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A MODEL OF DIETARY FIBER UTILIZATION BY SMALL
MAMMALIAN HERBIVORES, WITH EMPIRICAL
RESULTS FOR *NEOTOMA*

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Abstract.—Allometric considerations have suggested that small herbivores are inefficient at or incapable of extracting energy from the microbial fermentation of structural carbohydrates. This notion is at odds with accumulating empirical evidence that demonstrates well-developed fiber digestion abilities for a number of small rodent genera. To examine the apparent inconsistency, we have constructed a model of plant fiber utilization tailored specifically for hindgut fermenters. Computer simulations provide estimates of fiber and overall dry-matter digestibilities as a function of body size, energy demand, and diet. Our calculations indicate that small mammals can obtain significant benefit from fiber fermentation, especially at moderate fiber levels. Comparisons with literature data are in general agreement, although fiber digestion abilities are still underestimated for the smallest animals. In an empirical test of the model, *Neotoma* obtained over 21% of their digestible energy solely from the microbial fermentation of plant fiber. We also observed an interesting pattern of allometric sorting predicted by the model. Smaller woodrats significantly reduced the fiber content of their diet, a behavior presumably reflecting energy limitations.

Although cellulose and its related components are the most abundant organic compounds in most environments (Van Soest 1973, 1982; Demment and Van Soest 1985), a number of considerations have led to the belief that small herbivores cannot make effective use of structural carbohydrates as an energy source and must rely primarily on easily digested plant cell contents. First, microbial digestion of structural carbohydrates has been shown to be directly proportional to both the size of the animal's fermentation chamber and the residence time of particles within it. Although chamber size scales linearly with body mass (Parra 1978; Van Soest 1982; Demment 1983; Demment and Van Soest 1985), the higher mass-specific metabolic rate of smaller animals requires higher overall food passage rates (fig. 1). This has been interpreted by some to indicate that plant fibers can only be superficially processed by small herbivores and thus do not constitute a significant element of the diet (e.g., Batzli and Cole 1979; Batzli 1985). Second, the smaller absolute energy requirements of small herbivores suggest that energy needs could be largely met by selective feeding of plant materials without heavy dependence on microbial fermentation (Penry and Jumars 1987). A tacit assump-

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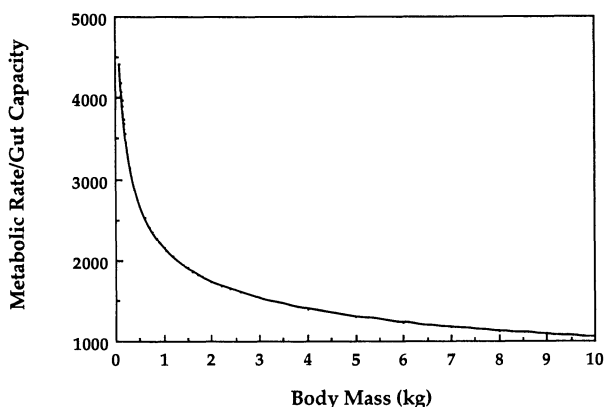


FIG. 1.—Metabolic-rate-to-gut-capacity ratio vs. body mass. This graph implies that, in general, smaller mammals must consume food that is more digestible than larger ones, or else they must consume more food relative to their size. Redrawn from similar curve by Demment (1983). Metabolic rate taken as $140 W^{0.75}$, gut capacity = $0.065 W^{1.06}$ as determined from literature values.

tion, of course, is that abundant quantities of moderate quality vegetation are readily available.

Some recent studies have indicated, however, that plant structural carbohydrates may provide an important energy source for small herbivorous mammals in natural populations. Significant fiber digestion abilities have been demonstrated for several small rodents in laboratory settings (Keys and Van Soest 1970; Servello 1981; Hammond 1989; present study). For example, using digestibility and intake data from Keys and Van Soest (1970), we estimate that voles (*Microtus pennsylvanicus*) can obtain approximately 34% of their maintenance energy from fiber. This is well within the range observed for large hindgut fermenters on analogous diets (Fonnesbeck 1968; Hintz et al. 1971). Additionally, highly modified gastrointestinal structures are observed in some rodents (Barry 1974; Carleton 1980; K. E. Justice and F. A. Smith, personal observation) and are presumably an adaptation for enhancing fiber fermentation capabilities.

Such evidence suggests not only that natural populations of small herbivores use plant fibers as a significant source of dietary energy but also that selection has resulted in the evolution of mechanisms that at least partially compensate for allometric constraints on fiber digestion. We have tested these hypotheses by formulating a model of fiber fermentation based on characteristics of hindgut herbivores that have not previously been treated quantitatively. For example, several key physiological parameters were permitted to vary allometrically with body mass. The predictive ability of the model was evaluated by comparing generated values with literature data and with data from a laboratory test involving different species of woodrat. Computer simulations were run using the range of body masses and percentage dietary fiber expected to be found among natural populations. In general, we found a strong correlation between model predictions

and observed values for medium to large species, but, even with our careful analysis, there was a tendency to underestimate fiber digestion abilities for the smallest herbivorous animals. The discrepancy probably reflects, at least partially, adaptations for fiber use that were not incorporated into our model, and it is suggestive of selection for enhanced fermentation abilities. Empirical results from a laboratory experiment corroborated our expectations that woodrats digest plant fibers and also revealed an interesting pattern of allometric food particle sorting. Despite homogenation of the experimental diet, smaller animals were able to significantly reduce the fiber content by selective feeding.

