J Comp Physiol B (1995) 164:609–617

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

Limits to food intake and fiber utilization in the prairie vole, *Microtus ochrogaster*: effects of food quality and energy need

K.T. Castle*, B.A. Wunder

Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

Accepted: 24 October 1994

Abstract. We fed prairie voles (*Microtus ochrogaster*) rat chow diluted with variable amounts of α-cellulose to determine 1) how much fiber the voles could tolerate in their diet; 2) changes in food intake and digestibility of dry matter and of fiber; 3) the extent to which voles utilized fiber as an energy source; and 4) whether any of these variables differed between groups of animals maintained at 5 or 22°C. Fiber content of the diets ranged from 20 to 84%. Animals held at 5°C maintained body mass through a diet containing 69% fiber, while animals held at 22°C maintained body mass through the 84% fiber diet. Dry matter intake increased with fiber level from 9.3 to 15.0 g·day^{-1} for animals at 5°C and from 5.6 to 14.0 g·day^{-1} for animals at 22°C; intake on the highest fiber diet eaten by either group was not different. Dry matter digestibility decreased significantly as the fiber in the diets increased, but was not affected by temperature treatments. Digestible dry matter intake for each group remained constant regardless of diet quality, but on each diet digestible dry matter intake for animals at 5°C was significantly higher than that of the animals held at 22°C. Digestibility of the fiber portion of the experimental diets remained constant as food quality decreased, so the percent of daily energy need met by fiber utilization increased with higher food intake. On the lowest quality diet each group tolerated, fiber digestion provided approximately 42 and 68% of the energy needs of voles at 5 and 22°C, respectively.

Key words: Diet digestibility – Food intake – Fiber – Herbivore – Vole, *Microtus*

* *Present address:* Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA

Abbreviations: BM, body mass; BMR, basal metabolic rate; DE, digestible energy; DM, dry matter; DMD, dry matter digestibility; DDMI, digestible dry matter intake; MR, metabolic rate; NDF, neutral detergent fiber (=cell walls); NDS, neutral detergent solubles (=cell solubles); SEM, standard error of mean; T_a, ambient temperature

Correspondence to: K.T. Castle

Introduction

There is considerable interest in the responses of herbivores to varying levels of food quality and how those responses are influenced by energy need. Typically, herbivores increase food intake as diet quality decreases and/or as energy need increases (Montgomery and Baumgardt 1965b; Keys and Van Soest 1970; Batzli and Cole 1979; Gross et al. 1985; Baker and Hobbs 1987; Woodall 1989; Hammond and Wunder 1991; Loeb et al. 1991; Nagy and Negus 1993). By increasing intake of low quality food, herbivores maintain a relatively constant intake of digestible energy and nutrients. Below some low level of food quality, however, intake decreases, and animals fall into negative energy balance. Figure 1 depicts a typical "intake-response" curve for an animal eating foods of decreasing quality. To the right of the "inflection point" intake is thought to be controlled by chemostatic or thermostatic mechanisms; to the left, intake may be controlled by palatability or gut fill (Montgomery and Baumgardt 1965a; Van Soest 1982; Weston and Poppi 1987).

Decreases in food quality may pose a more severe problem for small herbivores than for large herbivores. Theoretically, small herbivores should be constrained by their size to eating only high quality, low fiber foods (Demment and Van Soest 1985). In mammals BMR generally scales with BM$^{0.75}$ (Kleiber 1961), whereas gut capacity generally scales with BM$^{1.0}$ (Parra 1978). If the ability to digest fiber increases with increased retention time in the gut, as Sibly (1981) suggests, then animals with bigger guts should be able to digest fiber more effectively than those with smaller guts. Small mammals, with their relatively high ratio of MR to gut capacity should be less able to derive energy from the fiber portion of their diets because they need to process food quickly to meet their energy needs, but they have only the same relative gut capacity as large mammals with which to digest fiber.

Prairie voles are among the smallest mammals which feed primarily on the vegetative parts of plants, consuming mainly the leaves and stems of monocots and dicots

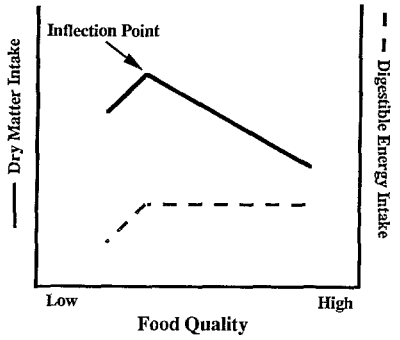

Fig. 1. Generalized scheme of the relationship between food quality and dry matter (—) and energy intake (- - -) in a herbivore. Note that diet quality decreases from right to left

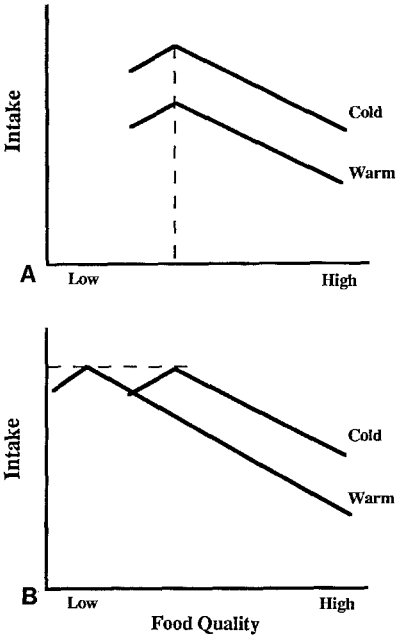

Fig. 2A,B. Hypothetical intake-response curves for herbivores held at cold or warm temperatures as influenced by diet quality: **A** possible response if maximal intake is limited by some aspect of the diet, such as palatability or nutrient content; **B** possible response if maximal intake is limited by some aspect of the animal, such as maximal gut size or maximal processing rate

(Batzli 1985; Hammond 1989). These plant parts frequently contain high levels of fiber, especially during winter when cell solubles are translocated to underground storage organs (Short et al. 1974; Van Soest 1982). Unlike many small mammals, microtine rodents have no demonstrated ability for torpor (Wunder 1985). Thus, they are faced with decreased T_a and concomitant increased energy needs at the very time that food quality is at its lowest. Prairie voles should therefore exhibit adaptations to cope with both decreased food quality and increased energy need.

