 to 6	61.7	2.2	192.82	13.36	128.81	8.76	126.23	8.59	66.85	0.80
6 to 9	63.1	1.5	234.96	18.30	160.82	13.26	157.61	12.99	68.39	1.26
9 to 12	61.8	2.2	222.92	22.03	152.07	15.72	149.03	15.41	68.08	0.73
12 to 15	59.7	3.2	256.10	20.25	184.01	12.85	180.33	12.59	72.27	2.96
15 to 18	55.9	3.1	380.62	46.61	248.11	37.98	243.15	37.23	63.73	4.33
18 to 21	51.5	2.7	534.17	57.21	341.05	29.23	334.23	28.65	64.50	1.65
Mean of total lactation period	59.4	1.1	259.39	22.90	174.37	14.43	170.88	14.14	68.07	0.93
Controls	45.2	1.6	122.75	6.37	80.80	4.09	78.99	3.99	66.10	1.33

[a] For each group, $n = 5$.
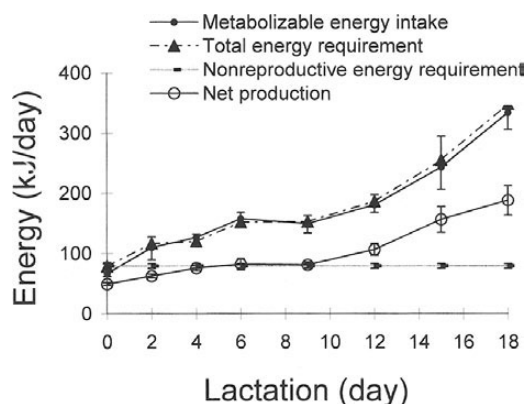
FIG. 1.—Metabolizable energy intake, total energy requirement, nonreproductive energy requirement, and net production energy (kJ/day) during lactation in Brandt's voles (*Microtus brandtii*). Values are means ± SE (for clarity, SE is not shown for all means). $n = 5$ for each sample.

reproducing controls (Table 1). During lactation (days 0–21), metabolizable energy intake was significantly lower than total energy requirement (paired samples t-test, $t = -2.804$, $d.f. = 39$, $P = 0.008$; Fig. 1), suggesting that voles perhaps used their body reserve to compensate for the energy cost of lactation. Maternal body reserve was based on dry energy content and body water content in the lactating females of 23.5 kJ/g and 63.3% of fresh body mass, respectively (Table 2). Digestibility did not differ significantly between lactating and control voles ($t = 1.138$, $d.f. = 53$, $P = 0.260$; Table 1).

Energy requirement of young.—Growth of young correlated positively with maternal total energy requirements ($r = 0.925$, $d.f. = 40$, $P < 0.001$; Fig. 1). Maternal metabolizable energy intake generally paralleled the incremental increase in net production calculated from Eq. 5 (19.79 ±

TABLE 2.—Body mass, net fresh body mass, net dry body mass, whole body water content, whole body lipid mass, lipid content, and caloric values of control, pregnant, and lactating Brandt's voles.

	Control ($n = 7$)		Pregnant ($n = 10$)		Lactating ($n = 11$)	
	Mean	SE	Mean	SE	Mean	SE
Body mass (g)	41.43[Aa]	2.03	67.86[B]	3.05	48.02[A]	1.81
Net fresh body mass (g)	31.10[A]	1.72	42.89[B]	2.17	33.43[A]	1.39
Net dry body mass (g)	13.97[A]	1.34	18.90[B]	1.34	12.25[A]	0.58
Water content (%)	55.64[A]	2.34	56.19[AB]	1.18	63.33[B]	1.09
Lipid mass (g)	5.50[A]	2.35	8.04[A]	2.95	3.59[B]	1.07
Lipid content (%)	37.79[A]	2.81	41.59[A]	2.02	28.70[B]	1.53
Caloric value (kJ/g)	24.74[A]	0.57	25.61[A]	0.70	23.49[A]	0.44

[a] Within each row, values with different superscripts are significantly different between periods ($P < 0.05$).

0.14 kJ/g dry mass and 79.87 ± 0.86% water, respectively). At peak lactation, metabolizable energy intake significantly correlated with litter size ($n = 35$, $r = 0.544$, $P < 0.001$; Fig. 2). Mean litter size was 7.9 ± 0.4 ($n = 35$). Individual maternal body mass at day 0 correlated positively with litter size ($n = 35$, $r = 0.395$, $P = 0.019$).

