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ORIGINAL PAPER

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Selective digesta retention and coprophagy in Brandt's vole (*Microtus brandti*)

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Abstract Digestive performance, gut morphology and rate of digesta passage were measured in Brandt's voles (*Microtus brandti*) offered pelleted diets of low (25% neutral-detergent fibre) and high (38%) fibre content. Digestion coefficients of dry matter, crude fat, crude protein, energy and fibre were all significantly lower on the higher fibre diet. Although not significantly higher, dry matter intakes were more than maintained when extra cellulose was included in the diet, so that intakes of digestible energy were only 22% lower on the higher fibre diet. Total length and total gut tissue weight increased significantly, and the length and tissue weight of the caecum, proximal colon, and distal colon were significantly greater on the higher fibre diet as well. Total tract mean retention time (MRT) of a solute marker (Co-EDTA) was significantly greater than that of a particle marker (Cr-cell walls) on the lower fibre diet, and in the same direction on the higher fibre diet. The ratio of solute to particle MRTs (the solute/particle differential retention ratio) was 1.45 on the lower fibre diet and 1.19 on the higher fibre diet. There were no significant differences in marker MRTs between diets. Examination of marker concentrations in the stomach, small intestine, caecum and colon of voles killed at 0.5-h intervals after a pulse dose of Co-EDTA indicated that the marker was recycled to the stomach by coprophagy. Thus, as in other microtine rodents, an increase in gut capacity, selective digesta retention and recycling of digesta via coprophagy enables Brandt's voles to utilise diets of higher fibre content than may be expected for such a small (45 g) mammalian herbivore.

Keywords Mean retention time · Digestibility · Coprophagy · Brandt's vole

Abbreviations *ADF* acid-detergent fibre · *Cr-cell walls* Cr-mordanted cell walls · *CSM* colonic separation mechanism · *MTR* mean retention time · *NDF* neutral detergent fibre · *TT* transit time

Introduction

It has been shown that, within certain limits, mammalian herbivores increase food intake and rate of passage of digesta, at the cost of decreased digestibility, as diet quality decreases and/or energy needs increase (Woodall 1989; Loeb et al. 1991; Nagy and Negus 1993). Castle and Wunder (1995) suggested that decreases in food quality might pose a more severe problem for small than for larger herbivores. This is because the smaller the animal, the greater its energy need per unit of body mass, while the rate of fermentation is the same in small and large animals on a common diet (Björnhag 1994). However, some small mammalian herbivores, most of which are hindgut fermenters (Cork et al. 1999), overcome the disadvantage of small size by separating fluid, solutes and small particles from large particles in their proximal colon, and selectively retaining the former components in a capacious caecum (Hume 1989). This concentrates digestive effort on the potentially more digestible fractions of the digesta, while the passage of larger particles through the colon is facilitated. Clearance of indigestible bulk from the colon allows the animal to maintain higher rates of food intake which partially compensates for the lower nutrient density of lower-quality forage diets (Hume 1989; Cork et al. 1999).

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In many caecum fermenters (small hindgut fermenters), selective retention of digesta components is combined with coprophagy (ingestion of faeces) or caecotrophy (ingestion of high-nutrient faeces derived from caecal contents). Recycling of nutrients in this way also helps to explain the ability of several small mammalian herbivores to subsist on high fibre diets (Takahashi and Sakaguchi 1998). Coprophagy would be expected to increase mean retention time (MRT) in these animals, especially of fluid digesta and dissolved solutes (Björnhag and Sjöblom 1977).

Brandt's vole is a small (40–50 g) mammalian herbivore that feeds on grass. It is distributed primarily in the Inner Mongolian grasslands of China, Mongolia and in the Beigaer Lake region of Russia (Zhang and Wang 1998). Despite its small size, Brandt's vole has been observed to consume about 40 g fresh grass per day. During winter, when diet quality decreases and energy requirements for thermoregulation increase, the amount of food consumed daily can even exceed its body mass (Zhang and Wang 1998).