BACKGROUND

In this article, the term *fiber* is synonymous with neutral detergent fiber (NDF), the solid remaining after digestion of vegetation in a neutral detergent solution at 100°C (Goering and Van Soest 1970). It forms the structural basis of plants and consists primarily of cellulose, hemicellulose, and lignin. In general, this is the fraction of forage that cannot be digested enzymatically but that is at least partially degradable by microbial fermentation (Van Soest 1977, 1978). Soluble fractions produced during the detergent treatment are known as neutral detergent solubles (NDS), referred to here simply as *solubles*. They consist primarily of cell contents such as proteins, sugars, and storage carbohydrates and are highly digestible enzymatically.

Herbivory is defined, in its strictest sense, as plant consumption by animals that obtain a substantial proportion of their energy needs from the microbial degradation of plant fiber. Mammals lack cellulolytic enzymes capable of digesting the structural carbohydrates of plants (McBee 1970; Van Soest 1973; Janis 1976) and thus, to exploit this resource, have evolved fermentation chambers that house symbiotic microflora. The fermentation chamber can be situated either anterior to the stomach, as in ruminants, or posterior to the main site of enzymatic digestion, as in horses and rodents. The location is important in terms of energy efficiency. While large ruminants may be efficient at fermenting a high-fiber diet, *all* food ingested is subject to microbial degradation, even that potentially enzymatically available. As a mammal's size decreases, its diet must increasingly be enriched with solubles to provide more digestible energy per gram of mass. Eventually a body mass is reached where energy gained from fiber fermentation is completely offset by energy loss through the microbial trophic level. At this point, mechanisms favoring retention of the digesta in the rumen should become dysfunctional, and enzymatic digestion should be the dominant alimentary mode. Parra (1978), Van Soest (1982), and Demment and Van Soest (1985) have predicted that this lower limit of body mass in ruminants is at 5–10 kg; indeed, the smallest herbivorous ungulates (the dik-dik, *Madoqua guenthera*, and suni, *Nesotragus maschatus*) attain adult masses of 4–6 and 6–8 kg, respectively (Nowak and Paradiso 1983). In smaller animals, the need to pass large amounts of highly digestible material through the rumen is not compatible with the requirement that fiber spend a significant amount of time in the fermentation chamber.

While hindgut fermenters are subject to the same metabolic rate/gut capacity

allometry as ruminants, the location of the fermentation chamber in the cecum results in a different situation as body size decreases. Solubles are digested enzymatically *before* reaching the fermentation chamber. Thus, not only is energy conserved, but since the fermentation chamber contains almost exclusively plant fiber, a more efficient cellulolytic microbial community ensues. Consequently, small animals should be able to consume moderately high-fiber diets while still maintaining a reasonable fermentation time, and significant levels of fiber digestion may occur at smaller sizes than the lower limits predicted for ruminants.

METHODS

Model Derivation

The general model was partially derived from work by previous investigators, notably Demment (1982), Van Soest (1982), and Demment and Van Soest (1985), although they concentrated more specifically on ruminants or generalized mammalian herbivores rather than mammals with hindgut fermentation chambers. Penry and Jumars (1987) recently constructed an interesting digestion model based on chemical engineering principles. It is of limited use for herbivores, however, since the reaction kinetics treat food as a homogeneous entity and ignore the distinction between different fractions.

For an estimate of basal metabolic rate (BMR, in kilocalories per day), we follow the usual expression of Kleiber (1932):

$$\text{BMR} = 70 W^{0.75}, \quad (1)$$

where W is body mass (in kilograms). The maintenance energy, M (in kilocalories per day), is usually taken as roughly twice this amount (Crampton and Harris 1969; Van Soest 1982):

$$M = 140 W^{0.75}. \quad (2)$$

The total digestible energy, DE (in kilocalories per day), we specify as

$$\text{DE} = CI (D_f F + D_s S), \quad (3)$$

where I represents the mass ingested in kilograms of dry matter per day; D_f the digestibility of the plant fiber; F the proportion of fiber in the diet; D_s the digestibility of cell solubles; $S = 1 - F$, the proportion of solubles in the diet; and $C = 4,400$, the average caloric content of a kilogram of forage (Crampton and Harris 1969). The digestible energy that can be obtained from fiber, DE_f , is

$$\text{DE}_f = CID_f F, \quad (4)$$

and the proportion of energy obtained from fiber is the ratio of DE_f to DE. Thus, the modeling effort reduces to finding expressions for D_f and D_s and to adjusting the ingestion rate, I , to achieve a total digestible energy rate equivalent to the maintenance energy.

Our model reflects the assumption that digestibility of fiber is a function of fermentation time. An estimate of the chamber holding capacity and the material

TABLE 1
BODY MASSES AND WET MASS OF CONTENTS OF FERMENTATION CHAMBER
FOR VARIOUS HINDGUT FERMENTERS

Species	Body Mass (kg)	Fermentation Mass (kg)	Reference
Elephant	2,337	278.1	Hungate et al. (1959)
Horse	426	47.7	Elsden et al. (1946)
Capybara	40.5	5.14	Parra and Gonzalez (1972)
Swine	20.0	.92	Elsden et al. (1946)
Beaver	17.5	1.07*	Hoover and Clarke (1972)
Koala	7.25	.757	Cork and Warner (1983)
Rabbit	1.63	.111	Carmichael et al. (1945)
Rabbit	1.17	.101	Elsden et al. (1946)
Guinea pig	.683	.043	Slade (1970)
Woodrat	.157	.0116	This study
Vole	.042	.0025†	Gross et al. (1985)

* Cecum and upper colon, maximum observed.

