

Effects of Dietary Fibre on Digesta Passage, Nutrient Digestibility, and Gastrointestinal Tract Morphology in the Granivorous Mongolian Gerbil (*Meriones unguiculatus*)

Yan-Xin Pei¹

De-Hua Wang^{1,*}

Ian D. Hume²

¹State Key Laboratory for Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, People's Republic of China;

²School of Biological Sciences A08, University of Sydney, New South Wales 2006, Australia

Accepted 6/4/01

ABSTRACT

To investigate digestive tract performance in Mongolian gerbils (*Meriones unguiculatus*), food intake and digestibility, digesta passage rate, and gastrointestinal tract morphology were measured in captive animals fed low- or high-fibre diets. We used two markers (Co-ethylene diamine tetra-acetic acid for solutes and Cr-mordanted cell walls for particles) to measure differential passage rates of digesta fractions in order to test for the presence of a colonic separation mechanism (CSM). Although dry-matter intakes on the high-fibre diet did not differ from those on the low-fibre diet, digestibilities of dry matter, neutral-detergent fibre, acid-detergent fibre, crude protein, and crude fat were all significantly lower on the high-fibre diet. Gross energy intake on the high-fibre diet also did not differ from that on the low-fibre diet, but energy lost in faeces was much higher than on the low-fibre diet; thus, energy digestibility and digestible energy intake were significantly lower on the high-fibre diet. The lengths and dry-tissue masses of all segments of the gastrointestinal tract tended to enlarge in response to increased dietary fibre, but only the total tract contents, contents of the small intestine, and length and dry-tissue mass of the caecum increased significantly. The mean retention time (MRT) of the particle marker was significantly greater than that of the solute marker on the low-fibre but not the high-fibre diet; the solute/particle differential retention ratio was 0.62 on the low-fibre diet and 0.90 on the high-fibre diet. Thus, there was no

evidence for selective retention of the solute marker on either diet. The MRT of the particle marker was significantly lower on the high-fibre diet and in the same direction as the MRT of the solute marker. These results suggest that the granivorous Mongolian gerbil has no CSM but can adjust its digestive tract capacity to accommodate greater quantities of low-quality food.

Introduction

Fibre of plant material affects many aspects of gastrointestinal function in mammals (Southgate 1990; Hansen et al. 1992). The model of Illius and Gordon (1992) suggests that mammals below a body mass of 1–3 kg should not be able to rely on microbial fermentation of structural plant parts in their digestive tract as a primary source of metabolic energy. This is because digesta retention times are too short for sufficient microbial breakdown of plant cell walls (Cork 1994). Nevertheless, as Justice and Smith (1992) noted, a number of small herbivorous and omnivorous rodents have well-developed abilities to digest fibre. Some small mammalian herbivores 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.

When small rodents are faced with declining diet quality, they have three options. First, they can select among diet components seasonally to maximize energy intake (Phillipson et al. 1980; Batzli 1985). Second, they can increase food intake to process more food even though digestibility decreases (Batzli and Cole 1979). Third, they can increase gut size and absorptive capacity to compensate for the lower digestibility of low-quality food (Lee and Houston 1993). Some or all of these strategies have been found in several small herbivorous rodents, particularly microtines (voles and lemmings) from North America and Europe (Björnhag 1994). Recently, Pei et al. (2001) found evidence for similar adaptations in the Asian microtine *Microtus brandti* (Brandt's vole).

Within families of mammals, granivores (seed eaters) tend to have lower gut capacity relative to strict herbivores (Parra 1978) and have a comparatively smaller caecum and colon

* Corresponding author; e-mail: wangdh@panda.ioz.ac.cn.

(Schieck and Millar 1985). These characteristics constrain granivores in their ability to digest plant cell walls relative to herbivores (Cork et al. 1999). One group of predominantly granivorous rodents consists of the gerbils, jirds, and sand rats (subfamily Gerbillinae in the family Muridae). The Gerbillinae are distributed through savanna, steppe, and desert biotopes in sub-Saharan Africa, the hot deserts and semideserts of northern Africa and southwest Asia, and in the colder deserts, semideserts, and steppes of central Asia (MacDonald 1984). Gerbils are well known for their well-developed water conservation abilities (Edwards et al. 1983). However, little is known of their digestive tract function.