Prairie voles increase intake in response to decreased diet quality (Hammond and Wunder 1991) but maximal intake values are unknown. In addition, on a given diet, animals maintained at low temperatures have higher intakes than animals maintained at relatively high temperatures, in order to compensate for costs of thermoregulation (Hammond and Wunder 1991). This permits tests of hypotheses about whether maximal intake points might be related to palatability or maximal gut fill. Thus, the objective of this study was to generate intake-response curves for voles maintained at 22 or 5°C. We hypothesized that if the inflection point is determined by some aspect of the diet, such as palatability, then animals at both temperatures would reach their inflection point at the same level of diet quality (but different levels of intake) because the food would taste equally bad to all voles (Fig. 2A). If the inflection point is determined by some aspect of the animal, such as maximal gut size or maximal processing rate, then the inflection point should occur at different levels of diet quality (but at the same level of intake) because all voles should have similar abilities to adjust their gut size or processing rate (Fig. 2B). From the intake-response curves generated, we planned to determine the maximum rate of food intake and the lowest quality (highest fiber) diet which voles could eat and on which they would maintain BM, and whether those measurements varied with energy need. Additionally, we measured changes in DM, fiber, and cell soluble digestibility. We were particularly interested in the effect of increased energy need on fiber digestibility because, presumably, as energy needs increase, voles need to process food more quickly, and hence retention time and utilization of fiber would be decreased.

Materials and methods

Animals. We live-trapped prairie voles from a mixed grass and mountain scrub community 10 km northwest of Ft. Collins, Larimer County, Colo., USA. Trapping took place from late August until early October 1991. Animals were held in the animal care facility at Colorado State University where they were placed individually in cages (25cm×14cm×12 cm) and given food and water ad lib until the start of the experiment. Photoperiod during the study was 12L:12D.

Diets. The basal diet for this study was Agway Prolab 3200 Rat Chow in milled form containing approximately 20% NDF (=cell walls), 22% crude protein, and 5% fat. We used powdered α-cellulose from Bioserve, (Frenchtown, N.J., USA) as the added fiber for all experimental diets. Experimental diets were made by adding α-cellulose to the basal diet to achieve dilutions of 20–80% (by mass). The actual NDF percentage of each diet was determined using a modified Goering and Van Soest method (Hammond 1989). Sodium sulphite and decalin were omitted from the procedure and 0.1 ml heat-stable α-amylase (Sigma Chemical #3306) was added to 35 ml detergent solution in each test tube in order to decrease starch interference. The composition of the rat chow and the experimental diets are given in Table 1. We measured the DM content of each diet by drying a sample of each diet to constant mass at 55°C. All measurements and calculations are presented on a DM basis.

Experimental procedures. All voles were maintained in the lab for at least 30 days prior to the start of the experiment, so that they could adjust to lab conditions and adjust gut size to the lab diet. After this acclimation period we ranked 28 animals (16 males, 12 females) according to BM and assigned voles, in order, to one of two groups; these groups did not differ in mean BM. One group was placed in a constant temperature cabinet and held at 5°C, while the other group was maintained in a constant temperature cabinet at 22°C.

Table 1. Composition of the diets fed to prairie voles

% of the diet (as dry mass) composed of α-cellulose	% NDF in diet	% NDS in diet
0	20.3	79.7
20	35.2	64.8
30	43.7	56.3
40	51.2	48.8
50	60.4	39.6
60	69.1	30.9
70	77.1	22.9
80	83.6	16.4

We fed the voles powdered food instead of pelleted food or fresh forage in order to maintain consistent diet quality and to decrease the possibility of food-sorting by the voles. Powdered food was placed in a food dish fitted with a lid that allowed the voles access to the food but which minimized spillage of food from the dish as the animal ate. Results from a preliminary trial demonstrated that there were no differences in DMD or intake between powdered and pelleted forms of the rat chow.

During experiments voles were held individually in metabolism cages that facilitated separation of food and feces from urine. A piece of absorbant cardboard was placed at the bottom of each mouse cage; a piece of window screen and a piece of hardware cloth were then placed over the cardboard. That portion of the orts (food not eaten) remaining in the food dish was collected each day. Any orts which spilled and feces trapped on either the window screen or cardboard were collected each day into vials using a fine hair brush then dried to constant mass at 55°C. When dry, the spilled orts and feces were separated by sieving the vial contents through window screen and rolling individual feces on the screen by hand to remove the powdered food. This method allowed us to very clearly separate food from feces.

We removed animals from a feeding trial if either of two criteria were met: 1) if an animal lost 10% of its BM daily for 2–3 days, and 2) if an animal refused the diet for more than 1 day. These criteria resulted in the removal of four animals during the trials.

We maintained the animals at their respective temperatures for 18 days before the feeding trials began. After 18 days we conducted a 5-day food intake and digestibility trial for each group. Every day we collected orts and feces from each animal; orts and feces were dried at 55°C for 48–72 h (to constant mass), and later separated and weighed. Animals were weighed on days 1, 3, and 5 of each collection period so we could determine whether they were maintaining BM.