† Mean of two experimental conditions.

TABLE 2
PERCENTAGE DRY MATTER IN THE CONTENTS OF THE RUMEN OR CECUM OF REPRESENTATIVE
MAMMALIAN HERBIVORES

Species	Body Mass (kg)	Dry Matter (%)	Reference
Cow	600	12	Short (1963)
Mule deer	57	14	Prins and Geelen (1971)
Whitetail deer	51	15.8	Short (1963)
Fallow deer	40	15	Prins and Geelen (1971)
Beaver	17.5	15.8	Hoover and Clarke (1972)
Roe deer	14	24	Prins and Geelen (1971)
Porcupine	8.25	21.9	Johnson and McBee (1967)
Koala	7.25	18.8	Cork and Warner (1983)
Woodrat	.157	21.7	This study
Vole	.041	27.5*	Gross et al. (1985)

* Average of two experimental regimes.

entering per unit time is necessary to calculate fermentation time. The holding capacity, V (in kilograms), can be estimated from the regression of wet mass of the cecum and colon contents versus body mass. By using the data in table 1 we obtain

$$V = 0.065 W^{1.06}, \quad (5)$$

with $r^2 = 0.993$. The actual amount of material undergoing fermentation is determined by both the wet mass and percentage dry matter (DM) of the contents. Although Demment (1983) used an overall figure of 10% DM, observed DM is inversely related to body size. Table 2 gives the proportion of DM in the rumen

or cecum for mammals of various body masses. From these we calculate a regression of

$$DM = 0.22 W^{-0.08}, \quad (6)$$

with $r^2 = 0.71$. The amount of material entering the fermentation chamber is taken as the amount ingested, I , less the solubles digested in the stomach and small intestine. The average time in the chamber is the amount contained in the chamber divided by the quantity entering per unit time. The average retention time in the fermentation chamber, T (in days), is given as

$$\begin{aligned} T &= (DM/100) V/[I(1 - D_S S)] \\ &= 0.0139 W^{0.98}/I(1 - D_S S). \end{aligned} \quad (7)$$

The form of the relationship between average retention time and proportion of fiber digested is based on the results of ruminant *in vitro* fermentation studies, as no information is available on the time dynamics in the cecum. Waldo (1969) first suggested that *in vitro* fiber digestion could be described by first-order kinetics acting on a potentially digestible fraction, in the presence of an indigestible portion. The indigestible material is usually taken as the amount remaining after 48–72 h of fermentation. Later workers (e.g., Mertens and Ely 1979) showed that the process can better be approximated by assuming fast and slow fractions, each controlled by first-order kinetics. However, for the short to intermediate retention times of concern here, the former model is completely satisfactory. Mertens (1973) has shown that the *in vitro* process is also characterized by a lag phase, which is adequately described by a discrete time delay before initiation of first-order kinetics. Presumably, this induction period is associated with growth and acclimation of the bacteria and hydration of the substrate. There is some question whether the time lag is also characteristic of *in vivo* systems. It seems reasonable to assume so for ruminants, because the ingesta enters the rumen first and eating occurs intermittently (Mertens 1973). However, in hindgut fermenters ingesta are hydrated in the gastrointestinal tract prior to reaching the cecum and presumably enter continuously. Thus, there is likely to be little or no time lag after the material enters. Accordingly, we assume simple first-order kinetics acting on a potentially digestible fraction. That is,

$$\frac{dD}{dt} = -kD, \quad (8)$$

where D is the proportion of potentially digestible fiber and k is the rate constant. In integrated form,

$$D_t = D_0 e^{-kt}, \quad (9)$$

where D_0 is the proportion of the fiber potentially degradable. If $U = 1 - D_0$ is the undigestible fraction of the fiber, then the relationship between the time in the fermentation chamber and fiber digestibility is

$$D_f = 1 - U - D_0 e^{-kt}. \quad (10)$$

The digestibility parameters k and U vary with the degree of lignification and other forage characteristics and are thus specific to the food consumed. We have picked values of $U = 51.3$ and $k = 0.114$ for medium-maturity alfalfa hay as determined by Smith et al. (1971, 1972).

In contrast to fiber, the degradation of solubles does not appear to be a function of retention time, at least for the range of concern in herbivores. Fonnesbeck (1969) has shown that the true digestibility of cell solubles is essentially 100% in the horse. However, because of endogenous excretion of cell contents, the apparent value is less and is a function of the relative levels of fiber and solubles in the diet. If metabolic excretion is a constant proportion of dry matter intake, the apparent digestibility (D_S) of cell solubles is given by

$$D_S = d - c/S, \quad (11)$$

where d is the true digestibility, c is the metabolic excretion as a fraction of dry matter intake, and S is the proportion of solubles in the diet (Van Soest 1982). Apparent digestibility data can be fitted to this function if we use linear regression by transforming to

$$SD_S = Sd - c, \quad (12)$$

as is commonly done for the "Lucas test" (Van Soest 1982). The data of Fonnesbeck (1969) and Hintz et al. (1971) yield values of $c = 0.127$ and $d = 1.02$ with $r^2 = 0.96$, with both c and d given as proportional rather than percentage values. Accordingly, equation (11) can be simplified to

$$D_S = 1.02 - 0.127/S. \quad (13)$$

We have now defined all of the functions needed for the model. Setting equation (2) equal to equation (3), we obtain

$$140 W^{0.75} = CI (D_f F + D_S S). \quad (14)$$

Replacing D_f and D_S with the formulations presented in equations (10) and (13) and setting $t = T$ yields

$$140 W^{0.75} = CI [(1 - U - D_0 e^{-k((0.0139 W^{0.98})/I(1 - D_S S))}) F + (1.02 - 0.127/S) S]. \quad (15)$$