The Mongolian gerbil (*Meriones unguiculatus*) is a small (60–80 g) Asian species distributed primarily in the Inner Mongolian grasslands of China, the desert region of Mongolia, and the Beigaer Lake region of Russia. It feeds mainly on plant seeds; during summer, green stems and leaves are also consumed, but during autumn and winter, its diet is dominated by grass seeds (Zhang and Wang 1998). It is well known as a seed hoarder, with one animal storing as much as 20 kg of seeds in its burrow in order to survive the winter (MacDonald 1984). Sun and Jing (1984) and Wang et al. (2000) examined their resting and average daily metabolic rates. The aim of this study was to examine the effect of food with different fibre levels on food intake and digestibility, rate of digesta passage, and gastrointestinal tract size in the Mongolian gerbil. We used two markers (Co-ethylene diamine tetra-acetic acid [EDTA] for solutes and Cr-mordanted cell walls for particles) to measure differential passage rates of digesta fractions and to test for the presence of a colonic separation mechanism (CSM).

Material and Methods

Animals and Diets

Adult Mongolian gerbils were livetrapped in Inner Mongolia in May 1999 and transported to the Institute of Zoology, Chinese Academy of Sciences in Beijing. They were maintained on standard rat pellets (Beijing Ke Ao Feed Co.) in plastic cages at $24^{\circ} \pm 1^{\circ}\text{C}$ under a 15L:9D cycle with lights on at 0600 hours. Food and water were available ad lib. throughout the experiment. After 2 wk of acclimation, 15 animals were housed individually in stainless steel mesh metabolism cages ($0.24 \times 0.24 \times 0.24$ m) over a device to collect faeces and urine separately. The animals were randomly assigned one of two diets: **eight animals were offered a low-fibre diet** of standard rat pellets (13.5% neutral-detergent fibre [NDF]) and **seven animals a high-fibre diet** of rat pellets with additional fibre (27.4% NDF). The gender ratio was similar on the two diets, and no female was pregnant or lactating. The **high-fibre diet** was prepared by grinding the standard rat pellets and then thoroughly **mixing them with** an amount of **alfalfa powder** equal to 50% of the weight of rat pellets. The dry mixture was moistened and then warmed until dry in

order to adhere the **alfalfa powder** to the rest of the diet, and then it was repelleted (Table 1).

Food Intake and Digestibility

After an adaptation period of 2 wk on the experimental diets, food residues and faeces were collected from each animal for 5 d. The animals were weighed at the beginning and end of the experiment.

All food residues and faeces and samples of the diets were oven dried for 48 h at 60°C , weighed to determine dry-matter content, and then ground through a 1-mm screen. Portions of each sample were used to determine contents of crude fat, crude protein, NDF, acid-detergent fibre (ADF), and gross energy. NDF and ADF were determined by the procedures of Goering and Van Soest (1970) after pretreatment with heat-stable α -amylase (Sigma A3306) to remove starch (Van Soest et al. 1991). Total nitrogen was determined following the Kjeldahl procedure, and crude protein was calculated as total nitrogen $\times 6.25$. Crude fat was measured with the Soxhlet procedure using diethyl ether. The gross energy content was determined in a Parr 1281 adiabatic bomb calorimeter (Parr Instrument, Moline, Ill.), using benzoic acid as the standard.

Digesta Passage Rate

Digesta passage rate was measured immediately after the digestibility collection period. Two inert markers were used. The **solute phase of the digesta** was marked with Co-EDTA (Dojindo, Osaka, Japan), and the **large-particle phase** with Cr-mordanted cell walls (Cr-cell walls). The cell walls were prepared from ground oats (*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) screens, and those particles that passed the $600\text{-}\mu\text{m}$ screen but were retained on the $300\text{-}\mu\text{m}$ 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 mixed with a small amount (<2 g) of wheat flour to make a pellet that was offered to each of 12 animals at 1600 hours, after removing the experimental diet. One of the animals on the low-fibre diet

Table 1: Nutritional analysis of pelleted Mongolian gerbil diets (dry-matter basis)

Nutrients	Low-Fibre Diet	High-Fibre Diet
Crude fat (%)	$6.1 \pm .8$	$7.8 \pm .9$
Crude protein (%)	34.3 ± 3.5	23.7 ± 3.3
NDF (%)	13.5 ± 1.3	27.4 ± 1.9
ADF (%)	$6.5 \pm .5$	19.4 ± 1.1
Gross energy (kJ g^{-1})	$18.0 \pm .8$	$17.9 \pm .5$

Note. NDF: neutral detergent fibre; ADF: acid detergent fibre. Values are means \pm SE ($n = 6$).