After this initial collection period, we randomly selected four animals from each temperature group to serve as control animals for time effects; these voles received ground rat chow for the duration of the study. The remaining ten animals at each temperature made up the experimental groups. Every 15 days thereafter both experimental groups received a new, higher fiber diet. The first 10 days on the new diet served as an acclimation period, and the last 5 days served as a collection period to determine intake and digestibility (as described above).

Calculations. Daily food intake was calculated by subtracting the mass of orts from the mass of food given, corrected for dry matter.

We calculated the digestibility of different diet components, based upon the total 5-day digestibility trial, using the formula:

$$\%Digestibility = \frac{(X_{eaten} - X_{feces})}{X_{eaten}} \times 100$$

where X is the dry mass of the component (DM, NDF, or NDS).

Gut size measurements were made on the experimental animals following the methods of Gross et al. (1985), and were made after the animals had been on the highest fiber diets each group had been fed. All animals were killed at approximately 0900 hours to control for possible intake cycles.

Statistical analyses. We used a repeated measures analysis with linear contrasts to test for overall differences between the responses of animals to decreased T_a and either decreased or constant diet quality. For each variable, we first regressed individual animal responses against diet quality, or "time step" for comparisons between control groups, and determined the slope and intercept of each regression line. We then calculated the average slope and intercept for each temperature group using the individual regressions and compared those measures using two-tailed *t*-tests for unpaired samples [P. Chapman, personal communication; Milliken and Johnson (1984)]. Differences between groups on a given diet were tested by one-way analysis of variance. Results are given as mean ± SEM.

Results

Sample sizes

Twelve experimental animals (five held at 22°C and seven at 5°C) and six control animals (three in each group) completed all treatments up to the highest fiber levels or last time step. Only data from these animals were used in statistical analyses.

Control animals

Data collected from the control animals are given in Table 2. Regression analysis of these results indicates that DMD was the only variable that changed at any point during the study; DMD by animals at 5°C decreased slightly during the study, and DMD by animals at 22°C was lower during "time-step" six than at any other time. There was little or no change in the responses of the "time" controls in this study, so we conclude that the responses of the experimental animals are due to the diet treatments.

Experimental animals

When voles at 22°C were fed a diet with approximately 90% NDF, and voles at 5°C were fed a diet containing 77% NDF (data not shown), all animals either stopped eating or greatly reduced their daily intake. We were not able to quantify this decrease in intake because voles quickly lost BM (or died) on those lowest quality diets, and were therefore removed from the study before intake measurements could be taken. We thus concluded that voles had reached their respective inflection points on the previous diet, and stopped the experiment.

Body mass

BM did not vary during the experiment with T_a or diet except on the lowest quality diet a group could tolerate, where mean BM of each group decreased (Table 3).

Intake

Daily DM intake of all experimental animals increased significantly as diet quality decreased (Fig. 3). We plotted

Table 2. Body mass, intake, and digestibility for control animals maintained at 22 or 5 °C (mean±1 SEM)

	Time step							
	1	2	3	4	5	6	7	8
Body mass (g)								
22 °C	54.0±7.7	56.6±6.8	56.5±7.2	58.8±7.9	59.1±6.5	58.4±6.9	58.7±6.4	58.6±6.9
5 °C	47.0±7.9	47.6±7.9	48.8±8.0	49.4±8.6	49.6±8.4	49.6±8.3		
Intake (g · day^{-1})								
22 °C	6.3±0.3	6.0±0.4	5.7±0.6	5.8±0.6	5.8±0.3	5.7±0.2	5.9±0.6	5.5±0.3
5 °C	9.0±0.4	8.8±0.7	9.1±0.7	8.9±0.7	9.1±0.6	9.4±0.6		
	***	***	***	***	***	***		
%DMD								
22 °C	82.9±0.4	80.8±0.7	82.2±0.2	85.3±0.1	80.2±0.3	75.5±2.7	82.1±0.4	82.5±0.8
5 °C	80.7±0.5	78.3±1.3	80.0±0.4	79.3±0.7	78.5±0.4	75.4±1.2		
				***				
DDMI (g · day^{-1})								
22 °C	5.2±0.3	4.8±0.3	4.7±0.5	4.9±0.5	4.7±0.3	4.3±0.3	4.8±0.5	4.6±0.3
5 °C	7.3±0.3	7.0±0.7	7.3±0.6	7.1±0.6	7.1±0.5	7.1±0.4		
	**	**	***	**	***	***		
% NDF digestibility								
22 °C	60.6±0.9	53.7±1.9	60.6±0.9	64.4±0.4	52.3±0.9	47.1±10.2	59.3±0.8	59.5±1.7
5 °C	57.3±0.8	51.2±4.0	55.0±1.4	53.1±2.1	51.2±1.8	44.3±2.9		
% NDS digestibility								
22 °C	88.6±0.2	87.7±0.3	88.3±0.1	90.6±0.1	87.3±0.1	84.4±2.6	88.0±0.4	88.4±0.6
5 °C	86.7±0.4	85.3±0.6	86.3±0.3	85.9±0.5	85.5±0.2	83.3±0.8		
% of DDMI from NDF								
22 °C	14.8±0.1	13.5±0.3	15.0±0.2	15.3±0.1	13.2±0.2	12.4±2.0	14.6±0.1	14.6±0.3
5 °C	14.4±0.1	13.2±0.8	14.0±0.3	13.6±0.5	13.2±0.4	11.9±0.6		

n= 3 for both groups; n=2 animals at 22 °C during time step 6[1]

