Digesta Retention and Digestive Performance in Sciurid and Microtine Rodents: Effects of Hindgut Morphology and Body Size

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Abstract

To examine the effects of hindgut morphology and body size on the digestive performance of rodents, we fed diets of three different fiber contents (7%, 22%, and 28%) to three species of sciurids—yellow-pine chipmunks (Eutamias amoenus) (55–60 g body mass), Columbian ground squirrels (Spermophilus columbianus) (600–700 g), and hoary marmots (Marmota caligata) (2,000–3,000 g)—and to Townsend voles (Microtus townsendii) (55–60 g), a microtine rodent. All species generally maintained body mass on all three diets, except that chipmunks lost mass on the high-fiber diet. We measured intake and digestibility of the three diets and compared rates of passage of fluid digesta (marked with Co-EDTA) and large particles (marked with Cr-mordanted plant cell walls) on the 7% fiber diet. For voles, the mean retention time (MRT ± SE) of fluid (14.8 ± 1.9 h) was greater (P = 0.02, paired t-test) than that of large particles (13.1 ± 2.4 h). This indicates separation of digesta phases in the proximal colon and selective retention of fluid digesta, probably in the cecum, which means that small, highly digestible food particles as well as bacteria are preferentially held in the cecum, which results in a more effective digestion by this system. In contrast, in the three sciurids, MRTs of fluid were the same or less than those of large particles, indicating no selective fluid retention. Among all species, MRTs increased with increasing body size. Dry matter digestibility was greater in the voles than in the chipmunks for all three diets and was greater in marmots than in voles for the low-fiber diet. Our results confirm the general prediction that voles can utilize more fibrous foods than chipmunks because of separation of digesta in a more complex proximal colon and selective retention of fluid in a larger cecum. Within the Sciuridae, increasingly larger body size (and hence a larger absolute gut capacity relative to metabolic rate) offsets the disadvantage of the relatively simple sciurid hindgut.

Introduction

The ratio of absolute gut capacity to total energy requirements increases with body size in mammalian herbivores (Demment and Van Soest 1985). Thus, larger animals can use more fibrous diets by means of longer retention of digesta in the gut, particularly in regions with microbial fermentation such as the proximal colon and the cecum. Furthermore, morphological diversity of the digestive tract can contribute to differences in processing of food by different species according to the match between design of the gut and the general diet to which the species is adapted (Hume 1989).

The ability of many microtine rodents (voles and lemmings: subfamily Microtinae, family Arvicolidae) to utilize low-quality diets largely composed of grasses and sedges is unusual for small mammals (<100 g). Several factors contribute to this ability, including a complex dentition (Vorontsov 1967) and a large cecum and complex proximal colon (Vorontsov 1967; Lange and Staaland 1970; Behmann 1973; Snipes 1979). For example, the proximal colon of the lemming (*Lemmus lemmus*) has a separation mechanism that results in selective retention of fluid and fine particles in the cecum (Sperber, Björnhag, and Ridderstrale 1983). *Lemmus lemmus* is also coprophagic, ingesting feces at intervals throughout the day and night (Björnhag and Sjöblom 1977). A similar pattern of coprophagy occurs in *Microtus pennsylvanicus* (Ouellette and Heisinger 1980), *Microtus californicus* (Kenagy and Hoyt 1980), and *Microtus pinetorum* (Cranford and Johnson 1989).

In contrast, the smaller sciurid rodents (family Sciuridae), in the same size range as typical microtines, do not feed on grasses to any great extent but instead select a variety of seeds, fruits, and inflorescences (Broadbooks 1958; Trombulak 1985), all of which are generally of much lower fiber content and thus are more highly digestible (Cork and Kenagy 1989*a*). The sciurid digestive system is simpler than that of the microtines, and the cecum smaller (Cork and Kenagy 1989*b*). The presence of a separation mechanism in the sciurid proximal colon has not been established to our knowledge. Although coprophagy appears to have little importance in small sciurids (Kenagy and Hoyt 1980), its extent and nutritional significance are unknown.