Table 2: Body mass change, intake, and digestibility in Mongolian gerbils

	Low-Fibre Diet (n = 8)	High-Fibre Diet (n = 7)	P
Body mass (g):			
Initial body mass	55.6 ± 4.0	47.0 ± 1.9	.089
Final body mass	58.8 ± 3.8	44.8 ± 1.9	.008
Body mass change	3.2 ± 1.8	-2.2 ± .6	.016
Dry matter:			
Intake (g d ⁻¹)	6.7 ± .3	5.9 ± .4	.179
Intake (g kg ^{-.67} d ⁻¹)	45.0 ± 2.8	47.6 ± 2.9	.534
Faecal output (g kg ^{-.67} d ⁻¹)	9.8 ± .5	22.0 ± 1.2	<.001
Apparent digestibility (%)	78.0 ± 1.0	53.6 ± 1.6	<.001
Fibre:			
Intake of NDF (g d ⁻¹)	.9 ± .0	1.6 ± .1	<.001
Intake of NDF (g kg ^{-.67} d ⁻¹)	5.8 ± .2	13.0 ± .8	<.001
Faecal output (g kg ^{-.67} d ⁻¹)	3.0 ± .1	11.1 ± .7	<.001
Digestibility of NDF (%)	47.9 ± .9	14.2 ± 3.7	<.001
Intake of ADF (g d ⁻¹)	.4 ± .0	1.2 ± .1	<.001
Intake of ADF (g kg ^{-.67} d ⁻¹)	2.8 ± .1	9.2 ± .6	<.001
Faecal output (g kg ^{-.67} d ⁻¹)	1.4 ± .1	7.9 ± .4	<.001
Digestibility of ADF (%)	49.8 ± 1.6	14.3 ± 2.9	<.001
Crude fat:			
Intake (g d ⁻¹)	.4 ± .0	.5 ± .0	.051
Intake (g kg ^{-.67} d ⁻¹)	2.6 ± .1	3.7 ± .2	<.001
Faecal output (g kg ^{-.67} d ⁻¹)	.7 ± .0	1.2 ± .1	<.001
Apparent digestibility (%)	72.1 ± .7	66.4 ± 1.7	.009
Crude protein:			
Intake (g d ⁻¹)	2.2 ± .1	1.4 ± .1	<.001
Intake (g kg ^{-.67} d ⁻¹)	14.7 ± .5	11.3 ± .7	.002
Faecal output (g kg ^{-.67} d ⁻¹)	7.9 ± .2	4.1 ± .3	.012
Apparent digestibility (%)	80.1 ± 1.2	63.3 ± .9	<.001
Energy:			
Intake (kJ d ⁻¹)	115.00 ± 5.34	106.92 ± 7.11	.370
Intake (kJ kg ^{-.67} d ⁻¹)	773.07 ± 28.27	857.51 ± 51.32	.163
Faecal output (kJ kg ^{-.67} d ⁻¹)	157.23 ± 9.19	359.65 ± 19.94	<.001
Digestible intake (kJ kg ^{-.67} d ⁻¹)	615.78 ± 20.08	497.32 ± 35.51	.010
Apparent digestibility (%)	79.7 ± .5	57.8 ± 1.2	<.001

Note. Values are means ± SE.

ingested insufficient markers within the 30 min allowed in order that the dose could be described as a pulse dose and was removed from the experiment. After dosing, the experimental diets were offered as during the digestibility experiment. The collection trays beneath the metabolism cages were inspected, and any faeces present 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 (a total of 72 h). Defaecation times were taken as the midpoint of each inspection interval. Collected faeces were oven dried at 60°C for 48 h and then ashed in a muffle furnace at 550°C for 4 h. Ashed samples were digested in conical flasks on a hot plate with 10-mL 1.5 N nitric acid containing 2 g

KCl. The clear digests were transferred quantitatively to 25-mL volumetric flasks and diluted to the mark with 1.5 N nitric acid. The concentrations of Co and Cr in the diluted digests were determined by flame atomic absorption spectroscopy (Siman180-80, Hitachi, Tokyo, Japan).