[1] Within a time step, different numbers of asterisks indicate significant differences between groups (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; no asterisk $P > 0.05$)

% NDS in the diet on the x-axis in order to show the negative correlation between diet quality and intake, and to facilitate comparison to Figs. 1 and 2. Analysis of intake as a function of NDS in the diet showed that the responses of the two groups were the same as diet quality decreased (slopes were not different; P=0.44), but that the animals at 5°C consistently ate more food on any given diet than animals at 22°C (adjusted intercepts: 12.5±0.3 g·day^{-1} versus 8.7±0.4 g·day^{-1}; P=0.0001). We adjusted the "y-intercepts" to reflect intake at an intermediate diet quality (49% NDS=51% NDF); this adjustment allowed us to calculate the average difference in intake between the groups since neither group was fed a diet containing 0% NDS.

Maximal daily DM intakes by voles at 5°C (15.0±0.6 g·day^{-1} on the 31% NDS diet) and by voles at 22°C (14.0±0.8 g·day^{-1} on the 16% NDS diet) were not significantly different (unpaired t-test; P=0.33). The shaded region of Fig. 3 indicates 1 SEM maximal intake by animals at 5 and 22°C.

Dry matter digestibility

DM digestibility decreased significantly in both experimental groups as diet quality decreased (Table 3). The responses of the two groups as diet quality decreased were not different (slopes: –0.75±0.02 and –0.72±0.05, for animals at 22 and 5°C, respectively; P=0.68; intercepts: 68.2±0.8 and 68.4±0.8, respectively; P=0.82). Voles at 22°C digested 81.3% of DM in undiluted rat chow (20.3% NDF) but only digested 32.5% of DM in the 77% NDF diet. There was no significant difference in DMD for voles at 22°C eating the 77% and 84% NDF diets (32.5 and 33.8%, respectively). Animals at 5°C digested 80.6% of DM in undiluted rat chow (20.3% NDF) but DMD was only 43.4% when fed a diet containing 69% NDF. These results indicate that decreased diet quality, but not decreased temperature, had a negative effect on DM digestibility.

Table 3 also contains our calculations of % digestible energy of the diets of experimental animals on each diet; these values were included in calculations used to compare fiber utilization in various species of small mammal. Because there is a strong correlation between DM digestibility and energy digestibility (Robbins 1983, Table 13.3; Hammond and Wunder 1991) we calculated DE values by multiplying the DMD of each diet by 18.4 kJ·g^{-1} which is the gross energy value of the rat chow (Agway).

Daily digestible dry matter intake

There was no overall change in DDMI for either group of experimental animals throughout the study (slopes were not different from zero; slopes=–0.004±0.01 and 0.01±0.009 for voles at 22 and 5°C, respectively). In addition, the slopes were not different from each other (P=0.27). The intercepts, however, were significantly

Table 3. Body mass, intake, and digestibility for experimental animals maintained at 22 °C or 5 °C (mean±1 SEM)

	Percent NDF in diet							
	20.3	35.2	43.7	51.2	60.4	69.1	77.1	83.6
Body mass (g)								
22 °C	49.9±4.1	49.6±3.7	49.6±3.7	49.5±3.2	49.8±3.0	49.0±1.9	48.8±1.6	46.4±0.9
5 °C	44.0±1.8	44.6±1.6	44.5±1.9	44.3±1.8	43.4±1.4	42.5±1.3		
			*	*				
Intake (g · day^{-1})								
22 °C	5.2±0.6	6.3±0.4	7.4±0.4	8.5±0.4	10.1±0.8	11.1±0.8	13.4±0.5	14.0±0.8
5 °C	9.2±0.3	10.1±0.3	11.4±0.4	13.1±0.5	13.7±0.3	15.0±0.6		
	***	***	***	***	***	***		
% DMD								
22 °C	81.3±0.2	67.1±0.6	62.2±1.0	57.0±0.7	50.3±1.0	41.4±0.7	32.5±1.0	33.8±1.4
5 °C	80.6±0.5	67.7±0.8	62.6±0.9	57.8±1.3	50.2±2.0	43.4±2.1		
DE in diet (kJ · g^{-1})								
22 °C	14.9±0.03	12.4±0.1	11.4±0.2	10.5±0.1	9.3±0.2	7.6±0.1	6.0±0.2	6.2±0.3
5 °C	14.8±0.1	12.5±0.1	11.5±0.2	10.6±0.2	9.1±0.4	8.0±0.4		
DDMI (g · day^{-1})								
22 °C	4.2±·0.5	4.2±·0.3	4.6±·0.3	4.9±·0.3	5.1±0.4	4.6±0.4	4.4±0.3	4.8±0.4
5 °C	7.4±0.3	6.8±0.2	7.2±0.3	7.5±0.3	6.8±0.3	6.5±0.3		
	***	***	***	***	***	***		
% NDF digestibility								
22 °C	59.1±0.2	32.4±0.8	32.5±1.2	31.4±1.2	29.9±1.3	23.0±1.1	21.1±1.0	27.4±1.9
5 °C	57.4±1.0	33.9±1.6	34.1±1.9	33.2±2.3	32.1±2.9	27.2±3.1		
% NDS digestibility								
22 °C	86.9±0.2	86.0±0.6	85.3±0.9	83.8±1.3	81.4±0.6	82.3±0.7	70.6±1.3	66.0±1.7
5 °C	86.5±0.5	86.0±0.4	84.8±0.4	83.6±0.3	77.6±0.9	79.7±1.0		
					**	*		
% of DDMI from NDF								
22 °C	14.8±0.02	17.0±0.3	22.8±0.5	28.2±1.0	35.8±0.9	38.4±1.2	50.1±1.0	67.6±1.8
5 °C	14.5±0.2	17.6±0.6	23.7±1.0	29.2±1.4	38.3±1.8	42.4±2.9		

n=5 for animals at 22 °C and 7 for animals at 5 °C[1]