On the basis of the above, it can be predicted that, on a common diet, voles should digest a greater proportion of total dry matter than sciurids of similar body size, particularly if they are on diets of high fiber content. We tested this prediction by feeding Townsend voles (*Microtus townsendii*) and yellow-pine chipmunks (*Eutamias amoenus*) of similar body mass (55–60 g) diets of three different fiber levels and monitoring intake and digestibility of the diets. Rate of passage of digesta was also measured in order to compare gut function. Large sciurid rodents such as the larger ground

squirrels (*Spermophilus* spp.) and the marmots (*Marmota* spp.) include more grasses, sedges, and forbs in their diet than do chipmunks (Ingles 1965; Ritchie 1990). We therefore studied three species of sciurids to test the prediction that greater body size should offset the disadvantage of the simpler gut of sciurids. In addition to the yellow-pine chipmunks we also studied Columbian ground squirrels (*Spermophilus columbianus*) (mass 600–700 g) and hoary marmots (*Marmota caligata*) (mass 2,000–3,000 g).

Material and Methods

Animals. The Townsend voles were trapped in grassland in the vicinity of Seattle, King County, Washington, in November 1990. The yellow-pine chipmunks were caught near Fish Lake, Chelan County (elevation 600 m), in September 1990. The Columbian ground squirrels and hoary marmots were trapped near Harts Pass, Okanogan County (elevation 2,000 m), in August 1990.

Six animals of each species were used in the experiments. All were adults except the marmots, which were juveniles from the current year. All animals were maintained in individual stainless steel mesh metabolism cages (25 cm × 30 cm × 25 cm high for the voles, chipmunks, and ground squirrels, 50 cm × 50 cm × 40 cm high for the marmots) at 20° ± 0.5°C under a 14L: 10D cycle. The constant long day length was used to simulate summer conditions in an effort to delay hibernation in the sciurids for as long as possible (Kenagy 1986). This was successful in the chipmunks and marmots but not in the ground squirrels (see below).

Diets. The three experimental diets were Purina laboratory chows: Rodent Laboratory Chow, Rabbit Chow, and High Fiber Rabbit Chow (see table 1 for compositions). The diets were analyzed for fiber fractions by the methods of Goering and Van Soest (1970) and for crude protein (i.e., total nitrogen × 6.25) by an automated semimicro Kjeldahl method (Clare and Stevenson 1964). The distribution of dietary particle sizes was determined by wet sieving of 0.2–0.4 g of dry sample through a set of 4-cm-diameter Endicott (London) sieves. All samples were analyzed in duplicate. Food and water were available ad lib. throughout the study.

Digestibility. Intake and apparent digestibility of the dry matter of each of the three diets were measured by total collection of uneaten food and feces of six animals of each species over 5 d, following a premeasurement period of at least 5 d on each diet. Animals were weighed at the beginning and end of each collection period, and the body mass of each individual for the collection period was taken as the mean of the two weights. Dry matter

TABLE 1

*Composition and distribution of particle sizes
in the three experimental diets*

	Percentage of Dry Matter		
	Rodent Laboratory Chow[a] (Cubes)	Rabbit Chow[a] (Pellets)	High Fiber Rabbit Chow[a] (Pellets)
Chemical composition:			
Fiber (neutral-detergent)	16.9	33.5	34.5
Fiber (acid-detergent)	7.4	22.3	27.8
Lignin	2.0	5.6	6.1
Crude protein	23.5	16.2	14.0

	Percentage of Particles (Dry Weight) Held on Screen		
	Rodent Laboratory Chow[a] (Cubes)	Rabbit Chow[a] (Pellets)	High Fiber Rabbit Chow[a] (Pellets)
Screen size (μm):			
1,000	11.0	12.7	15.8
500	22.7	33.2	27.2
250	16.4	12.0	12.1
125	10.7	8.2	11.2
75	8.7	2.4	2.2
45	3.5	.7	2.5
<45	27.1	30.8	29.1

[a] Purina.

content of food offered, uneaten food, and feces was determined by drying at 95°C to constant mass.