Gastrointestinal Tract Morphology

The animals were killed by decapitation after the measurement of digesta passage rate. Their complete gastrointestinal tracts were quickly removed and dissected free of mesenteric attachments but without stretching the tissue (Freehling and Moore

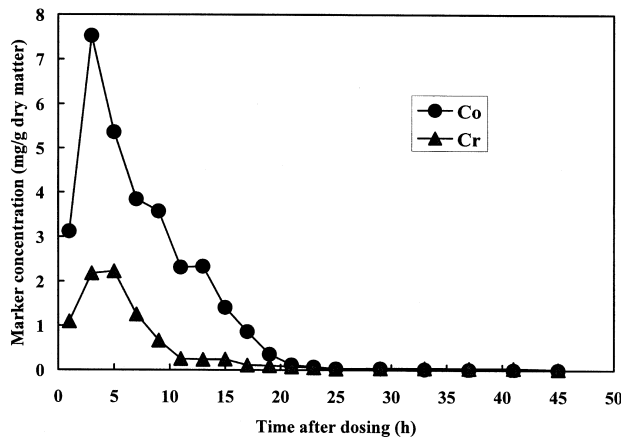


Figure 1. Faecal marker concentration versus time after dosing of Co-EDTA and Cr-cell walls in Mongolian gerbils on the low-fibre diet. Values are the means of five individuals. Co-EDTA represents the solute phase of the digesta; Cr-cell walls represent the large particles (300–600 μm) in digesta.

1987). The lengths and fresh weights with contents and fresh weights without contents of the stomach, small intestine, caecum, proximal colon, and distal colon were recorded. The junction between proximal and distal colon was taken to be the point where segmentation of contents first became apparent (Hume et al. 1993). The content-free tissues were dried at 60°C for 48 h and weighed. The weight of contents was assumed to be the difference between the wet weights of a segment with and without contents.

Calculations and Statistical Analysis

Apparent digestion and digestibility of energy and nutrients of the food were calculated as follows (Sibly 1981):

$$\begin{aligned} \text{amount digested (g d}^{-1}\text{)} &= \text{amount ingested (g d}^{-1}\text{)} \\ &\quad - \text{amount defaecated (g d}^{-1}\text{)}, \\ \text{digestibility (\%)} &= \frac{100 \times \text{amount digested (g d}^{-1}\text{)}}{\text{amount ingested (g d}^{-1}\text{)}}. \end{aligned}$$

The term “digestibility” is used for fibre because there is no endogenous source of fibre, but “apparent digestibility” is used for dry matter, crude fat, crude protein, and energy to indicate that no correction was made for endogenous sources of these dietary fractions.

Transit time (TT) was taken to be the time for the appearance of 5% of the marker in the faeces (Balch 1950). Mean retention time (MRT), the best single measure of passage rate through the entire gastrointestinal tract (Warner 1981), was calculated by the formula

$$\text{MRT} = \frac{\sum_{i=1}^n m_i t_i}{\sum_{i=1}^n m_i},$$

where m_i is the amount of marker in the i th defaecation at time t_i after the dose and n is the total number of defaecations to recover the whole of the marker dose (Blaxter et al. 1956).

Values are presented as mean \pm SE. In order to minimize any effect of body size and for ease of comparisons across rodent species, all intake data are scaled to the 0.67 power of body mass ($\text{kg}^{0.67}$); Hayssen and Lacy (1985) found this to be the most appropriate exponent for rodents. Differences in intake and digestibility between the low- and high-fibre diets were tested by independent-sample t -tests. Differences between MRTs of Co-EDTA and Cr-cell walls within diets were tested by paired t -tests, and differences between diets were tested by independent-sample t -tests. All t -tests were two tailed. All statistical tests were performed with a computerized statistical software package (SPSS 1988). Differences were considered significant at the 5% level.

Results

Food Intake and Digestibility

Body mass changes, intake and digestibility of each dietary component, and parameters of energy metabolism were measured on the two diets (Table 2). There was no significant difference in the initial body mass of the two groups of gerbils, but those on the low-fibre diet gained mass ($t = -1.84$, $P = 0.109$) over the 5-d collection period, while those on the high-fibre diet lost mass ($t = 3.86$, $P = 0.008$).

Dietary-fibre content had no significant effect on intakes of dry matter, but intakes of NDF, ADF, and crude fat were all

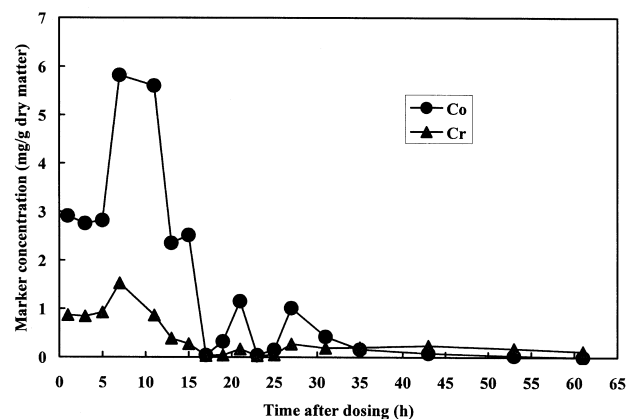


Figure 2. Faecal marker concentration versus time after dosing of Co-EDTA and Cr-cell walls in Mongolian gerbils on the high-fibre diet. Values are the means of six individuals. Co-EDTA represents the solute phase of the digesta; Cr-cell walls represent the large particles (300–600 μm) in digesta.