This equation is difficult to solve explicitly. We thus iterate to convergence on a computer, making an initial low guess for I and then raising it by an appropriate amount until the expression is satisfied to within a small error term, which indicates that energy balance has been attained.

Digestibility Trial

Woodrats (*Neotoma* spp.) were chosen for a laboratory test of our model. All members of the genus appear to consume bulky herbivorous diets (see Vorhies and Taylor 1940; Linsdale and Tevis 1951; Fitch and Rainey 1956; Finley 1958; Thompson 1982), although no field studies have attempted to measure actual fiber consumption. Preliminary work in our laboratory demonstrated that *Neotoma* were able to maintain weight on a high-fiber diet (ca. 45%). Four species and subspecies were chosen to provide a range of body sizes and also to allow testing

for differences in digestive performance that might be due to dietary specializations. *Neotoma fuscipes* (131–246 g) is considered to be an oak specialist (Atsatt and Ingram 1983) and typically lives in oak woodland or dense chaparral. *Neotoma albigula* (130–225 g) is found in the Sonoran desert and feeds primarily on cactus (Vorhies and Taylor 1940; Justice 1985). Two subspecies of *N. lepida* were selected. *Neotoma l. lepida* (78–157 g) consumes a variety of desert shrubs and is perhaps the most xerically adapted of the woodrats (Thompson 1982), whereas *N. l. intermedia* (119–228 g), a more mesic subspecies, is commonly found inhabiting large *Opuntia* patches in coastal sage scrub.

Woodrats had been in captivity from 2 to 3.5 mo prior to the experiment. During this time they were fed commercial horse pellets (ground alfalfa hay, grain, vitamins, and minerals) and alfalfa hay cubes, which contained approximately 40% fiber. The experimental diet was made from alfalfa hay cubes ground through a 2-mm screen, with 10% cornstarch used as a binder. It contained 39.5% fiber (23.6% cellulose, 10.2% hemicellulose, and 5.7% lignin). The animals were fed this diet for a 6-d acclimation period, followed by 6 d in which input and output were measured. Fecal pellets and orts (discarded food) from each woodrat were dried at 50°–60°C, and 10-g aliquots of each were homogenized for subsequent analyses. Water and mineralized salt were provided ad lib. Ambient temperature remained approximately 22°C throughout the experiment, and lights were on a 12L:12D cycle. Chemical analyses of the diet, orts, and feces followed the method of Goering and Van Soest (1970) with the exception that decalin and sodium sulfite were omitted (Robertson and Van Soest 1981).

RESULTS

Computer Simulations

Although we are most interested in the behavior of the model at small body masses, simulations were conducted over a broader range to check for validity with literature data. In the following sections, we examine the effects of dietary fiber content on fermentation times, digestibility, and obtainable energy for herbivores of various sizes.

The variation in fiber digestibility over the mass range of 0.1–1,000 kg is illustrated in figure 2 for diets of 40% and 60% plant fiber, respectively. As body size is decreased, the concomitant rise in mass-specific metabolic requirements results in greater mass-specific food consumption and, consequently, shorter retention time in the fermentation chamber (fig. 2A). Shorter particle residence period depresses fiber digestibility (fig. 2B), which intensifies the need for higher ingestion rates. The impact is greatest at low body mass because fermentation times lie within the steeper region of the exponentially decaying function (eq. [9]). As both the 40% and 60% diets approach their fullest digestibility ($1 - U$) at extended fermentation times, convergence occurs (fig. 2B). Thus, not only are structural carbohydrates generally less usable at lower body sizes, but the energy value is reduced disproportionately in high- versus low-fiber diets. At sufficiently small body masses the ingestion rate required to meet metabolic demands may