The aim of this study was to measure the digestive responses of Brandt's vole to an increased dietary fibre content in terms of food intake and digestibility and rate of passage of digesta, and to determine if the species is coprophagic. Results are compared with similar data on other microtine rodent species in other parts of the world, and with data of Sperber et al. (1983) on the nature and effectiveness of the colonic separation mechanism in myomorph rodents.

Materials and methods

Animals and diets

Eleven non-reproductive adult Brandt's voles were live-trapped in the Inner Mongolian grasslands of China in May 1999. They were transported to the Institute of Zoology, Chinese Academy of Sciences, Beijing, where they were maintained in an air-conditioned room at 24 ± 1 °C under a 15:9-h L:D cycle. Food and water were available ad libitum throughout, and the animals were weighed at the beginning and end of each experiment.

Animals were divided randomly into two groups. Group I ($n = 6$) was offered commercial rabbit pellets (Beijing Ke Ao Feed) as a low fibre diet. Group II ($n = 5$) was offered the same diet with an increased content of the cellulose as a high-fibre diet. The high-fibre diet was prepared by grinding rabbit pellets, then thoroughly mixing in 67% alfalfa powder. The dry mixture was slightly moistened, warmed until dry in order to adhere the alfalfa powder to the other dietary components, and then re-pelleted. The chemical composition of the two experimental diets is shown in Table 1.

Table 1 Nutritional analysis (means ± SE)of the diets offered to Brandt's voles (dry matter basis). *ADF* acid-detergent fibre, *NDF* neutral-detergent fibre. $n = 6$

	Low fibre diet	High fibre diet
Crude fat (%)	5.1 ± 1.0	4.8 ± 0.9
Crude protein (%)	24.3 ± 2.2	21.7 ± 1.5
NDF (%)	25.0 ± 2.8	37.6 ± 2.5
ADF (%)	13.6 ± 2.1	26.3 ± 3.3
Gross energy (kJ/g)	17.2 ± 4.5	17.4 ± 2.1

Food intake and digestibility

During experiments the voles were housed individually in stainless steel mesh metabolism cages (24 cm×24 cm×24 cm) with metal trays placed underneath to collect the faecal pellets. Measurements of food intake and faecal output lasted 5 days after a pre-measurement period of 14 days on each diet. During the collection period, food residues, faeces and urine were collected quantitatively and bulked for each animal; residues and faeces were dried at 60 °C for 48 h, then ground through a 1-mm screen. Dried samples of food, food residues and faeces were analysed for their contents of crude fat by the Soxhlet method, total nitrogen by the Kjeldahl method, and neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) by the methods of Goering and Van Soest (1970) after pre-treatment with heat-stable α-amylase (Sigma A3306) (Van Soest et al. 1991). The gross energy contents of food, food residues and faeces were determined in a Parr 1281 oxygen bomb calorimeter (Parr Instrument, USA), with benzoic acid as the standard. Crude protein was assumed to be 6.25 times total nitrogen.

Rate of passage of digesta

Rate of digesta passage was measured immediately following the collection period. Two inert markers were used. The solute phase of digesta was marked with Co-EDTA (Dojindo, Japan), and the large particle phase with Cr-mordanted cell walls (Cr-cell walls). The cell walls were prepared from ground oaten (*Avena sativa*) hay using the NDF procedure of Goering and Van Soest (1970). The cell walls were then washed through a stack of Endecott (London, UK) screens, and those particles that passed through the 600-μm screen but were retained on the 300-μm screen were mordanted with chromium following the procedure of Udén et al. (1980). The two markers, 0.05 g Co-EDTA and 0.1 g Cr-cell walls, were offered to each animal in a small piece of apple. After the dose had been consumed the animals were offered their experimental diets. One animal from Group II consumed only a small amount of the markers and was removed from the experiment. Collection trays beneath the cages were inspected, and any faeces present were collected, every 2 h for the first 24 h, every 4 h for the next 24 h, and then every 8 h for the next 24 h. Defecation times were taken as the midpoint of each inspection interval. Collected faeces were dried to constant mass at 60 °C, then converted into ash at 550 °C for 4 h. The ashed samples were digested in conical flasks on a hot plate with 10 ml concentrated nitric acid, followed by 2 ml hydrogen peroxide. The clear digests were transferred quantitatively to 25-ml volumetric flasks and diluted to the mark with de-ionised water. The concentrations of Co and Cr in the diluted digests were determined by flame atomic absorption spectroscopy (Siman 180–80, Japan).