Table 3: Transit times (TT) and mean retention times (MRT) of two digesta markers in the gastrointestinal tracts of Mongolian gerbils

	Co-EDTA Solute Marker		Cr-CWC Particle Marker	
	TT (h)	MRT (h)	TT (h)	MRT (h)
Low-fibre diet	1.0 ± .1	10.1 ± 1.6 ^A	1.2 ± .1	16.4 ± 1.7 ^B
High-fibre diet	1.3 ± .1	8.2 ± 1.1 ^A	1.0 ± .1	9.1 ± 1.6 ^A

Note. Means of MRT with different superscripts differ significantly ($P < 0.05$). Values are means ± SE. $n = 5$ for low-fibre diet; $n = 6$ for high-fibre diet.

higher, while intakes of crude protein were lower on the high-fibre diet. The apparent digestibility of dry matter, crude fat, and crude protein and the digestibility of NDF and ADF were all lower on the high-fibre diet (Table 2).

As with dry matter, intakes of gross energy were not significantly different between the two groups, but faecal energy loss was much greater on the high-fibre diet. As a result, energy digested and apparent digestibility of energy were both lower on the high-fibre diet (Table 2).

Rate of Marker Passage

The patterns of appearance of the two markers in the faeces with time after dosing are shown in Figures 1 and 2. Both markers were present in faeces collected 2 h after dosing. Their concentrations increased rapidly thereafter to reach peaks within 3 and 7 h after dosing, and then they declined and reached background levels at 21 h after dosing on the low-fibre diet and between 17 and 35 h after dosing on the high-fibre diet.

TTs and MRTs of the two markers on the two diets are shown in Table 3. There were no significant differences in TT either between markers or between diets. The MRT of the particle marker was greater than that of the solute marker on the low-fibre diet ($t = 5.186$, $P = 0.007$) but not on the high-fibre diet ($t = -1.118$, $P = 0.315$). The ratio of the average solute to particle marker MRTs (the solute/particle differential retention ratio) was 0.62 on the low-fibre diet but 0.90 on the high-fibre diet. The MRT of the particle marker was significantly lower for the high-fibre than for the low-fibre diet ($t = 0.350$, $P = 0.014$), but MRT of the solute marker did not differ between diets ($t = 1.014$, $P = 0.337$).

Gastrointestinal Tract Size

There were no significant differences in total length or total dry mass of the gastrointestinal tract between the two diets (Table 4), although the 28% greater total tract tissue dry mass on the high-fibre diet approached significance ($t = -1.915$, $P = 0.085$). The responses of the component parts of the tract to increased dietary fibre were different. The dry-tissue mass of the stomach and caecum was 32% greater on the high-fibre

diet ($t = -3.838$, $P = 0.003$ and $t = 22.313$, $P = 0.043$, respectively), and the length of the caecum was 51% greater ($t = -6.862$, $P = 0.001$). Although the length and dry-tissue mass of the small intestine, proximal colon, and distal colon also tended to increase on the high-fibre diet, none of the differences reached significance at $P = 0.05$.

The total mass of gastrointestinal contents was significantly greater ($t = -2.231$, $P = 0.050$), but of the component tract segments, only the small intestine contents were significantly greater (by 122%; $P = 0.025$) on the high-fibre diet.

Discussion

Results are consistent with the highly granivorous dietary habit of the Mongolian gerbil. The MRT of Cr-cell walls was greater than that of Co-EDTA, which reflects the slower release of particles than of solutes from the stomach, a phenomenon that is common among vertebrates (Stevens and Hume 1995), but there was little selective retention of either digesta phase in the remainder of the tract. Thus, there was no evidence for a CSM in the gerbil hindgut. A CSM would be expected to result in selective retention in the caecum of solutes and small particles (Björnhag 1987) and thus a greater MRT of the solute marker rather than the particle marker.