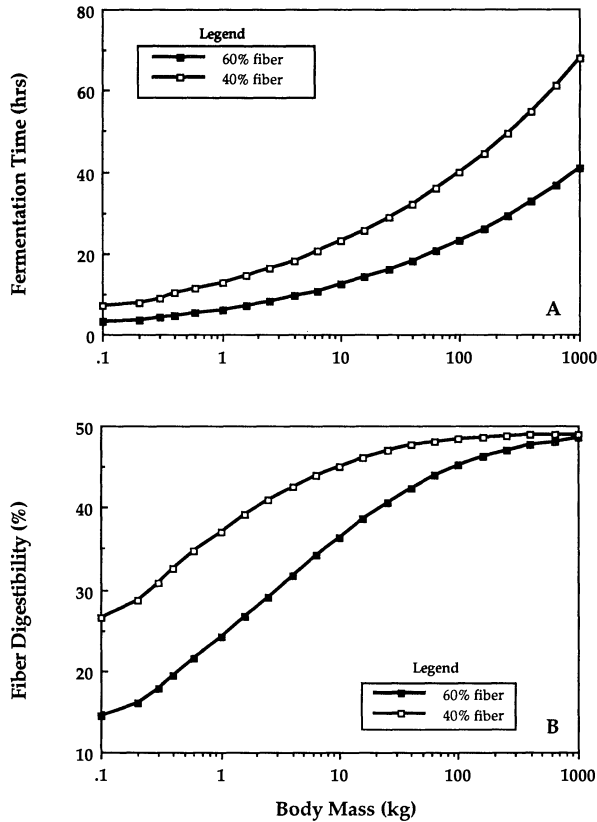


FIG. 2.—Model predictions for diets of 40% and 60% fiber and body masses from 100 g to 1,000 kg. For figs. 1–4, the digestibility parameters for medium-maturity alfalfa hay ($U = .51$, $k = 0.011$) were used, and energy expenditure of $2 \times \text{BMR}$ is assumed. A, Fermentation time (in hours); B, fiber digestibility.

be impossible to attain. Indeed, small rodents cannot survive on 60% fiber diets (Keys and Van Soest 1970).

Our simulations indicate that retention times and fiber digestibilities are primarily dependent on *fiber* ingestion rates and not on the overall consumption of organic matter. Accordingly, we have plotted fermentation time and fiber digestibility versus diet for animals of 0.15, 1.5, and 15 kg (fig. 3). The drop-off in maximal fermentation time with increased fiber consumption is felt at all masses (fig. 3A), but effects on digestibility are more pronounced for smaller animals (fig. 3B). This is because retention times become short, and without compensating mechanisms, only limited microbial fermentation can occur. Conversely, at low fiber levels, sufficient time is available to obtain maximal energy from the fiber contained in the diet.

The relationship between diet quality and energy derived from fiber fermentation is illustrated in figure 4, again with herbivores of 0.15, 1.5, and 15 kg. At

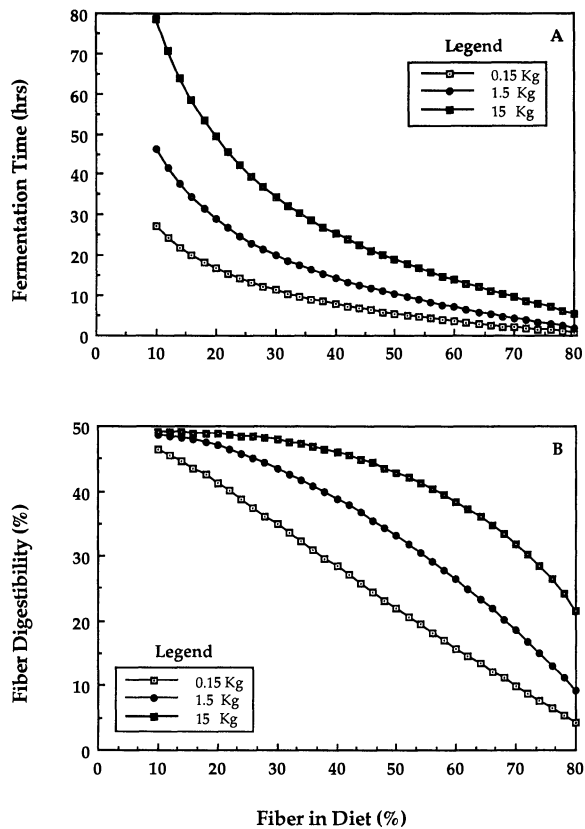


FIG. 3.—Model predictions for diets of 10%–80% fiber at body masses of 0.15, 1.5, and 15 kg (i.e., woodrat, rabbit, and beaver, respectively). *A*, Fermentation time; *B*, fiber digestibility.

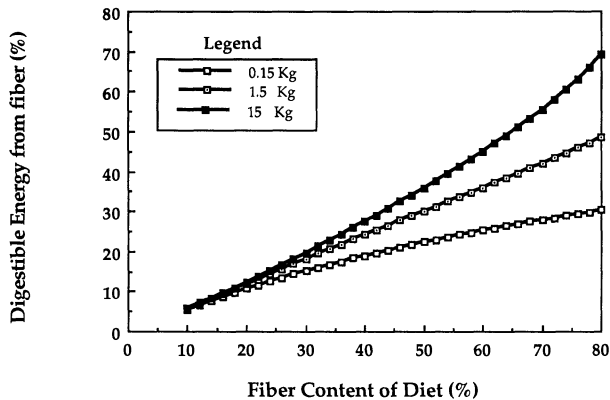


FIG. 4.—Digestible energy obtained from fiber fermentation vs. fiber content of the diet. Curves for three different body masses are represented. Note that although the slope remains positive, it diverges at high fiber levels.

very low plant fiber levels (ca. 10%–20%) the percentage of digestible energy obtained is similar for all three sizes, but as the diet becomes progressively coarser, the slopes diverge. At high levels of fiber, the sign of the second derivative changes for the smallest and largest animals, while remaining constant at the intermediate size. Thus, the small herbivore becomes less efficient at extracting energy from the microbial fermentation of fiber, even though overall more energy is obtained from this source (i.e., the slope is still positive).