Gut morphology

The animals were killed by decapitation after the measurement of digesta passage rate. Their complete digestive tracts were quickly removed and dissected free of mesentery. The lengths of the stomach, small intestine, caecum, proximal colon and distal colon with contents were measured to the nearest 1 mm, without stretching the tissue (Freehling and Moore 1987). Then the organs without contents were dried for 48 h at 60 °C and weighed to the nearest 1 mg using a Mettler Analytical Balance. The junction between proximal and distal colon was taken to be the point where faecal pellets were first apparent (Hume et al. 1993).

Coprophagy

Fifteen animals were maintained on standard rabbit pellets. The solute marker Co-EDTA (0.05 g) was offered in apple to each animal, and the time taken to ingest the marker was recorded. Of the 15 animals, 12 were killed by decapitation at intervals of

0.5, 1.0, 1.5 and 2.0 h after dosing (three at each time). The digestive tract of each animal was exposed through a ventral midline incision, and the stomach, small intestine, caecum and colon were ligated to isolate their contents. The concentration of marker present in dried (at 60 °C to constant weight) contents from each gut region was determined by flame atomic absorption spectroscopy. The total mass of dry contents was used to calculate the amount of marker in each region of the tract at each time.

Calculation and statistical analysis

Transit time (TT) was taken as the time of appearance of 5% of the marker in the faeces (Balch 1950). MRT, the best single measure of rate of passage through the entire digestive tract (Warner 1981), was calculated using the equation:

$$\mathrm{MRT} = \sum_{i=1}^{n} m_i t_i \Big/ \sum_{i=1}^{n} m_i$$

where m_i is the amount of marker excreted in the ith defecation at time t_i, and n is the total number of defecations to recover the whole of the dose (Blaxter et al. 1956).

Values are presented as means ± SE. In order to minimise any effect of body size, and for comparisons across rodent species, intake data are scaled to the 0.67 power of body mass ($M^{0.67}$); this was found by Hayssen and Lacy (1985) to be the most appropriate exponent for rodents. The effects of treatment (diet) on intake and digestibility were tested by independent-samples t-test. Differences between MRT for Co-EDTA and Cr-cell walls within groups were tested by paired-samples t-test, and differences between groups by independent-samples t-test. Statistical significance was taken as $P < 0.05$.

Results

Food intake and digestibility

Body mass changes, food intakes and digestibilities are shown in Table 2. The magnitude of body mass loss was similar on both diets; although it was not significant on the low fibre diet, the loss approached significance on the high fibre diet. Although dry matter intake was not significantly different between the two diets, faecal output increased by 80% with the increase in dietary cellulose, and thus apparent digestibility of dry matter decreased by 25%. As with dry matter, intakes of crude fat, crude protein and gross energy were also not significantly different between diets, but apparent digestibilities fell by 26% for fat, 13% for crude protein and 24% for energy. Consequently, intake of digestible energy fell by 22% on the higher fibre diet.

In contrast, although intakes of NDF and ADF both increased as a result of the increased cellulose content of the diet, digestibility of NDF fell by 37% and that of ADF by 41%.