Lipid content.—Body mass, net fresh body mass, and net dry body mass differed significantly among periods (ANOVA, $F = 24.293$, $d.f. = 2, 25$, $P < 0.001$; $F = 9.924$, $d.f. = 2, 25$, $P < 0.001$; $F = 8.242$, $d.f. = 2, 25$, $P < 0.001$, respectively; Table 2). Whole-body lipid mass also differed significantly among periods (ANCOVA, $F = 2.962$, $d.f. = 2, 25$, $P = 0.046$). Lipid mass of lactating voles was lower than control

and pregnant voles (LSD = 2.363, $d.f. = 16$, $P = 0.031$ and LSD = 4.691, $d.f. = 19$, $P < 0.001$, respectively; Table 2). Mass specific lipid contents (lipid mass/net dry body mass) of lactating voles were lower than those of control females (ANCOVA $F = 4.432$, $d.f. = 2, 25$, $P = 0.010$; Table 2). There were no significant differences in caloric value of maternal tissues among these groups (ANCOVA, $F = 2.339$, $d.f. = 2, 25$, $P = 0.091$; Table 2). Water content per gram of mass ([net fresh body mass − net dry body mass]/net fresh body mass), corrected for effects of body mass, was significantly different among groups (ANCOVA, $F = 4.060$, $d.f. = 2, 25$, $P = 0.015$), with body water content of lactating females being the highest (Table 2).
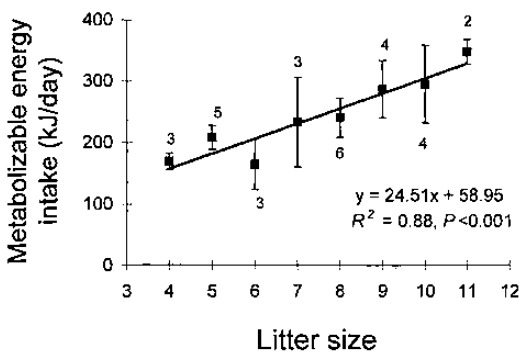

FIG. 2.—Relation between metabolizable energy intake and litter size at day 21 during lactation in Brandt's vole (*Microtus brandtii*). Values are means ± 1 *SE*. Number of litters of each size are indicated.

DISCUSSION

Energy requirements of pregnant female Brandt's voles are, as expected, higher than those of nonreproductive females. Lactating females had an even greater energy requirement. Similar patterns have been reported for several species of rodents (Innes and Millar 1981; Kaczmarski 1966; Konig et al. 1988). Postparturition maternal metabolizable energy intake of Brandt's vole increases roughly in parallel with growth of young voles, peaking at end of lactation. Other lactating small rodents have been reported to increase their food intake 2- or 3-fold to meet energy demands of young (Genoud

and Vogel 1990; Gittleman and Thompson 1988; Peters 1983).

Metabolizable energy intake during lactation not only depends on the stage of lactation but on litter size as well in Brandt's voles. Kenagy et al. (1990), working with golden-mantled ground squirrels (*Spermophilus saturatus*), found maternal energy expenditure at peak lactation similarly increased significantly with litter size. In contrast, Genoud and Vogel (1990) suggested that peak energy intake was not significantly influenced by litter size in shrews (*Soricidae*).

Maternal body mass of Brandt's vole at day of birth also positively correlates with litter size. After that, body mass gradually decreased from parturition to weaning. In particular, during late lactation loss of mass was due to use of body fat reserves, as has been reported for ground squirrels (*S. saturatus*; Kenagy et al. 1989). Pregnant voles had the highest lipid content and lactating voles had the lowest lipid mass (Table 2), suggesting that lipid was stored during pregnancy and was consumed during lactation. Similar exploitation of body fat reserves to meet heavy lactating energy demand occurs in other species (*S. saturatus*, Kenagy 1987; *Sigmodon hispidus*, Mattingly and McClure 1985; *Phodopus sungorus*, Weiner 1987).

Glazier (1985) indicates that species with larger litters were no more associated with greater body fat use than were species with smaller litters. However, our data indicated that voles with large litters used more maternal body fat reserves. Likewise, Kenagy et al. (1990) indicate that exploitation of body fat reserve directly correlates with litter size in golden-mantled ground squirrels.

Under most conditions fat reserves are short-term buffers against energy imbalances during breeding seasons (Gittleman and Thompson 1988; Millar 1987). Generally, small mammals (including other voles; Millar 1987) meet their energy requirements during reproduction almost exclusively by increasing energy intake rather

than using body fat reserves (Kenagy 1987; McClure 1987). Djungarian hamsters (*P. sungorus*, Weiner 1987) and cotton rats (*S. hispidus*, Mattingly and McClure 1985) exploit lipid reserves only after they have reached the upper limit of their ability to assimilate energy from food. However, Brandt's voles depleted their body fat reserves before they reached maximum metabolizable energy intake. Thus, it appears that small quantities of stored lipid may routinely supplement ingested energy to support reproduction in small species that live in harsh climatic conditions (Weiner 1987).

In their natural habitat, Brandt's voles need to produce large numbers of offspring within a few months once conditions become suitable. Field studies show that mean litter size is around 8 (Zhang and Zhong 1979), similar to the present observations in the laboratory. Brandt's voles start to reproduce while ground temperature is low. This requires that voles deposit energy before and during pregnancy to meet high lactation energy costs so as to reduce time and energy spent foraging during lactation and increase time available for nursing offspring. Lactating animals also reduce their exposure to cold and predators (Degen 1997; Kam and Degen 1993; Weiner 1987). Although Brandt's voles were provided unrestricted access to food in our experiment, body fat reserves were still used during lactation.

In summary, energy requirements of female Brandt's voles during lactation parallel growth of the young. Dams increase food intake and use body fat reserves to meet energy demands during lactation at rates that depend on litter size. Although the contribution of body fat reserves to the total energy cost of reproduction is relatively small, it likely represents an important energy supplement.

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