The simulations converge on 49% fiber digestibility at higher body masses (figs. 2 and 3) because the fermentation time becomes sufficient for complete degradation of the digestible fraction, which we held constant at $1 - U = 49\%$. For the empirical studies, of course, U varies depending on the nature of the fodder and typically ranges from 45% to 80% (Van Soest 1982). Values for medium-maturity alfalfa from Smith et al. (1971, 1972) were chosen to match the fiber content of the alfalfa used in preparing the experimental diet. The model is very sensitive to this parameter, however, and other forage values from Smith et al. (1971, 1972) bracket the empirical results.

Model Predictions and Literature Values

We compared computer-generated predictions with literature values to evaluate the model's performance over a broad range of body sizes. To minimize inevitable differences in methodology and experimental design, we concentrated on digestion studies that used alfalfa-based diets with similar U , the total collection method of assaying input and output, and the standard analysis for fiber (Goering and Van Soest 1970) or a close derivative. The ratios of observed and predicted fiber digestibilities are graphed in figure 5 for hindgut herbivores that range from 0.025 (pine voles) to 3,400 kg (Asian elephant). At higher body masses, the model appears not to be particularly biased, although the Asian tapir (*Tapirus indicus*) performs more poorly than predicted. Foose (1982) has suggested that the tapir relies on fermentation primarily for nitrogen and not as a substantial source of energy, but not much is known about the nutritional ecology of natural populations. The model has a general tendency consistently to underestimate fiber fermentation abilities of the very smallest animals (1–3 in fig. 5), all of whom are members of the rodent genus *Microtus*. Unfortunately, little published information is currently available for other small herbivorous species, but we suspect they too will perform better than predicted.

Digestibility Trial with Woodrats

The results of the digestibility experiment are summarized in table 3. Overall, woodrats digested 35.0% of the total fiber consumed (approximately 70% of the available fiber), which represented 21.3% of digestible energy requirements. Our model simulations predicted slightly lower values of 29.8% and 18.4%, respectively, an underestimate of about 15% (fig. 5).

We wished to examine possible correlations between consumption, digestion, selectivity, and body mass (table 4) and, moreover, to determine whether the form of any such relationship was allometric or isometric. It seemed likely, however, that body mass would be correlated with both sex and taxonomic group,

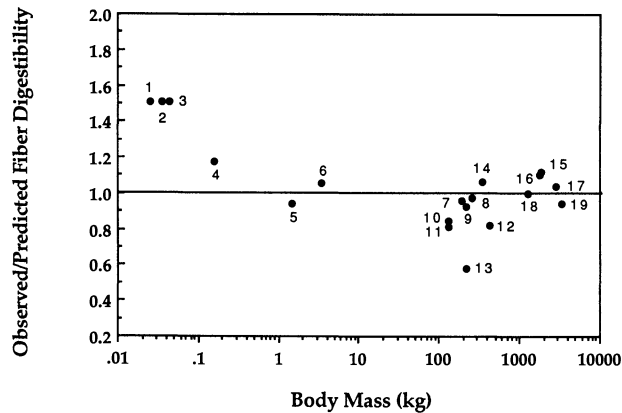


FIG. 5.—Comparison of observed with predicted fiber digestibilities, based on data from the literature. Plotted is the ratio of observed to predicted vs. mass in kilograms (log scale). Legend: 1—pine vole (Servello 1981); 2—meadow vole (Keys and Van Soest 1970); 3—California vole (K. E. Justice, unpublished data); 4—woodrat spp. (this study); 5—domestic rabbit (Paul-Murphy et al. 1982); 6—rock hyrax (Paul-Murphy et al. 1982); 7—Asian wild ass (Foose 1982); 8—mountain zebra (Foose 1982); 9—plains zebra (Foose 1982); 10—pony (Hintz et al. 1971); 11—American tapir (Foose 1982); 12—horse (Fonnesbeck 1968); 13—Asian tapir (Foose 1982); 14—grevy zebra (Foose 1982); 15—Indian rhino (Foose 1982); 16—white rhino (Foose 1982); 17—African elephant (Foose 1982); 18—black rhino (Foose 1982); 19—Asian elephant (Foose 1982).

TABLE 3
RESULTS OF DIGESTION TRIAL WITH WOODRATS

Variable	Mean	SE	Range
Body mass (g)	156.6	6.6	78.0–245.7
Change in mass (g)	1.38	.95	–16.4–9.9
Consumption (g/g/d)	.092	.003	.055–.131
% Fiber consumed	38.2	.25	34.1–39.6
% Fiber in orts	44.3	.37	40.3–51.5
% Fiber in scats	66.7	.30	63.0–69.0
% Dry matter digestibility	62.8	.42	58.8–69.6
% Fiber digestibility	35.0	.69	25.8–43.7
% Soluble digestibility	79.9	.31	76.2–84.2
Digestible energy (kcal/g/d)	.254	.008	.143–.365
% Digestible energy from fiber	21.3	.37	16.6–25.1

NOTE.—Data are pooled over sexes and taxonomic groups. $N = 36$.

so we first investigated these possible confounding factors. Analysis of variance confirmed the highly significant effect of sex on mass ($P < .001$) but failed to demonstrate any further effects on consumption, digestion, or selectivity (table 4) after removal of mass by linear regression. Accordingly, data for both sexes were pooled in all subsequent analyses.