One of the several advantages of a CSM to a small mammal (Cork et al. 1999) is the facilitated passage of large particles through the colon. This results in higher levels of food intake than would otherwise be possible on a forage diet. The gerbils in our study were not able to increase food intake when the fibre content of the food was increased but digestibility, and, consequently, digestible-energy intake, fell (Table 2), and they lost body mass.

Although the high-fibre diet was lower in crude-protein content than the low-fibre diet (Table 1), and the apparent digestibility of the protein was lower, its digestible-crude-protein content was still 15.0%. Edwards et al. (1983) showed that Mongolian gerbils maintained body mass on a diet of only 9.8% crude protein (and lower on a digestible basis). This suggests that, even on the high-fibre diet, our gerbils were consuming protein at above maintenance levels. Therefore, the difference in crude-protein content between the two experimental diets is unlikely to have influenced our results. The two

Table 4: Effect of dietary-fibre content on the gut length and dry-tissue mass of Mongolian gerbils

	Low-Fibre Diet (<i>n</i> = 5)		High-Fibre Diet (<i>n</i> = 6)		<i>P</i>
Totals for gut:					
Length with contents (cm)	46.5 ±	3.1	51.9 ±	2.0	.174
Dry-tissue mass (mg)	635.3 ±	75.9	814.5 ±	54.6	.085
Contents (mg)	656.0 ±	126.9	1085.0 ±	144.4	.050
Gut segments:					
Length with contents (cm):					
Stomach	2.5 ±	.1	2.7 ±	.1	.236
Small intestine	30.5 ±	2.5	32.2 ±	1.7	.609
Caecum	4.1 ±	.1	6.2 ±	.2	.001
Proximal colon	2.9 ±	.3	3.7 ±	.8	.369
Distal colon	6.2 ±	.4	6.9 ±	.1	.208
Dry-tissue mass (mg):					
Stomach	104.0 ±	6.9	137.5 ±	5.3	.003
Small intestine	347.5 ±	64.5	455.1 ±	46.5	.202
Caecum	90.6 ±	8.7	119.1 ±	8.7	.043
Proximal colon	43.8 ±	2.6	50.1 ±	11.6	.608
Distal colon	49.3 ±	2.5	52.5 ±	2.4	.395
Contents (mg):					
Stomach	327.3 ±	85.8	509.8 ±	78.8	.147
Small intestine	102.6 ±	25.2	228.0 ±	40.4	.025
Caecum	149.6 ±	19.1	236.0 ±	44.1	.103
Proximal colon	31.8 ±	9.7	41.5 ±	14.2	.587
Distal colon	44.5 ±	9.9	69.7 ±	13.6	.167

Note. Values are means ± SE.

diets were similar in crude fat and gross-energy content; however, apparent digestibility of energy was lower, and hence, the intake of digestible energy was also lower on the high-fibre diet, which is consistent with the lack of a CSM in the gerbil hindgut.

Among rodents, there is evidence for a CSM in the hindgut of the strictly herbivorous microtines (Hume et al. 1993; Pei et al. 2001), which allows these small mammals to process plant material of much higher fibre content than would be predicted from models based on cell wall digestion, such as that of Illius and Gordon (1992). However, other rodent groups such as the Sciuridae (squirrels) do not appear to have a CSM (Hume 1994), and the smaller members of this family are, like gerbils, granivores rather than strict herbivores (e.g., Trombulak 1985). On forage diets, food intake is limited by the slow passage of large particles. Larger sciurids such as the marmots are more herbivorous because the disadvantage of a lack of a CSM is partially offset by larger body size and thus greater fermentation capacity (Parra 1978; Hume et al. 1993).

On the low-fibre diet, our Mongolian gerbils digested dry matter to the same extent as more herbivorous rodents of similar body size such as the Townsend vole (*Microtus townsendii* [Hume et al. 1993]; both 77% on a 7% ADF diet). Although

dry-matter digestibility fell to similar levels (54%) in both rodents on a higher-fibre diet (19%–22% ADF), dry-matter intake increased by 20% in the voles, whereas in the gerbils it did not change. The increase in the voles suggests the presence of a CSM that facilitates the passage of large particles through the hindgut and probably also an increase in total gastrointestinal tract capacity. Hume et al. (1993) did not measure gut fill in the Townsend vole. However, the length and mass of the contents of the caecum of several other *Microtus* species have been found by Gross et al. (1985) and Lee and Houston (1993) to increase by as much as 42% in response to increased dietary fibre. We found similar increases in caecal size in Mongolian gerbils (Table 4), which may explain why dry-matter intake did not decline on the high-fibre diet despite the absence of a CSM.