Measurements for the voles, chipmunks, and marmots were taken on animals first on the Rodent Laboratory Chow (7% fiber), followed by the Rabbit

Chow (22% fiber), and then the High Fiber Rabbit Chow (28% fiber), because responses of the animals, especially the chipmunks, to increasing fiber content were unknown. The ground squirrels received the medium-fiber diet twice, in late August 11 d after capture (fattening phase) and then as the animals prepared to enter hibernation in early October (hibernation phase). The high- and low-fiber diets were given to them between these times, in early and late September, respectively.

Rates of Passage of Digesta. The fluid phase of digesta was marked with Co-EDTA, and the large particle phase with Cr-mordanted cell walls (Udén, Colucci, and Van Soest 1980). The Co-EDTA was prepared by the method of Udén et al. (1980), and the Cr-mordanted cell walls by the method of Ellis and Beever (1984). Cell walls were prepared from annual ryegrass (*Lolium* sp.) hay ground through a 1-mm screen and refluxed with neutral detergent solution (Van Soest and Wine 1967). Once prepared, the cell walls were washed through a set of Endicott sieves, and only the fraction that passed through the 1,000-μm screen and was retained on the 500-μm screen was used for preparation of the large particle marker. Rate of passage was measured immediately before the collection period for digestibility for animals on the low-fiber diet. The two markers, together with a small amount of peanut butter, were fed to all animals except one marmot that refused peanut butter but accepted cubes of apple containing the markers. Doses used were approximately 0.3 g Co-EDTA and 0.6 g Cr-mordanted cell walls per kilogram of body mass for all four species. After ingestion of the markers, feces were collected at 2-h intervals for 48 h, then every 6 h for 24 h, then every 12 h for 24 h, and once more after a further 24-h period. Excretion times were taken as the midpoint of each collection interval. Collected feces were dried to constant mass at 95°C.

The concentrations of Co and Cr in each collection were determined after wet ashing of up to 0.6 g of dry sample (as little as 0.1 g in the case of the voles and chipmunks) in a 100-mL volumetric flask with 10 mL HNO_3, followed by 5 mL concentrated H_2SO_4. The clear (though sometimes colored) digest was finally made up to 100 mL, and Co and Cr concentrations were determined by inductively coupled plasma emission spectroscopy (ICP) (Sakaguchi and Hume 1990).

The best overall measure of rate of digesta passage is mean retention time (MRT) (Warner 1981). Mean retention time in hours was calculated in two ways: first by the equation

$$\text{MRT} = \sum_{i=1}^{n} M_i t_i \Big/ \sum_{i=1}^{n} M_i, \tag{1}$$

where M_i is the amount of marker excreted in the ith defecation at time t_i after dosing (Blaxter, Graham, and Wainman 1956), and second by the equation

$$\text{MRT} = \text{TT} - \frac{1}{k}, \tag{2}$$

where TT is transit time (time of first appearance of marker, in hours) and k is the slope of the semilogarithmic plot of marker concentration versus time after peak concentration of the marker (Brandt and Thacker 1958). The term $1/k$ is the turnover time of the marker in the primary mixing pool in the gut.

Differences between MRTs of the two markers within animals were tested by paired t-tests (Snedecor and Cochran 1967). Differences between animal species on each diet were tested by one-way ANOVA. Statistical comparisons were not made between diets for two reasons: First, the same animals were used for all diets, and thus measurements on each diet were not independent. Second, the sciurids undergo marked seasonal cycles in growth, fat deposition, and energy expenditure (Kenagy and Barnes 1988; Kenagy, Sharbaugh, and Nagy 1989) that confound comparisons between diets made at different times. This was particularly evident with the ground squirrels (see table 4 below).

Results

Intake and Digestibility. All voles, chipmunks, and marmots maintained body mass on all three diets, with the notable exception that the chipmunks lost mass on the high-fiber (28%) diet (table 2). We present the results for ground squirrels separately, below, because their intake declined precipitously during the time of the measurements, in association with the onset of hibernation; data from the ground squirrels thus cannot be compared with those for the other three species, none of which entered hibernation during the period of study.