Table 2 Body mass change, intake and digestibility in Brandt's vole

	Low fibre diet	High fibre diet	P value
Animals	6	5	
Initial body mass (g)	46.1 ± 3.4	41.7 ± 2.9	0.371
Final body mass (g)	45.9 ± 3.8	40.0 ± 2.4	0.330
Dry matter			
Intake (g/day)	8.0 ± 0.4	8.4 ± 1.1	0.715
Intake (g/kg$^{0.67}$ per day)	64.9 ± 8.1	72.0 ± 14.4	0.301
Faecal output (g/kg$^{0.67}$ per day)	18.3 ± 2.2	32.9 ± 5.1	< 0.001
Apparent digestibility (%)	71.7 ± 1.1	54.0 ± 1.1	< 0.001
Fibre			
Intake of NDF (per gram)	2.0 ± 0.1	3.2 ± 0.9	0.017
Intake of NDF (g/kg$^{0.67}$ per day)	16.2 ± 2.0	28.0 ± 10.3	0.022
Faecal output (g/kg$^{0.67}$ per day)	8.0 ± 0.5	18.8 ± 3.1	0.004
Digestibility of NDF (%)	50.3 ± 2.1	31.9 ± 5.2	0.007
Intake of ADF (g/day)	1.1 ± 0.1	2.2 ± 0.2	0.003
Intake of ADF(g/kg$^{0.67}$ per day)	8.8 ± 1.1	18.9 ± 3.8	< 0.001
Faecal output (g/kg$^{0.67}$ per day)	4.8 ± 0.9	13.7 ± 2.1	< 0.001
Digestibility (%)	45.6 ± 2.4	27.1 ± 2.1	< 0.001
Crude fat			
Intake (g/day)	0.4 ± 0.0	0.4 ± 0.1	0.950
Intake (g/kg$^{0.67}$ per day)	3.3 ± 0.4	3.5 ± 0.7	0.665
Faecal output (g/kg$^{0.67}$ per day)	1.0 ± 0.1	1.7 ± 0.2	< 0.001
Apparent digestibility (%)	68.9 ± 1.5	50.7 ± 4.7	0.003
Crude protein			
Intake (g/day)	1.9 ± 0.1	1.8 ± 0.2	0.648
Intake (g/kg$^{0.67}$ per day)	15.8 ± 2.0	15.6 ± 3.1	0.928
Faecal output (g/kg$^{0.67}$ per day)	3.2 ± 0.7	4.8 ± 0.9	0.006
Apparent digestibility (%)	79.5 ± 1.6	69.1 ± 0.9	0.001
Energy			
Intake (kJ/day)	1.4 ± 0.1	1.5 ± 0.2	0.650
Intake (g/kg$^{0.67}$ per day)	11.2 ± 1.4	12.6 ± 2.5	0.280
Faecal output (g/kg$^{0.67}$ per day)	3.0 ± 0.4	5.5 ± 0.7	< 0.001
Digestible intake (g/kg$^{0.67}$ per day)	8.2 ± 1.1	7.1 ± 2.5	0.363
Apparent digestibility (%)	73.2 ± 0.2	55.5 ± 0.8	0.001

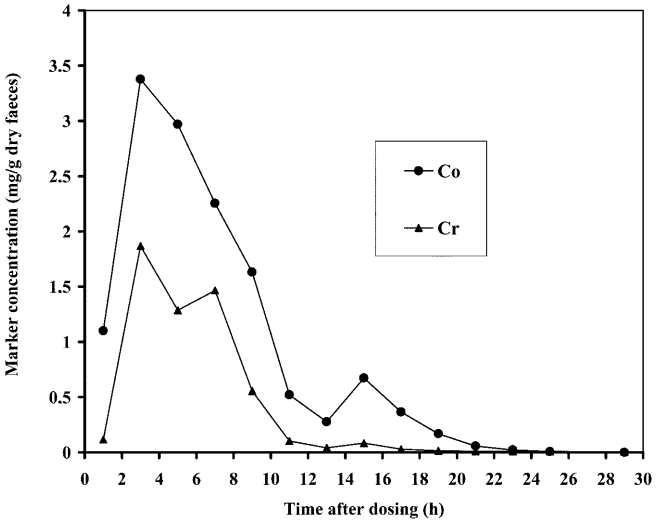

Fig. 1 Faecal marker concentration versus time after dosing of Co-EDTA and Cr-cell walls in Brandt's voles on a low fibre diet. Values are means of six individual measurements. Co-EDTA represents the solute phase of the digesta; Cr-cell walls represent large particles (300–600 μm) in digesta

Rate of passage of digesta

The patterns of marker appearance in the faeces after dosing are shown in Figs. 1, 2. Both markers appeared in collected faeces within the first 2 h after dosing, and their concentrations increased rapidly thereafter, to reach peaks within 3 h and 7 h after dosing. The primary peaks were followed by a slower decline, with small subsidiary peaks in marker concentration 7 h and 15–19 h after dosing.