Increases in gut capacity in response to lower diet quality appear to be a general phenomenon among animals. Penry and Jumars (1987) described it as a moderating mechanism that maintains or defends digestibility of the diet. An increase in gut size with the diet quality reduced can theoretically result in several benefits to small mammals. First, at a similar rate of food intake, digesta passage rate should decrease (i.e., digesta retention time should increase) so that digestibility of refractory

components of the diet may be maintained or even increased (Sibly 1981). Second, rate of food intake may be maintained or even increased despite a decline in rate of digestion. Third, even if digestibility declines, greater quantities of food can be processed by the gut, which may result in increased quantities of nutrients being absorbed (Ferraris and Diamond 1986; Karasov and Diamond 1988).

Although the Mongolian gerbil does not appear to have a specialised CSM, the increase in gut capacity observed in this study in response to increased dietary fibre should allow it to cope with modest fluctuations in diet quality between a peak in summer to lower levels in autumn and winter. In this it is similar to small sciurid rodents, the ground and tree squirrels and chipmunks (Hume et al. 1993). Both groups appear to have some capacity to deal with fluctuations in diet quality throughout the year, but neither group has the capacity to process enough dry forage in its gastrointestinal tract to be a successful herbivore; instead, they are predominantly granivores.

Acknowledgments

We are grateful to Professor Y. Shi of Beijing Normal University for carrying out the marker analyses, to Z. Song and Y. Wang for their help with the experiments, and to Dr. G. J. Faichney, University of Sydney, for his helpful comments on a draft of this article. The study was supported in part by the National Natural Science Foundation of China (39770122 and 39970128), the Chinese Academy of Sciences (KSCX2-1-03, STZ-01-06), and the Project of Science and Technology Committee of the People's Republic of China (FS200-009).

Literature Cited

- Balch C.C. 1950. Factors affecting the utilization of food by the dairy cow. I. The rate of passage of food through the digestive tract. *Br J Nutr* 4:361–388.
- Batzli G.O. 1985. Nutrition. In R.M. Tamarin, ed. *Biology of the New World Microtus*. Spec Publ Am Soc Mammal 8: 779–811.
- Batzli G.O. and F.R. Cole. 1979. Nutritional ecology of microtine rodents: digestibility of forage. *J Mammal* 60:740–750.
- Björnhag G. 1987. Comparative aspects of digestion in the hindgut of mammals: the colonic separation mechanism (CSM) (a review). *Dtsch Tierärztl Wochenschr* 94:33–36.
- . 1994. Adaptations of the large intestine allowing small mammals to eat fibrous diets. Pp. 287–309 in D.J. Chivers and P. Langer, eds. *The Digestive System of Mammals: Food, Form and Function*. Cambridge University Press, Cambridge.
- Blaxter K.L., N.M. Graham, and F.W. Wainman. 1956. Some observations on the digestibility of food by sheep, and on related problems. *Br J Nutr* 10:69–91.
- Cork S.J. 1994. Digestive constraints on dietary scope in small and moderately-small mammals: how much do we really understand? Pp. 337–369 in D.J. Chivers and P. Langer, eds. *The Digestive System in Mammals: Form, Food and Function*. Cambridge University Press, Cambridge.
- Cork S.J., I.D. Hume, and G.J. Faichney. 1999. Digestive strategies of nonruminant herbivores: the role of the hindgut. Pp. 210–260 in H.-J.G. Jung and G.C. Fahey, Jr., eds. *Nutritional Ecology of Herbivores*. American Society of Animal Science, Savoy, Ill.
- Edwards B.A., K. Donaldson, and A.P. Simpson. 1983. Water balance and protein intake in the Mongolian gerbil *Meriones unguiculatus*. *Comp Biochem Physiol* 76A:807–815.
- Ferraris R.P. and J.M. Diamond. 1986. Use of phlorizin binding to demonstrate induction of intestinal glucose transporters. *J Membr Biol* 94:77–82.
- Freehling M.D. and J. Moore. 1987. A comparison of two techniques for measuring gut length. *J Wildl Manag* 51:101–108.
- Goering H.K. and P.J. Van Soest. 1970. *Forage Fibre Analysis*. U.S. Dept. Agric. Handb. 379. 20 pp.
- Gross J.E., Z. Wang, and B.A. Wunder. 1985. The role of diet quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. *J Mammal* 66:661–667.
- Hansen I., K.E.B. Knudsen, and B.O. Eggum. 1992. Gastrointestinal implications in the rat of wheat bran, oat bran and pea fibre. *Br J Nutr* 68:451–462.
- Hayssen V. and R.C. Lacy. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp Biochem Physiol* 81A:741–754.
- Hume I.D. 1989. Optimal digestive strategies in mammalian herbivores. *Physiol Zool* 62:1145–1163.
- . 1994. Gut morphology, body size and digestive performance in rodents. Pp. 315–323 in D.J. Chivers and P. Langer, eds. *The Digestive System in Mammals: Form, Food and Function*. Cambridge University Press, Cambridge.
- Hume I.D., K.R. Morgan, and G.J. Kenagy. 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. *Physiol Zool* 66:396–411.
- Illius A.W. and I.J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89:428–434.
- Justice K.E. and F.A. Smith. 1992. A model of dietary fibre utilization by small mammalian herbivores, with empirical results from *Neotoma*. *Am Nat* 139:398–416.
- Karasov W.H. and J.M. Diamond. 1988. Interplay between physiology and ecology in digestion: intestinal nutrient transporters vary within and between species according to diet. *BioScience* 38:602–611.
- Lee W.B. and D.C. Houston. 1993. The effect of diet quality on gut anatomy in British voles (Microtinae). *J Comp Physiol* 163B:337–339.
- MacDonald D. 1984. *The Encyclopedia of Mammals*. Facts on File Publications, New York.