On a metabolic body-mass basis ($\text{kg}^{0.67}$, an exponent for rodents given by Hayssen and Lacy [1985]), chipmunks ate less ($P < 0.025$) of the low-fiber diet than did either the voles or marmots. Dry matter intake did not differ among the three species on the medium-fiber diet, but on the highest-fiber diet, chipmunks ate more ($P < 0.01$) than did the voles or marmots (table 3). Voles digested a greater ($P < 0.05$) proportion of total dry matter than did chipmunks on both the 7%- and 22%-fiber diets, and marmots digested more ($P < 0.05$) than did voles on the 7%-fiber diet. On the 28%-

TABLE 2

Body mass and body mass change during 5-d collection period for voles, chipmunks, and marmots on three diets

	Diet		
	7% Fiber	22% Fiber	28% Fiber
Mean body mass (g):			
Vole	54.9 ± 4.4	55.6 ± 4.5	61.0 ± 3.9
Chipmunk	61.9 ± 2.0	54.2 ± 3.1	54.7 ± 3.1
Marmot	2,308 ± 134	2,314 ± 121	2,522 ± 131
Body mass change (%):			
Vole	+10.3 ± 1.5	+.5 ± 3.2	+2.5 ± 1.5
Chipmunk	+2.9 ± 1.6	+.6 ± 1.5	−4.4 ± 1.0
Marmot	+7.5 ± 1.1	+5.5 ± 1.1	+2.4 ± 1.1

Note. Values are mean ± SE ($n = 6$).

fiber diet, digestibility did not differ between voles and marmots, and both were higher ($P < 0.01$) than chipmunks. Consequently, intake of digestible dry matter (or dry matter assimilated) on a metabolic body-mass basis was higher ($P < 0.01$) in the marmots than in the voles and chipmunks on the low-fiber diet, but, on the higher-fiber diets, intakes were similar across the three species.

Digestibility values for the ground squirrels were similar to those of the chipmunks for all three diets (cf. table 4 and table 3). The difference between ground squirrels while entering hibernation and while fattening is apparent in the fivefold greater intakes of the animals during fattening (table 4).

Digesta Retention. The forms of the marker excretion curves were generally similar in the four species, although the curves from the chipmunks were less regular than those from the other three species (fig. 1). Within a species, there was relatively little variation between individual animals, as reflected in the small standard errors of the means in table 5.

There were no significant differences in TTs between the two markers in any species (table 5). In the voles, the MRT of the large particle marker (Cr-mordanted cell walls) was less ($P < 0.05$) than that of the fluid marker (Co-EDTA), which indicated that fluid was selectively retained in this species (table 5). In contrast, in the three sciurids, the MRT of Cr-mordanted cell

TABLE 3

Dry matter intake, digestibility of dry matter, and digestible dry matter intake by voles, chipmunks, and marmots

	Diet		
	7% Fiber	22% Fiber	28% Fiber
Dry matter intake (g/d):			
Vole	8.1 ± .6	9.7 ± 1.1	12.1 ± .8
Chipmunk	7.7 ± .3	10.4 ± .6	12.7 ± .7
Marmot	112 ± 11	103 ± 10	131 ± 10
Dry matter intake (g/kg$^{0.67}$ · d):			
Vole	56.7 ± 1.3^a	68.3 ± 7.4^a	78.8 ± 4.4^a
Chipmunk	50.0 ± 2.2^b	73.1 ± 3.2^a	88.9 ± 2.3^b
Marmot	64.0 ± 4.8^c	63.2 ± 6.1^a	70.4 ± 4.4^a
Digestibility of dry matter (%):			
Vole	77.4 ± 1.4^a	54.6 ± 1.0^a	50.9 ± 1.0^a
Chipmunk	74.6 ± .4^b	47.6 ± 1.3^b	40.6 ± 3.0^b
Marmot	81.0 ± .5^c	57.6 ± 1.6^a	50.3 ± 1.2^a
Digestible dry matter intake (g/kg$^{0.67}$ · d):			
Vole	43.8 ± 1.0^a	37.0 ± 3.7^a	40.0 ± 2.1^a
Chipmunk	37.2 ± 1.5^a	34.7 ± 0.9^a	36.0 ± 2.6^a
Marmot	51.8 ± 3.9^b	36.2 ± 3.1^a	35.3 ± 2.1^a