While there was no a priori reason for expecting differential digestive performance on the basis of sex alone, the disparate dietary specializations of the

TABLE 4
ANALYSIS OF COVARIANCE

Factor	Body Mass	Sex	Taxonomic Group
Consumption related:			
Mass change (g)	NS	NS	NS
Food intake (g/d)	***	NS	*
Scats produced (g/d)	***	NS	**
Digestible energy (kcal/d)	***	NS	NS
Digestion related:			
% Dry matter digested	NS	NS	NS
% Fiber digested	NS	NS	NS
% Solubles digested	NS	NS	NS
% Digestible energy from fiber	NS	NS	NS
Selectivity related:			
% Fiber consumed	**	NS	**
Orts produced (g/d)	**	NS	NS

NOTE.—The effect of body mass was removed first. The mass column reflects the significance of the regression of the dependent variable on body mass. The other columns show the significance of sex or taxonomic group on the dependent variable. Ratio data were arcsine-transformed prior to parametric testing. $N = 36$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

woodrat species suggested they might respond differently to the experimental regime. Analysis of variance again revealed a highly significant effect of taxonomic group on body mass ($P < .01$); even after removal of mass, food intake and scat production were still significantly related to group (table 4). Since these two variables also displayed significant heterogeneity of variance (Cochran's C , Bartlett-Box F ; $P < .01$), effects were reassessed using a nonparametric Kruskal-Wallis ANOVA, which confirmed the result. A Scheffé multiple-comparison test suggested this was due to greater food consumption and elimination by *Neotoma albigula* relative to either subspecies of *N. lepida*. Thus, further investigations were conducted using ANCOVA between groups with mass as the independent variable and each of the consumption, digestion, and selectivity-related factors as dependent variables. Final results are summarized in table 4.

Regressions of the dependent variables against body mass revealed allometric relationships for both the selectivity-related factors (fiber consumed and Orts produced). The experimental diet was ground through a 2-mm screen to discourage selective feeding, but many animals still sorted their food to some degree (fig. 6). Accordingly, discarded food was analyzed and used to calculate actual consumption of fiber. Results indicated that smaller animals significantly reduced the fiber content eaten by rejecting higher fiber particles. The relationship with mass was nonlinear, however, and most pronounced within *N. l. lepida* (fig. 6; table 4).

The predicted scaling of mass and fiber digestibility was not detected (table 4). The correlation may have been obscured, however, by the lower-fiber diet se-

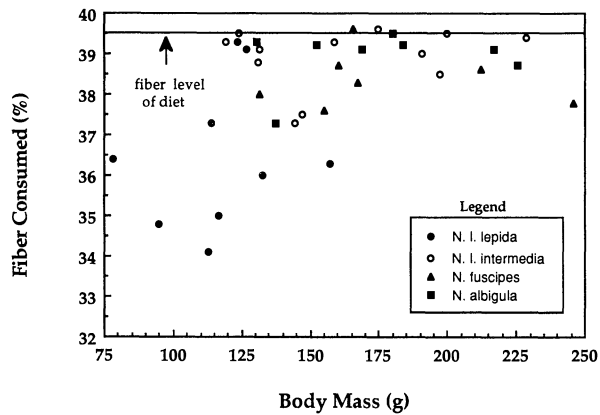


FIG. 6.—Percentage fiber in diet consumed in the laboratory digestion trial as a function of body mass. Smaller woodrats lowered the fiber content of their diets by sorting out and discarding high-fiber particles. After we log-transformed the X-axis to linearize the relationship, the regression obtained is fiber consumed (%) = $24 (\pm 4.3) + 6.7 (\pm 2.0) \log(\text{body mass})$, where the figures in parentheses are the SEs. The regression is significant at $P < .001$, with $r^2 = 0.6$.

lected by *N. lepida*. The sample size ($N = 36$) and mass range (78–246 g) in the present study lack the statistical power necessary for application of multivariate statistics. Inclusion of a broader mass range (e.g., the addition of *N. cinerea*, the largest species of woodrat) would probably allow further exploration of this question.

DISCUSSION

Our model simulations clearly indicate that small hindgut mammals can obtain a substantial fraction of their energy needs by the microbial fermentation of fiber. Although a progressively lower fraction of metabolic costs are met as body size decreases, even a rodent as small as the pine vole (25 g) acquires substantial benefits from plant fiber (predicted 15% DE; observed 20% DE). The resolution of the apparent paradox between empirical observations and earlier theoretical work (based primarily on foregut animals) is the result of careful consideration of the hindgut fermentation process. The location of the fermentation chamber posterior to the site of enzymatic digestion is crucial to fiber digestion abilities, since it permits full extraction of energy from solubles. In addition, the digestion and absorption of solubles in the small intestine allow a greater holding capacity for fiber in the cecum, which hence increases particle retention time.

Although our model generated predictions that we believe represent reasonable approximations of the digestive process, the fiber fermentation capabilities of very small mammals were consistently underestimated (fig. 5). In retrospect, this may not be surprising. Structural carbohydrates represent a ubiquitous and predictable resource in terrestrial environments. Thus, small herbivores have

probably experienced some sort of selection to derive energy from the most abundant constituent of their diet.

The precise nature of selection for mechanisms enhancing fiber digestion remains unclear. Sensitivity analysis that we conducted on our model indicated that the fermentation process is very responsive to the parameters V , k , U , and F . The latter two are not under physiological control and can only be influenced insofar as the choice of forage is concerned. If our model formulations are correct, this suggests that selection has most likely acted to increase the effective size of the fermentation chamber (V) or the fermentation rate (k) to compensate for the higher ingestion required at small body masses. In fact, Gross et al. (1985) and Hammond (1989) have shown that *Microtus* enlarge cecum tissue mass in response to increased fiber intake, and Hammond (1989) has demonstrated that this is accompanied by a rise in fiber digestibility. We have not included this adaptation in our model because it has not yet been demonstrated for other species.