- Parra R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pp. 205–229 in G.G. Montgomery, ed. *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, D.C.
- Pei Y.X., D.H. Wang, and I.D. Hume. 2001. Selective digesta retention and coprophagy in Brandt's vole *Microtus brandti*. *J Comp Physiol* 171B (in press).
- Penry D.L. and P.A. Jumars. 1987. Modeling animal guts as chemical reactors. *Am Nat* 129:69–96.
- Phillipson J., M. Sarrazin-Comans, and C. Stomatopoulos. 1980. Food consumption by *Microtus agrestis* and the unsuitability of faecal analysis for the determination of food preference. *Acta Theriol* 28:397–416.
- Schieck J. and J.S. Millar. 1985. Alimentary tract measurements as indicators of diets of small mammals. *Mammalia* 49: 93–104.
- Sibly R.M. 1981. Strategies of digestion and defecation. Pp. 109–139 in C.R. Townsend and P. Calow, eds. *Physiological Ecology: An Evolutionary Approach to Resource Use*. Sinauer, Sunderland, Mass.
- Southgate D.A.T. 1990. Dietary fibre and health. Pp. 10–19 in D.A.T. Southgate, K. Waldron, I.T. Johnson, and G.R. Fenwick, eds. *Dietary Fibre: Chemical and Biological Aspects*. Royal Society of Chemistry, Cambridge.
- SPSS. 1988. SPSS. Publishing House of Electronics Industry, Beijing.
- Stevens C.E. and I.D. Hume. 1995. *Comparative Physiology of the Vertebrate Digestive System*. Cambridge University Press, Cambridge.
- Sun R.Y. and S.L. Jing. 1984. Relation between average daily metabolic rate and resting metabolic rate of the Mongolian gerbil *Meriones unguiculatus*. *Oecologia* 65:122–124.
- Trombulak S.C. 1985. The influence of interspecific competition on home range size in chipmunks *Eutamias*. *J Mammal* 66:329–337.
- Udén P., P.E. Colucci, and P.J. Van Soest. 1980. Investigation of chromium, cerium and cobalt as markers in digesta rate of passage studies. *J Sci Food Agric* 31:625–632.
- Van Soest P.J., J.B. Robertson, and B.A. Lewis. 1991. Methods of dietary fibre, neutral detergent fibre, and non-starch polysaccharides in relation to animal nutrition. *J Dairy Sci* 74: 3583–3597.
- Wang D.H., Y.S. Wang, and Z.W. Wang. 2000. Metabolism and thermoregulation in the Mongolian gerbil *Meriones unguiculatus*. *Acta Theriol* 45:183–192.
- Warner A.C.I. 1981. Digesta passage rate through the gut of mammals and birds. *Nutr Abstr Rev* 51B:789–820.
- Zhang Z.B. and Z.W. Wang. 1998. Ecology and management for dominant pest rodent in the typical steppe of Inner Mongolia. Pp. 209–220 in *Ecology and Management of Rodent Pests in Agriculture*. Ocean, Beijing.