[1] Within a diet, different numbers of asterisks indicate significant differences between groups (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; no asterisk $P > 0.05$)

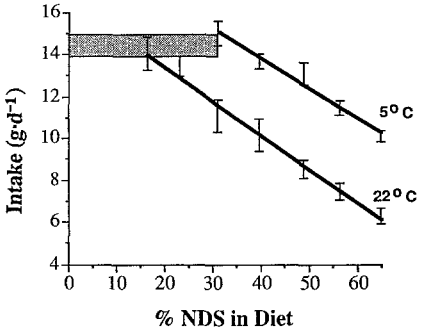

Fig. 3. Intake-response curves for prairie voles maintained at 5 and 22°C. Error bars represent 1 SEM for intake at each diet quality. The *stippled area* represents 1 SEM of intake on the last diet eaten by voles held at 22°C and indicates that maximal daily dry matter intake of the two temperature groups was not different ($P > 0.05$)

different from each other (intercepts=4.6±0.2 g·day^{-1} and 7.1±0.2 g·day^{-1} for animals at 22 and 5°C, respectively). The DDMI by voles at 5°C was approximately 2.5 g·day^{-1} higher than that of voles at 22°C throughout the study (Table 3). This difference reflects higher energy expenditure due perhaps to thermoregulation and/or activity by animals held at 5°C. These results indicate that T_a influenced DDMI, whereas diet quality did not.

NDF digestibility

On the experimental diets NDF digestibilities of the experimental animals were significantly lower than they had been on the rat chow diet (Table 3). After an initial drop in NDF digestibility, the digestibility of that fraction of the diet did not change significantly for animals at 5°C (slope=–1.54±0.67; P=0.06). In animals at 22°C, after the large initial drop in NDF digestibility, NDF digestibility varied considerably, but the overall trend was towards a decrease (slope=–1.63±0.24; P=0.002).

NDS digestibility

Digestibility of NDS by both groups decreased significantly as diet quality decreased (from 86.9 to 66.0% in animals at 22°C and from 86.5 to 77.6% in animals at 5°C). This large decrease may be somewhat misleading, however, because NDS digestibility was fairly high (over 80%) until the animals at 22°C were fed the diet

Table 4. Gut size measurements made on animals from previous studies and voles from the present study

	Gross et al. (1985)		Hammond and Wunder (1991)		This study	
	Warm low (9)	Cold low (9)	Warm low (10)	Cold low (10)	22 °C High (5)	5 °C High (4)
Body Mass (g)	41.6±2.2	41.1±1.9	47.6±3.7	48.8±3.2	39.8±0.69	42.5±2.23
Gut measurement:						
Length (mm)						
Stomach	37±1.0	36±1.4	39±2	39±1	30.8±2.7	42.7±2.7
Small Intestine	295±10.4	297±10.2	293±6	316±6	312.0±9.8	343.8±20.6
Cecum	162±11.0	176±8.2 *	148±6	173±6 *	204.0±7.5	223.8±24.5
Large Intestine	217±6.8	212±6.7	203±6	212±6	232.0±5.6	242.5±11.3
Total	711±23.2	720±17.5 *	683±12	738±12 *	787.8±15.8	842.8±46.0
Dry mass (g)						
Stomach	0.074±0.005	0.080±0.008	0.085±0.03	0.098±0.003 *	0.131±0.040	0.085±0.007
Small Intestine	0.112±0.010	0.144±0.013 *	0.175±0.009	0.211±0.009 *	0.091±0.018	0.220±0.010 *
Cecum	0.098±0.006	0.111±0.008 *	0.087±0.004	0.101±0.004 *	0.113±0.011	0.145±0.007
Large Intestine	0.064±0.004	0.069±0.006	0.068±0.004	0.077±0.004	0.082±0.007	0.102±0.008
Total	0.348±0.021	0.403±0.028 *	0.416±0.015	0.487±0.015	0.418±0.040	0.552±0.024 *
Wet Contents total (g)	3.49	4.50	3.68±0.31	5.27±0.31	7.52±0.94	7.49±0.56
Total Contents+Tissue (g)	5.21	6.41	5.97	9.11	11.19	11.57

"Low" and "high" refer to fiber levels in the respective studies. Values are given as mean ± SEM
Significant differences between temperature groups within a study are indicated by an asterisk, and sample sizes are given in parentheses[1]
[1] Within a study, different numbers of asterisks indicate significant differences between groups (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; no asterisk, $P > 0.05$)

containing 77% NDF, and until the animals at 5°C were fed the 60% NDF diet. A comparison of the responses of both groups indicated that the slopes, but not the intercepts, were significantly different (slopes=–0.13±0.01 and –0.23±0.03 for animals at 22 and 5°C, respectively; P=0.025; intercepts=85.9±0.8 and 86.3±0.4 for voles at 22 and 5°C, respectively; P=0.71). Thus, animals at both temperatures digested less of the NDS in their diet as diet quality reached the lowest levels fed each group, and when the responses are compared over the same range of diets, the decrease by voles at 22°C was less than that for voles at 5°C.