Transit times and MRTs of the solute and particle markers are shown in Table 3. Transit times were 0.7–0.8 h for both markers, and were similar for the two markers and both diets. The MRT of Co-EDTA was greater than that of Cr-cell walls on the lower fibre diet, but on the higher fibre diet there was no significant difference.

Gut size

The lengths and masses of the gastrointestinal tract are shown in Table 4. Total length and total mass of the gut tissue significantly increased on the higher fibre diet. The lengths and masses of the caecum, proximal colon and distal colon were all significantly greater, and no significant differences were found in stomach and small intestine lengths and masses.

Coprophagy

Data from the slaughter study (three individuals at each time) (Fig. 3), show that 0.5 h after dosing, 26% of the Co remained in the stomach, 27% in the small intestine, 19% in the caecum and 14% in the colon, while 15% had already been voided in faeces; after 1.0 h, the amount of markers were 9%, 34%, 15%, 9% and 33%, respectively; after 1.5 h, they were 15%, 35%, 14%, 19% and 18%, respectively, and after 2.0 h, they were 13%, 14%, 18%, 17% and 37%, respectively. Thus, the marker amount in the stomach had decreased after 1 h, but after 1.5 h it had increased again, suggesting that marked faeces had been eaten by the voles.

Discussion

Our results provide evidence for selective retention of solutes and fluid, and probably small particles of digesta, including bacteria, in Brandt's voles. The most likely site of selective retention is the large caecum. Data from the slaughter study also suggest that Brandt's voles ingest some faeces (coprophagy). Because they were housed individually in metabolism cages with wire mesh floors, the faeces eaten must have been their own.

Based on previous work, the colonic separation mechanism (CSM) responsible for the selective retention of digesta in the caecum of voles and lemmings is located

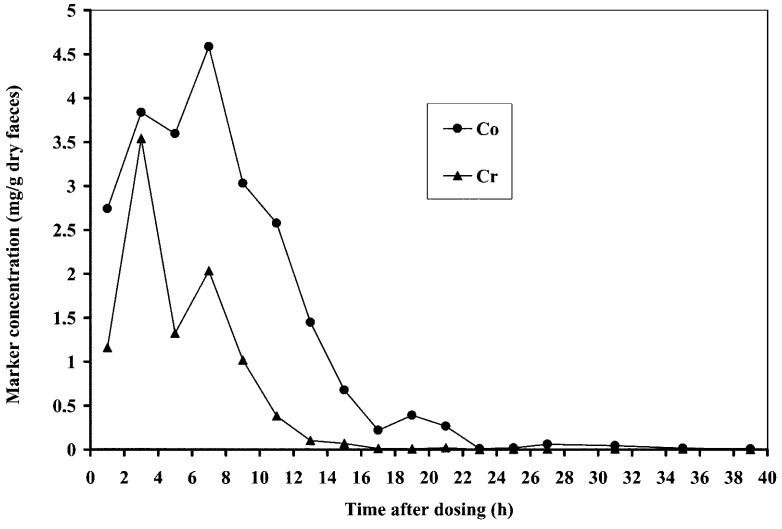

Fig. 2 Faecal marker concentration versus time after dosing of Co-EDTA and Cr-cell walls in Brandt's voles on a high fibre diet. Values are means of four individual measurements. Co-EDTA represents the solute phase of the digesta; Cr-cell walls represent large particles (300–600 μm) in digesta

Table 3 Transit times (*TT*) and mean retention times (*MRT*) of two markers in the gastrointestinal tract of Brandt's voles

	Co-EDTA		Cr-CWC	
	TT (h)	MRT (h)	TT (h)	MRT (h)
Low fibre diet	0.8 ± 0.1	7.4 ± 0.6^{a}	0.7 ± 0.1	5.1 ± 0.4^{b}
High fibre diet	0.8 ± 0.1	7.0 ± 0.6^{a}	0.7 ± 0.1	5.9 ± 0.6^{ab}