Note. Values are mean ± SE ($n = 6$). Species on the same diet show significant differences ($P < 0.05$) when they have different superscripts a, b, and c.

walls was greater (chipmunks $P < 0.01$, marmots $P < 0.05$) than that of Co-EDTA, or there was no difference between the markers (ground squirrels). This indicates selective retention of large particles, rather than fluid, in at least two of the three squirrel species, but this is probably the result of selective retention of large particles by the stomach, rather than the hindgut. Thus, retention times of large and fine particles in the cecum were probably similar. The TTs and MRTs of the ground squirrels are probably overestimates because of the low intakes on the low-fiber diet. Even lower intakes were recorded on the medium-fiber diet as the ground squirrels prepared to enter hibernation in early October, compared with intakes on the same diet in late August, soon after capture (table 4).

Average MRTs calculated by the second method (i.e., from TTs and marker concentrations in the feces, eq. [2]) were, for three species, similar to those calculated by the preferred method, on the basis of total marker excretion.

TABLE 4

Performance of ground squirrels on three diets

	Diet			
		22% Fiber		
	7% Fiber[a]	Fattening[b]	Hibernation[c]	28% Fiber[d]
Mean body mass (g)	663 ± 21	660 ± 20	580 ± 31	629 ± 17
Body mass change (%)	+1.8 ± 1.8	+1.4 ± 1.6	−2.6 ± .2	−4.7 ± 1.4
Dry matter intake (g/d)	26.0 ± 2.7	79.3 ± 3.9	14.0 ± 1.2	40.8 ± 3.3
Dry matter intake (g/kg$^{0.67}$ · d)	34.3 ± 3.7	104.8 ± 4.5	20.6 ± 2.5	55.6 ± 4.2
Digestibility of dry matter (%)	75.4 ± .9	48.7 ± .4	51.8 ± .7	40.9 ± 1.1
Digestible dry matter intake (g/kg$^{0.67}$ · d)	25.9 ± 2.9	51.1 ± 2.5	10.7 ± 1.2	22.6 ± 1.3

Note. Values are mean ± SE ($n = 6$).

[a] Late September.

[b] Late August, soon after capture.

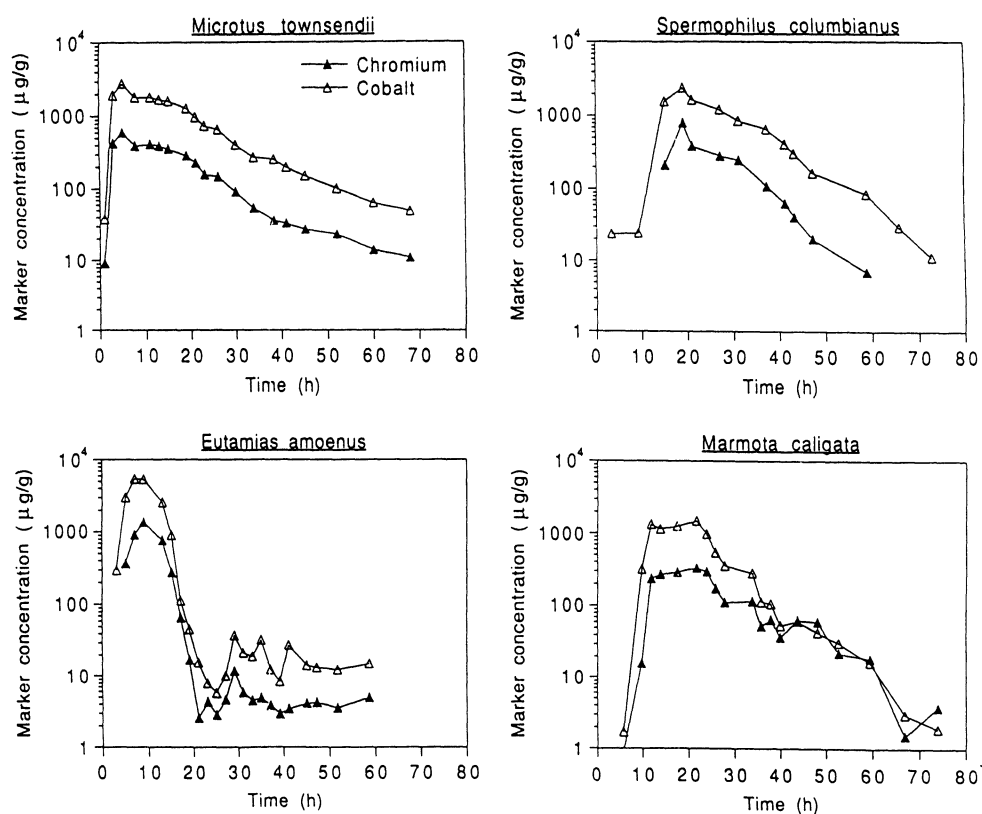[c] Early October, just before entering hibernation.