Gut size measurements

The only significant differences between gut measurements of animals held at different temperatures were for Dry mass of the small intestine (DM=0.091±0.018 g and 0.220±0.01 g for voles at 22 and 5°C, respectively; P=0.0007) and total DM of the gut (total mass=0.418±0.04 g and 0.522±0.024 g for animals at 22 and 5°C, respectively; Table 4). The large difference in small intestine DM probably accounted for the significant difference in total DM of the guts in the two groups.

Discussion

Recent nutritional theory suggests that small herbivores are constrained to eating only high quality, low-fiber diets because they have high metabolic needs relative to their gut capacity and therefore cannot extract energy from fiber fermentation fast enough to meet those needs (Parra 1978; Demment and Van Soest 1985). Small herbivores are therefore expected to maximize their net rate of energy gained from a diet by increasing their intake of low quality foods in order to "skim" the more quickly digestible cell solubles from the food (Janis 1976; Sibly 1981; Batzli 1985; Demment and Van Soest 1985). Clearly, prairie voles do not merely skim cell solubles for energy. Voles in our study were able to survive on diets containing 84% and 69% NDF when held at 22 or 5°C, respectively. Because the daily DDMI (and hence the daily digestible energy intake) of the voles was constant throughout the study, and the absolute amount of NDF digested per day increased, the percentage of digestible DM (and energy) obtained from NDF in the diet increased as diet quality decreased. Assuming that the daily digestible energy intake of voles is an estimate of maintenance energy requirements (since the animals did not gain mass), NDF fermentation accounted for approximately 42% of the daily energy needs of voles at 5°C on the 69% NDF diet, and accounted for approximately 68% of the daily energy needs of voles at 22°C on the 84% NDF diet. Previous estimates for the percent of maintenance energy provided by hindgut fermentation of fiber in small mammals ranged from 9 to 32% (Table 5).

In comparison, "concentrate-selective" and "intermediate-selective" ruminants derive approximately 40–65% of their daily energy needs from cell wall digestion, and "grazing" ruminants derive approximately 80–100% of their energy needs from fiber digestion (Van Soest 1982). Prairie voles in our study therefore gained proportionately as much energy from the fermentation of fiber as do many ruminant species.

Voles in this study were able to tolerate and utilize fiber to a much greater extent than previously reported for other small mammals (Table 5). One possible explanation is that the gradual increase in dietary fiber allowed

voles to acclimate to the higher fiber diets. However, we do not believe that this is a complete explanation because when two additional groups of voles (one at 22 and one at 5°C) were switched immediately from rat chow to the 69% NDF diet, they ate and digested the food as efficiently as the animals which were gradually acclimated (personal observation). Another possibility is that the fiber components of the diets which we used were more easily digested than those in other studies. The NDF fraction of a diet contains mostly hemicellulose, cellulose, and lignin (ash amounts are usually small), which are listed in decreasing order of digestibility (Van Soest 1982). Diets of natural forage fed to animals in previous studies may have contained more of the indigestible lignin in the NDF fraction, and therefore the animals were not able to digest those diets as well. A third possiblity is that the small particles of α-cellulose added to the diets in our study may have been digested more rapidly than more "natural-sized" particles of fiber (Robles et al. 1980; Bjorndal et al. 1990) and the voles were therefore able to meet their energy demands despite very high fiber intakes. However, voles chew food to a very small size and we are now investigating particle sizes and their effects on digestibility in these small herbivores.

We further evaluated the use of fiber by voles to meet their energy needs by calculating the food intake voles would need if they digested only cell solubles. We used the proportion of NDS in each diet and the NDS digestibility of each to calculate an "estimated" intake (Table 6). Because maximal daily intake for prairie voles is around 15 g·day^{-1}, animals attempting to survive only on NDS from their food would reach maximum intake on diets of much higher quality than actually observed. For voles at 22°C this would be a diet containing 60% NDF and voles at 5°C could only tolerate a diet containing 44% NDF. Thus, animals using only NDS to meet energy needs in the field would have to find food of much higher quality in winter than in summer (or at least when cold exposed).

One way to create a more favorable ratio of metabolic need to gut capacity is to increase the size of the fermentation vat (Sibly 1981; Penry and Jumars 1987). The extent of fiber digestion is a function of how long the fiber is exposed to microbes in the fermentation chamber (Sibly 1981; Penry and Jumars 1987; Allen and Mertens 1988; Sackaguchi et al. 1992; Hume et al. 1993). If the flow rate through the fermentation vat increases (due to increased rate of intake), then fiber digestion is decreased (Penry and Jumars 1987). If, however, the size of the vat increases as flow rate increases, then fiber digestion could be maintained (or increased if flow rate remained constant).

The size of the gastrointestinal tract of many small mammals increases in response to low food quality and/or exposure to situations that increase energy needs, such as cold-exposure or reproduction [voles: Gross et al. (1985); Woodall (1989); Hammond and Wunder (1991); Lee and Houston (1993); lemmings: Nagy and Negus (1993); mice: Green and Millar (1987); Hammond and Diamond (1992); jirds: Yahav and Choshniak (1990); pocket gophers: Loeb et al. (1991)]. Experimental voles in our study had longer and heavier ceca and large intestines (which make up the fermentation vat of voles) than previously reported for prairie voles eating relatively higher quality diets than those used here (Table 4). This result indicates that gut size of voles in this study increased in response to low diet quality and to cold exposure.