[ab]Means of MRT with different superscripts differ significantly ($P < 0.05$)

in the proximal colon (Sperber et al. 1983). Most of this region of the hindgut of *Lemnus lemnus* (the Scandinavian lemming) forms a double spiral, the lumen of which is almost completely divided into a narrow channel and the main lumen. Distal to the spiral, the proximal colon contains a longitudinal groove formed by two rows of oblique folds. This groove is continuous with the narrow channel of the spiral. Bacteria accumulate in the groove and are brought back to the spiral where they are trapped in mucus produced by tubular glands lining the narrow channel. The mixture of mucus and bacteria, with only few food particles, is brought back to the caecum, presumably by antiperistaltic movements (Sperber et al. 1983). This type of CSM is called the "mucus-trap" type (Cork et al. 1999). A similar mechanism is found in other myomorph rodents such as rats, and in caviomorph rodents such as guinea pigs, chinchilla and nutria (Björnhag 1987). It results in selective retention mainly of bacteria.

The other CSM described by Björnhag (1972) and Pickard and Stevens (1972) is the "wash-back" type (Cork et al. 1999). In this, a stream of water carries a mixture of solutes, small food particles and bacteria along the haustrated wall of the proximal colon to the caecum by antiperistaltic movements. The process is assisted by net secretion of water into distal parts of the proximal colon, and net absorption of water from the caecum (Björnhag 1981). This type of CSM is found in lagomorphs and in at least three folivorous marsupials (Björnhag 1987; Hume 1999). It results in selective retention not only of bacteria but also solutes, and small food particles.

Table 4 Effect of dietary fibre content on digestive tract morphology in Brandt's voles

	Low fiber diet	High fiber diet	*P* value
Sample size	6	5	
Total for gut			
Length (cm)	53.5 ± 2.6	70.8 ± 2.1	0.001
Dry mass of tissue (mg)	434.2 ± 14.6	553.8 ± 29.5	0.004
Gut segment			
Length (cm)			
Stomach	1.9 ± 0.1	2.0 ± 0.1	0.753
Small intestine	25.6 ± 1.7	28.7 ± 1.1	0.192
Caecum	8.9 ± 0.4	15.9 ± 0.4	0.001
Proximal colon	5.9 ± 1.1	9.2 ± 0.4	0.041
Distal colon	11.0 ± 0.8	14.8 ± 1.1	0.025
Dry mass of tissue (mg)			
Stomach	80.8 ± 1.9	89.2 ± 4.3	0.094
Small intestine	187.2 ± 7.0	200.0 ± 20.7	0.543
Caecum	93.3 ± 5.0	161.2 ± 4.0	0.001
Proximal colon	30.2 ± 6.1	49.0 ± 3.3	0.040
Distal colon	42.6 ± 2.5	54.4 ± 4.1	0.049

These two different types of CSM are reflected in the patterns of faecal appearance of pulse doses of inert markers that are specific for either unabsorbed solutes or food particles. There is much stronger selective retention of solute markers in the wash-back CSM than the mucus-trap CSM. Results from experiments based on the same or similar solute and particle markers as used in the present study are summarised in Table 5. For the wash-back type, the ratio of solute mean retention time to particle mean retention time (the solute/ particle differential retention ratio) ranges from 1.3 to 4.8. In contrast, for the mucus-trap type, reported ratios are only 1.2 at most for rats and guinea pigs (Stevens and Hume 1995). In voles, Hume et al. (1993) reported a ratio of 1.1 in the North American species *Microtus townsendii*. However, evidence that the ratio in voles can be higher than this is provided by the present study on *Microtus brandti* in China, in which ratios were 1.2 to 1.5.

Thus, although not as strongly retained as in species with wash-back CSMs, solute markers are selectively retained in at least two species of myomorph rodents. This is contrary to the conclusions of Sperber et al. (1983) and Björnhag (1987) that mucus-trap CSMs result in selective retention of bacterial cells but not of solutes, fluid or small food particles. There are two possible reasons for the conflict. One is the different markers and techniques used in the respective studies. The other is the possibility of subtle differences in the mucus-trap type of CSM among microtine rodents (lemmings and voles) that have yet to be discovered. Certainly there are differences between microtines and other myomorph rodents such as rats, even though practically all myomorph rodents have in their proximal colon two rows of oblique folds of mucosa that meet each other to form a longitudinal groove (Behmann 1973).