In several small mammals, a reverse peristalsis mechanism washes small particles from the colon back into the cecum, which increases the surface-to-volume ratio as well as reduces the washout of the microflora (Bjornhag 1972; Sperber et al. 1983; Chilcott and Hume 1985; Holtenius and Bjornhag 1985; Foley and Hume 1987). This apparently augments the fermentation efficiency of the cecum at high passage rates. Subtler adaptations that increase the effective surface area, such as evaginations of the cecal wall, may be difficult to detect, and their quantification could in fact pose a fractal geometry problem. In this context, it has been suggested that the short broad villi of *Microtus*, as well as their unique orientation, may slow the rate of passage of ingesta, which would allow maximal contact (Barry 1974). Coprophagy, which allows absorption of predigested materials and microbial recovery, is another surface area-related adaptation that could partially explain enhanced fiber digestion abilities.

Our sensitivity analysis also revealed a dependence on the fermentation rate constant, k . Physical factors that influence k include temperature and pH, but the concentration and species composition of the microflora also play a role. In general, the greater relative proportion of structural carbohydrates in the cecum has resulted in a more cellulolytic microbial community (e.g., higher k) than that found in the foregut, and there are reports that large hindgut fermenters are more efficient at degrading fiber than ruminants (Hungate 1966; Janis 1976). It is difficult, however, to envision a relevant mechanism that provides smaller hindgut herbivores with any physical or microbial advantage.

The woodrats in our study obtained over 20% of their digestible energy needs from fiber, which confirmed our model predictions and added another small mammal to the growing list of species shown to degrade structural carbohydrates (e.g., Keys and Van Soest 1970; Servello 1981; Hammond 1989). Despite the well-developed fermentation abilities of these herbivores, our model simulations predict that there are still fundamental physiological limits on the absolute fiber content of the diet. The lowest of the three curves in figure 4 illustrates this point, and our observation of food sorting may constitute evidence that smaller animals are forced to moderate their fiber intake (fig. 6). It is also possible, of course, that they sort simply because they can differentiate on a finer scale.

Field studies have not yet addressed the role of fiber in the energy budget of natural populations of small herbivores. Structural carbohydrates may become most important during times of the year when higher-quality food is not readily available or under particularly stressful conditions, as for example in a prolonged drought. In such circumstances, small herbivores are probably energy-limited, even with access to ubiquitous sources of low-quality forage. To investigate these ideas, we reran the model adjusting the metabolic rate to reflect increased demands. Reproduction, for example, has been reported to incur a 10%–70% rise in energy requirements (Grodzinski and Wunder 1975; McClure 1987). Using a 65% figure measured for *Neotoma floridana* (McClure 1987), we estimate that an animal weighing 157 g (the mean of woodrats in our empirical trial) would need to reduce fiber ingested from 38% to 24% to maintain constant fiber digestibility. Thus, our model suggests that reproduction by small herbivorous species may be seasonally restricted by dietary constraints.

Gross et al. (1985) have suggested that digestive restrictions limit the timing of reproduction in some small mammals. In *N. lepida*, breeding may be inhibited even during the normal reproductive season if perennial growth is curtailed by inadequate winter rains. Conversely, aseasonal reproduction has been reported only during extremely good environmental conditions (Kelly 1989, P. A. Kelly, personal communication; F. A. Smith, personal observation). Extremely high-fiber diets may not provide sufficient energy for reproduction and growth to occur, but they may permit survival to the next suitable breeding period.

SUMMARY

The allometry of metabolic rate versus body mass in mammals requires that smaller animals consume more digestible energy on a mass-specific basis than larger ones. Because gut volume is approximately isometric with body mass, smaller mammals must either achieve a greater throughput of digesta or consume food that is more digestible. This presents a special problem to herbivores, since their diets include large amounts of fiber. Plant fibers are refractory to enzymatic digestion and can be degraded only by symbiotic microorganisms in a suitable fermentation chamber. The degree of digestibility is directly related to chamber retention time, and increased throughput leads to decreased fermentation. Although this suggests that small herbivores cannot use high-fiber foods, laboratory studies have demonstrated that some small hindgut rodents (e.g., voles, woodrats) can survive on diets containing as much as 45%–50% plant fiber.

We have constructed a model of fiber digestion and energy utilization for mammalian herbivores that have hindgut fermentation chambers. The model takes into account the relationship between mass and metabolic rate, fermentation volume, and percentage dry matter in the fermentation chamber. Computer simulations allow prediction of fiber and dry matter digestibilities as a function of body size, energy demand, and diet. Our model suggests that hindgut fermenters can make economic use of fiber even at small body sizes, especially at moderate fiber levels. Model calculations were generally in agreement with literature data but underestimated capabilities of small mammals. This outcome may be a result of

natural selection acting on fermentation volume or surface area. In a related laboratory trial, members of the genus *Neotoma* obtained substantial digestible energy (21.3%) solely from microbial fermentation, with no apparent discernible sex or taxonomic group bias. We also found a tendency for the smaller animals in our study to significantly reduce the fiber content of their diet by food sorting, a behavior that may reflect energy limitations. In natural environments, energy restrictions imposed by dietary strategy may curtail reproduction.

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