[d] Early September.

Fig. 1. Concentration of Co (open symbols) and Cr (closed symbols) in
the dry feces of representative individuals of Microtus townsendii, Euta-
mias amoenus, Spermophilus columbianus, and Marmota caligata vs. time
after dosing. Cobalt (as Co-EDTA) represents the fluid phase of digesta to-
gether with fine particles; Cr (as Cr-mordanted cell walls) represents
large particles (500–1,000 μm).

Discussion

To our knowledge, this is the first study to compare directly digestive tract
performance of sciurid and microtine rodents. The results support the pre-
dictions made on the basis of the relative complexities of the digestive
systems of these two groups (Vorontsov 1967; Cork and Kenagy 1989a;
Hume 1989), and the influence of body size (Demment and Van Soest 1985)
and dietary fiber content.

   The individual voles all selectively retained the fluid marker, which means
that they preferentially retain bacteria, particularly in the cecum, which en-
hances overall digestive performance. This conclusion is based on the greater
MRTs of the Co-EDTA than of the large particle marker (table 5). Sakaguchi

TABLE 5

Transit times and MRTs of Co-EDTA (marker for fluid and fine [<75 µm] particles) and Cr-mordanted cell walls (large [500–1,000 µm] particle marker) in four rodents fed the low-fiber diet

	Co-EDTA			Cr-mordanted Cell Walls		
	TT (h)	MRT[a] (h)	MRT[b] (h)	TT (h)	MRT[a] (h)	MRT[b] (h)
Vole	1.4 ± .3	14.8 ± 1.9	15.3 ± 2.5	1.7 ± .4	13.1 ± 2.4*	12.9 ± 3.1
Chipmunk	3.0 ± .7	12.7 ± 1.0	5.5 ± .7	6.5 ± 2.1	14.1 ± 1.2**	9.1 ± 1.8
Ground squirrel	11.0 ± 1.7	22.5 ± 2.2	23.9 ± 1.1	13.6 ± 1.0	22.1 ± 1.1 (NS)	23.6 ± 3.1
Marmot	13.1 ± 2.5	24.8 ± 3.2	22.2 ± 2.7	17.1 ± 3.4	28.9 ± 3.4*	28.4 ± 4.2

Note. Values are mean ± SE ($n = 6$).

[a] Calculated from total collection of markers (eq. [1]).

[b] Calculated from TTs and marker concentrations (eq. [2]; see text).

* The difference between the MRTs for Cr calculated from total collection of markers and the MRTs for Co calculated from total collection of markers is significant at $P < 0.05$.

** The difference between the MRTs for Cr calculated from total collection of markers and the MRTs for Co calculated from total collection of markers is significant at $P < 0.01$.

and Hume (1990) showed that fine (less than 75 μm) particles, which include bacteria, moved with fluid in two species of marsupial folivores. Selective retention of fluid and fine particles in the cecum maintains higher concentrations of bacteria and small, potentially more fermentable particles (Bjorndal, Bolton, and Moore 1990) in the cecum and leads to more complete digestion of dry matter.