Selective retention of solutes, small food particles and bacteria in caecum fermenters is often associated with coprophagy. Our finding of coprophagy in Brandt's voles is in agreement with those of Björnhag and Sjöblom (1977) in the *Lemnus lemnus*, Ouellettte and Heisinger (1980) in *Microtus pennsylvanicus*, Kenagy and Hoyt (1980) in *Microtus californicus*, Cranford and Johnson (1989) in *Microtus pinetorum*, and Lee and Houston (1993) in *Microtus agrestis* and *Clethrionomys glareolus*. In all microtines studied, faeces are ingested at intervals throughout the day and night, interspersed with periods of eating and drinking. This pattern of feeding and digestive tract function is consistent with observations of ultradian activity patterns in microtines (e.g. Lehmann 1976; Gerkema and Daan 1985). Gerkema and Daan (1985) concluded that 6–12 short-term activity bouts are more or less evenly distributed over the 24 h. Halle (1995) found a clear-cut ultradian

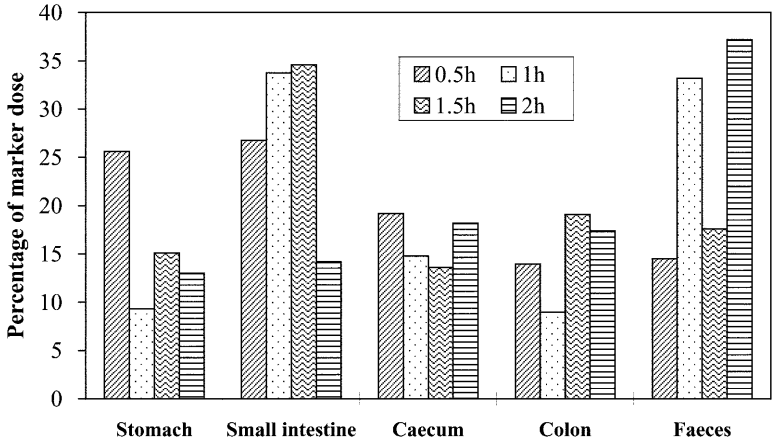

Fig. 3 The percentage of an oral pulse dose of Co-EDTA versus time in gut segments of Brandt's voles on commercial rabbit pellets

rhythm in root voles (*Microtus oeconomus*), with seven activity bouts per 24 h. These activity bouts are synchronous within family groups. Temporal synchrony in coprophagy bouts was also likely in the group of Brandt's voles in our study. If not, we would probably not have seen the increase in concentration of Co-EDTA in the stomach of all three animals killed 1.5 h after the oral pulse dose of the marker. Previous studies of coprophagy in microtines were based either on direct observation of individual animals (e.g. Kenagy and Hoyt 1980) or on radiographic observation of individuals over time after a pulse dose of barium sulphate directly into their caecum (Björnhag and Sjöblom 1977). Additional evidence for temporal synchrony is seen in the patterns of marker appearance in the faeces of groups of four or six animals (rather than of individuals) after the pulse dose of Co-EDTA and Cr- cell walls (Figs. 1, 2). On both diets there were small subsidiary peaks of marker concentration 7 h and 15–19 h after dosing. These peaks are indicative of an ultradian pattern of coprophagy. Without temporal synchrony within the group these small subsidiary peaks may not have been evident.