We believe that maximal intake by prairie voles is limited by some aspects of the animal, such as gut fill, maximum gut size or maximum processing rate because voles at 22 and 5°C reached their inflection points at the same level of food intake (Fig. 3), and the length and Dry mass of the fermentation vat did not differ between groups eating the lowest quality diet tolerated by each group. This suggests that gut sizes of animals in this study may represent the maximum attainable in prairie voles. One consequence of this result is that voles living at lower temperatures with consequently higher energy demands must either fill the gut much closer to capacity to meet energy needs or they must search for a higher

Table 5. Percentage of daily maintenance energy derived from fiber fermentation in small mammals

Rats	9%	Yang et al. (1969)
Rabbit	10–12%	Hoover and Heitmann (1971)
Beaver	19%	Hoover and Clark (1972)
Prairie vole	20%	Hammond and Wunder (1991)
Woodrat	21%	Justice and Smith (1992)
Pocket gopher	26%	Loeb et al. (1991)
Lemming	32%	Nagy and Negus (1993)
Prairie vole (5 °C)	42%	This study
Prairie vole (22 °C)	68%	This study

Table 6. Comparison of the intake of food needed (g · day^{-1}) by prairie voles if they utilized only the cell soluble component of a diet (a calculated value) versus actual intakes measured in this study (observed)

% NDF in diet	Warm (calculated)	Warm (observed)	*Difference*	Cold (calculated)	Cold (observed)	*Difference*
20.3	6.1	5.2	0.9	10.7	9.2	1.5
35.2	7.5	6.3	1.2	12.2	10.1	2.1
43.7	9.6	7.4	2.2	15.1	11.4	3.7
51.2	12.0	8.5	3.5	18.4	13.1	5.3
60.4	15.9	10.1	5.8	22.1	13.7	8.4
69.1	18.1	11.1	7.0	26.4	15.0	11.4
77.1	27.2	13.4	13.8			
83.6	44.3	14.0	30.3			

quality diet than needed when energy demand is not so high. Such a high quality diet may not be available during winter when above-ground plant material has senesced. Further, given that the inflection points occur at different quality-levels with different demands, we conclude that voles with energy demands approximating their maximal capacity will need to meet those demands with higher quality diets than animals with lower energy demands (Fig. 3).

Despite their higher intake on a given diet, animals at 5°C obtained the same DM and fiber digestibility as animals at 22°C. The results of this and previous studies (Table 4) suggest that on a given diet animals exposed to 5°C had bigger guts than animals at 22°C and were therefore able to defend DM and fiber digestibility. Other mechanisms that may allow mammalian herbivores to maintain digestibility in the face of increased intake include: 1) increased mastication to decrease the size of particles reaching the fermentation vat so that the rate of fermentation is increased (Robles et al. 1980; Bjorndal et al. 1990); 2) a colonic separation mechanism in the hindgut which allows the selective retention of small particles in the cecum (Bjornhag 1972; Holtenius and Bjornhag 1985) which will also increase the rate of fermentation; 3) increased activity and/or numbers of enzymes and transporters in the gut which can lead to increased digestion and absorption (Toloza et al. 1991); and 4) coprophagy or cecotrophy, which effectively increases the retention time of food in the gut and perhaps enhances digestibility (Hörnicke and Bjornhag 1980; Kenagy and Hoyt 1980; Chilcott and Hume 1985).

We demonstrated that prairie voles can circumvent the so-called rules governing the use of fibrous diets; many other small herbivores may do the same (Foley and Cork 1992). They do this by maintaining digestible energy intake through increased intake and by maintaining the digestibility of cell solubles and of fiber via long- and short-term adaptations. Existing models of fiber digestion by herbivores (Demment and Van Soest 1985; Fryxell 1991; Justice and Smith 1992) have neglected these processes, and consequently have consistently underestimated the digestive capabilities of small herbivores. Our data emphasize the importance of incorporating ostensible changes in behavior (possibly mastication), morphology (gut size) and physiology (enzyme-level adaptations) into models that seek to predict nutritional constraints. With the enhancements we propose, nutritional theory will be more faithful to the processes central to herbivore nutritional ecology.

Acknowledgements. This research was supported in part by NSF grant BSR 9006738 to B.A.Wunder and N.T. Hobbs. We would like to thank Drs. Tom Hobbs, Jim Detling, Gary Packard, John Gross, and Kim Hammond for helpful comments on early versions of this manuscript. We also thank two anonymous reviewers for their comments which also improved the manuscript. Dr. Phillip Chapman provided statistical advice. We are grateful to Mary Beth Voltura, Molly McLaughlin, Janelle Corn, Duncan Hopwood, and Ed Castro for help with animal care and pilot study data collection. Animals were studied under protocol approval of the Animal Care and Use Committee at CSU.

References

Allen MS, Mertens DR (1988) Evaluating constraints on fiber digestion by rumen microbes. J Nutr 118: 261–270

Baker DL, Hobbs NT (1987) Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can J Zool 65: 1978–1984

Batzli GO (1985) Nutrition. In: Tamarin RH (ed) Biology of new world *Microtus*. Am Soc Mammal, pp 779–811

Batzli GO, Cole FR (1979) Nutritional ecology of microtine rodents: digestibility of forage. J Mammal 60: 740–750

Bjorndal KA, Bolton AB, Moore JE (1990) Digestive fermentation in herbivores: effect of food particle size. Physiol Zool 63: 710–721

Bjornhag G (1972) Separation and delay of contents in the rabbit colon. Swed J Agricult Res 2: 125–136

Chilcott MJ, Hume ID (1985) Coprophagy and selective retention of fluid digesta: their role in the nutrition of the ringtail possum, *Pseudocheirus peregrinus*. Aust J Zool 33: 1–15

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminants and nonruminant herbivores. Am Nat 125: 641–672