That microtine rodents have a mechanism for separation of fine and large particles in the proximal colon has been demonstrated by Sperber et al. (1983). The proximal colon forms a double spiral; at the distal end of the spiral the mucosa is thrown into two rows of oblique folds and furrows (Vorontsov 1967) that direct a flow of bacteria trapped in mucus back toward the cecum (Björnhag 1987). Associated with this separation mechanism and selective retention of fluid and fine particles in the cecum is the ingestion of feces by microtines (Björnhag and Sjöblom 1977). The combination of a large haustrated cecum, selective retention of digesta, and coprophagy enables microtine rodents to utilize diets of much higher fiber content than expected for such small mammals. Microtines occur predominantly in grassland habitats (Batzli and Cole 1979), and their ability to maintain or even increase dry matter intake to compensate for the lower digestibility of higher-fiber diets (Batzli 1985; Cranford and Johnson 1989) is consistent with the above features of their digestive physiology.

The smallest of the sciurids, the chipmunks, exhibited MRTs generally similar to those of the voles but, in contrast, showed no selective retention of fluid and fine particles. This is probably the main reason why, on all three diets, apparent digestibility of dry matter was lower in the chipmunks than in the voles. Although they were able to increase absolute food intake to compensate for the decrease in digestibility on the high-fiber diet (so that intake of digestible dry matter remained almost constant across diets), they were not able to maintain body mass (table 2). These results are consistent with the relatively simple digestive system and the small size of chipmunks. Their natural diets are based primarily on low-fiber items, principally inflorescenses and seeds, and do not include grasses (Broadbooks 1958; Trombulak 1985).

In the marmots, the disadvantages of the relatively simple sciurid digestive tract were apparently overcome by greater body size and hence greater absolute gut capacity. Thus, although neither marmots nor chipmunks selectively retain fluid digesta in the cecum, the greater MRTs of marmots allowed more time for microbial digestion of fiber in their hindgut. Thus, dry matter digestibilities of marmots were greater than those of the chipmunks for all three diets and greater than those of the voles for at least the lower-fiber diets (table 3). This difference did not persist on the high-fiber

diet, on which digestibility in the 60-g voles was equal to that in the 2.5-kg marmots.

The ground squirrels cannot be compared in all ways with the other three species in this study because of their early entry into hibernation during the experiments. The low food intakes during the measurement of rate of passage of digesta would be expected to give rise to reduced passage rates, resulting in greater MRTs than expected (table 5). Thus, MRTs in the 600-g ground squirrels were almost as great as those in the 2.5-kg marmots. A seasonal change in the absorptive ability of the gut has also been demonstrated in ground squirrels (Carey 1989).

Mean retention times were calculated by two methods. The method based on total marker collection (eq. [1]) is preferred, but complete collection of marked feces is not always feasible, for instance, when retention is very long, as it is in some large herbivores (Warner 1981). In such cases, the alternative method (eq. [2]) may be the only choice. In this study, average MRTs calculated by the two methods agreed closely in the three species with relatively regular marker excretion curves (voles, ground squirrels, and marmots; fig. 1). This was not the case in the chipmunks, which had less regular marker excretion curves. Precision with the second method, based on the sum of transit and turnover times, is sensitive to errors in estimates of TT, which depend on defecation patterns of individual animals and collection intervals. When TT is a large proportion of MRT, as in the chipmunks (table 5), considerable error may arise, which may explain the poor agreement between the two methods in chipmunks. In species of greater body size, and thus greater MRT, when TT is expected to be only a minor component of MRT, the method based on transit and turnover times should be more reliable. The advantage of this method is that it may allow measurement of MRT in free-living animals, provided enough feces of individual animals can be identified and collected for definition of TT and turnover time.

The results broadly met predictions based on digestive tract morphology and body size. The ability of chipmunks to maintain intake of digestible dry matter (i.e., energy) on the high-fiber diet was surprising. Part of the explanation for this ability may lie in the similar particle size characteristics of the three commercially prepared diets (table 1). Natural foods that are high in fiber would be expected to break off in larger pieces during feeding and would have to be broken down by mastication before processing in the gut. Here the voles would have an advantage in that their molars all have flattened crowns and prisms of dentin surrounded by enamel and are open rooted—all adaptations for effectively chewing more abrasive grasses than

sciurids can with their simpler teeth (Vorontsov 1967). It would be useful to base future studies of this type on natural diets or on synthetic diets with a natural array of particle sizes.

Acknowledgments

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