Brandt's voles were able to partly compensate for the higher fibre content and lower digestible energy content of the high fibre diet by maintaining dry matter intakes at or slightly above levels measured on the low fibre diet (Table 2). This is consistent with results from other microtine rodents (Batzli 1985; Cranford and Johnson 1989; Hume et al. 1993), and with the facilitation of the passage of large food particles through the gastrointestinal tract of caecum fermenters with a CSM (Cork et al. 1999). Although the digestibility of fibre and other dietary components may decline, selective digesta retention enables these small herbivores to maintain intakes of digestible energy and nutrients on fibrous diets at higher levels than would otherwise be the case. In contrast, in caecum fermenters without a CSM, such as the golden-mantled ground squirrel (*Spermophilus lateralis*),

Table 5 MRT of solute (Co-EDTA) and particle markers (Cr-Cell walls) in several caecum fermenters with a "wash-back" (*A*) or a "mucus-trap" (*B*) colonic separation mechanism (CSM). References: *1* Sakaguchi et al. (1992a), *2* Cork et al. (1999), *3* Chilcott and Hume (1985), *4* Foley and Hume (1987), *5* Cork and Warner (1983), *6* Krockenberger (1993), *7* Sakaguchi et al. (1987), *8* Sakaguchi and Nabata (1992b), *9* Sakaguchi et al. (1992), *10* Sakaguchi and Ohmura (1992), *11* Hume et al. (1993), *12* This study – *a* low fibre diet, *b* high fibre diet

Species	MRT (h)		$\frac{MRT_{solute}}{MRT_{particle}}$	Ref
	Solute	Particle		
A. Wash-back CSM				
Rabbit (*Oryctolagus cuniculus*)	80.0	16.7	4.79	1
	62.6	38.5	1.29	2
Ringtail possum (*Pseudocheirus peregrinus*)	63	35	1.80	3
	206.0	102.6	2.01	2
Greater glider (*Petauroides volans*)	51	23	2.22	4
Koala (*Phascolarctos cinereus*)	200	130	1.54	5
	99	32	3.09	6
B Mucus-trap CSM				
Guinea pig (*Cavia porcellus*)	16.3	15.9	1.03	7
	22.6	30.7	0.74	8
	18.9	20.9	0.90	9
	20.4	17.1	1.19	10
	15.3	15.1	1.01	1
Nutria (*Myocaster coypus*)	45.0	44.2	1.02	8
Mara (*Dolichotis patagonium*)	26.8	27.3	0.98	9
Degu (*Octodon degus*)	19.4	15.5	1.25	10
Leaf-eared mice (*Phyllotis darwini*)	9.1	8.8	1.03	10
Townsend vole (*Microtus townsendii*)	14.8	13.1	1.13	11
Brandt's vole (*Microtus brandti*)	7.4	5.1	1.45	12(a)
	7.0	5.9	1.19	12(b)

food intake decreased on higher fibre diets (Cork and Kenagy 1989).

Another response often seen in many small herbivores when switched to diets of higher fibre content is an increase in gut capacity (Karasov and Hume 1997). Much of the increase is in the caecum (Cork et al. 1999). In many cases, the increased gut capacity and the resulting increase in retention time of digesta in the gut is sufficient to allow digestibility to remain relatively constant, even though food intake may have increased. Gut capacity in Brandt's voles increased on the higher fibre diet, but this was not sufficient to increase mean retention times (Table 3), and consequently digestibilities were consistently lower on the higher fibre diet. We think that the relatively small increase in gut capacity may be due to the rather short (14 days) acclimation period used; a longer period of acclimation may have increased gut capacity further.

Mean retention times in Brandt's voles were less than half those measured in another microtine (*M. townsendii*) by Hume et al. (1993; Table 4). Part of this difference may be due to the smaller body size of *M. brandti* (40–46 g) than of *M. townsendii* (55 g) and their higher dry matter intakes (65 $g/kg^{0.67}$ per day versus 57 $g/kg^{0.67}$ per day^{-1}). However, it is also likely that, relative to body size, *M. brandti* had a smaller gut volume. It would seem that all three explanations (viz. higher food intakes, smaller gut capacity, and a limited increase in gut capacity on the high fibre diet) would need to be invoked in order to account for the two-fold difference in MRTs between the two microtine species.

Thus, although the responses were not as great as those recorded in some other microtine rodents, Brandt's voles were able to partly compensate for the increased cellulose content of the diet by maintaining dry matter intakes and increasing digestive tract capacity despite large decreases in digestibility of all dietary components measured, especially fibre. Their ability to maintain food intakes must be due to the presence of a colonic separation mechanism, which facilitates the clearance of indigestible large particles from the hindgut (Sperber et al. 1983).

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