Foley WJ, Cork SJ (1992) Use of fibrous diets by small herbivores: how far can the rules be 'bent'? Trends Ecol Evol 7: 159–162

Fryxell JM (1991) Forage quality and aggregation by large herbivores. Am Nat 138: 478–498

Green DA, Millar SJ (1987) Changes in gut dimensions and capacity of *Peromyscus maniculatus* relative to diet quality and energy needs. Can J Zool 65: 2159–2162

Gross JE, Wang Z, Wunder BA (1985) Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. J Mammal 664: 661–667

Hammond KA (1989) The role of diet quality and energy need in the nutritional ecology of a small herbivore. Ph.D. Thesis, Colorado State University, Ft. Collins, USA

Hammond KA, Wunder BA (1991) The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. Physiol Zool 64: 541–567

Hammond KA, Diamond JM (1992) An experimental test for a ceiling on sustained metabolic rate in lactating mice. Physiol Zool 65: 952–977

Holtenius K, Bjornhag G (1985) The colonic separation mechanism in the guinea-pig (*Cavia porcellus*) and the chinchilla (*Chinchilla laniger*). Comp Biochem Physiol 82A: 537–542

Hoover WH, Clark SD (1972) Fiber digestion in the beaver. J Nutr 102: 9–16

Hoover WH, Heitmann RN (1972) Effects of dietary fiber levels on weight gain, cecal volume and volatile fatty acid production in rabbits. J Nutr 102: 375–380

Hörnicke H, Bjornhag G (1980) Coprophagy and related strategies for digesta utilization. In: Ruckenbush Y, Thivend P (eds) Digestive physiology and metabolism in ruminants. MTP Press, Lancaster, pp 707–730

Hume ID, Morgan KR, Kenagy GJ (1993) Digesta retention and digestive performance in Sciurid and Microtine rodents: effects of hindgut morphology and body size. Physiol Zool 66: 396–411

Janis C (1976) The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30: 757–774

Justice KE, Smith FA (1992) A model of dietary fiber utilization by small mammalian herbivores, with empirical results for *Neotoma*. Am Nat 139: 398–416

Kenagy GJ, Hoyt DF (1980) Reingestion of faeces in rodents and its daily rhythmicity. Oecologia 44: 403–409

Keys JE, Van Soest (1970) Digestibility of forages by the meadow vole *Microtus pennsylvanicus*. J Dairy Sci 53: 1502–1508

Kleiber M (1961) The fire of life. Wiley, New York

Lee WB, Houston DC (1993) The effect of diet quality on gut anatomy in British voles (Microtinae). J Comp Physiol B 163: 337–339

Loeb SC, Schwab RG, Demment MW (1991) Responses of pocket gophers (*Thomomys bottae*) to changes in diet quality. Oecologia 86: 542–551

Milliken GA, Johnson DE (1984) Analysis of messy data. Van Nostrand Reinhold, New York

Montgomery MJ, Baumgardt BR (1965a) Regulation of food intake in ruminants. 1. Pelleted rations varying in energy concentration. J Dairy Sci 48: 569–577

Montgomery MJ, Baumgardt BR (1965b) Regulation of food intake in ruminants. 2. Rations varying in energy concentration and physical form. J Dairy Sci 48: 1623–1628

Nagy TR, Negus NC (1993) Energy acquisition and allocation in male collared lemmings (*Dicrostonyx groenlandicus*): effects of photoperiod, temperature, and diet quality. Physiol Zool 66: 537–560

Parra R (1978) Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution, Washington, D.C., pp 205–230

Penry DL, Jumars PA (1987) Modeling animal guts as chemical reactors. Am Nat 129: 69–96

Robbins CT (1983) Wildlife feeding and nutrition. Academic Press, Orlando

Robles AY, Belyea FA, Martz FA, Weiss MF (1980) Effect of particle size upon digestible cell wall and rate of in vitro digestion of alfalfa and orchard-grass forages. J Anim Sci 51: 783–790

Sakaguchi E, Kaizu K, Nakamichi M (1992) Fibre digestion and digesta retention from different physical forms of the feed in the rabbit. Comp Biochem Physiol 102A: 559–563

Short HL, Blair RM, Segelquist CA (1974) Fiber composition and forage digestibility by small ruminants. J Wildl Manage 38: 197–209

Sibly RM (1981) Strategies of digestion and defecation. In: Townsend CR, Calow PA (eds) Physiological ecology: an evolutionary approach to resource use. Blackwell, Oxford, pp 109–139

Toloza EM, Lam M, Diamond JM (1991) Nutrient extraction by cold-exposed mice: a test of digestive safety margins. Am J Physiol 261: G608–G620

Van Soest PJ (1982) Nutritional ecology of the ruminant. O & B Books, Corvallis

Weston RH, Poppi DP (1987) Comparative aspects of food intake. In: Hacker JB, Ternouth JH (eds) The nutrition of herbivores. Academic Press, Sydney, pp 133–161

Woodall PF (1989) The effects of increased dietary cellulose on the anatomy, physiology, and behavior of captive water voles, *Arvicola terrestris* L. (Rodentia: Microtinae). Comp Biochem Physiol 94A: 615–621

Wunder BA (1985) Energetics and thermoregulation. In: Tamarin RH (ed) Biology of New World *Microtus*. Am Soc Mammal, pp 812–844

Yahav S, Choshniak I (1990) Response of the digestive tract to low quality dry food in the fat jird *Meriones crassus* and the levant vole *Microtus guentheri*. J Arid Environ 19: 209–215

Yang MG, Manoharan K, Young AK (1969) Influence and degradation of dietary cellulose in cecum of rats. J Nutr 97: 260–264