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Scaling of digestive efficiency with body mass in *Neotoma*

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Summary

1. Previous authors have suggested that larger animals are more efficient at extracting energy and nutrients from food resources because of their more favourable metabolic rate to gut capacity ratio (MR/GC). For herbivores in particular, the utilization of low quality vegetation becomes progressively more difficult with decreasing size because of the time-dependent nature of the microbial fermentation of plant fibre.

2. The relationship between fibre digestibility, a measure of digestive efficiency important to herbivores, and body size was investigated for three species of *Neotoma*. Animals ranged in mass from 80 to 400 g. A diagram was constructed which reflected allometric predictions, but also incorporated several mediating factors, such as intake and food sorting behaviour. Because of the high correlations between the variables, path analysis was utilized to evaluate the relative importance of each factor in affecting fibre digestibility.

3. Overall, a low correlation (0.105) was found between fibre digestibility and body mass. Path analysis revealed that this low correlation could be partitioned into a relatively strong direct influence of body mass (0.761) and opposing indirect effects through intake and food sorting (−0.563 and −0.094, respectively).

4. While it is clear from the analysis that body mass is of critical importance in influencing fibre fermentation, actual ecological or evolutionary implications are more difficult to assess. It is plausible, for example, that the apparent propensity towards insular gigantism common among small herbivores is at least partially the result of selection acting on digestive efficiency.

Key-words: Fibre digestibility, herbivory, insular gigantism, *Neotoma*, path analysis

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Introduction

Models of energy use in herbivorous mammals uniformly predict size-dependent restrictions on forage utilization and assimilation (i.e. Mertens 1973; Demment 1983; Penry & Jumars 1987). Such predictions largely stem from the asymmetrical scaling of metabolic rate (MR) and gut capacity (GC) with body mass, which results in an unfavourable situation for small animals. Not only are mass specific metabolic rates greater at smaller sizes (Kleiber 1961) but also the isometry between gut capacity and mass means more energy is required per unit digestive system (Parra 1978; Demment 1982, 1983; Demment & Van Soest 1985). Consequently, small herbivores generally tend to have rapid food passage rates (Parra 1978; Demment 1982, 1983; Van Soest 1982; Demment & Van Soest 1985).

While high passage rates may not be a significant problem for some types of nutritional strategies, the microbial fermentation of plant fibre is largely dependent on the residence time and size of the fermentation chamber (e.g. Parra 1978; Van Soest 1982). Thus, in small herbivores, passage rates and the size of the digestive system may eventually limit the energy available from plant fermentation (Van Soest 1982). Reasoning along these lines has prompted speculation that an inverse relationship exists between forage quality and body mass. That is, as mass decreases, herbivores become progressively more selective in their choice of forage, picking items higher in nutritional quality that require less microbial fermentation (e.g. Bell 1970; Mertens 1973; Jarman & Sinclair 1979; Van Soest 1982; Crawley 1983; Demment 1983; Penry & Jumars 1987).

Allometry notwithstanding, highly refined fibre fermentation abilities are found in several genera of small mammals (e.g. Keys & Van Soest 1970; Servello 1981; Hammond 1989; Justice & Smith

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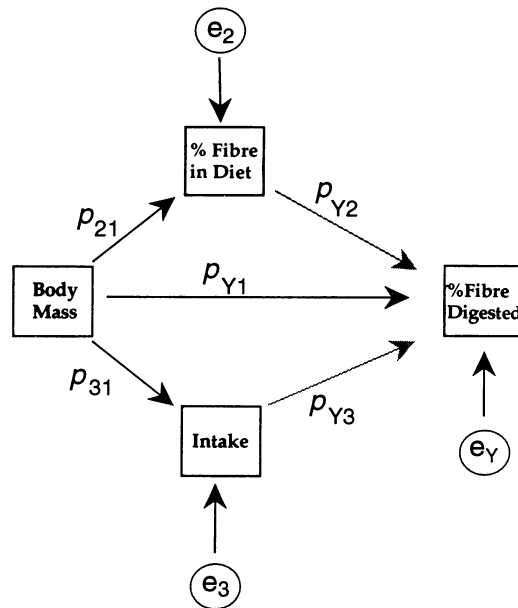


Fig. 1. Path diagram derived from the Justice & Smith model (1992) representing relationships between the three highly correlated independent variables (x_1 =body mass, x_2 =% fibre in diet and x_3 =intake) and the dependent variable (y =% fibre digested). Note that the diagram reduces to a standard multiple regression model when the paths p_{21} and p_{31} equal zero. All data were log transformed prior to analysis. The terms (e_2 , e_3 and e_y) represent unexplained variation.

1992), suggesting that physiological or morphological adaptations have occurred to increase the effective surface area and/or volume of the fermentation chamber, or to selectively retain food particles. In response to such observations, Justice & Smith (1992) recently developed a model of fibre digestion for hindgut herbivores that incorporates the basic MR/GC allometry and additional factors that may partially offset mechanical constraints on fibre digestion (Fig. 1). The model does predict digestive scaling, although calculations lead to higher estimates of fibre digestion abilities for small herbivores than expected solely on the basis of the standard MR/GC ratio.

The study reported here was designed to examine empirically the relationship between body mass and one measure of digestive efficiency unique to herbivores, fibre digestibility. Because recent work suggested that intake levels and food sorting were important mediating influences on fibre digestibility (e.g. Justice & Smith 1992), these factors were measured and incorporated into the analysis. Figure 1 illustrates the predicted relationships between body mass, fibre content of the diet, intake levels and fibre digestibility. Scaling of fibre digestibility is partially obscured by the two indirect negative paths. Larger animals can tolerate higher fibre diets ($+p_{21}$) but a higher overall intake of fibre reduces the proportionate digestibility of each particle ($-p_{Y2}$). Conversely,

sorting of food by small animals results in consumption of a lower fibre diet, increasing caecal retention time and elevating the digestibility of the remaining particles (Justice & Smith 1992). Likewise, intake rates increase with larger body mass ($+p_{31}$) but as they do, there is a corresponding rise in the amount of material entering the fermentation chamber and the overall digestibility of each particle is reduced ($-p_{Y3}$).

The diagram was analysed using path analysis (Sokal & Rohlf 1981; Pedhazur 1982), a linear regression technique originally developed by Sewall Wright (1921, 1934, 1960) for qualitative evaluation of causal models with highly correlated characters. Basically, the procedure decomposes the overall correlation between two variables into effects attributable to direct and indirect pathways. Fibre digestion abilities were determined by conducting a laboratory trial with *Neotoma* ranging in size from 80 to 400 g. Despite the limited mass range available, comparisons were restricted to a single genus to minimize the effect of divergent gastrointestinal morphology on digestive performance. Data derived from the empirical trial were subsequently used to calculate the magnitude and sign of the path coefficients and the influence of each path on fibre digestibility was evaluated.

Materials and methods

STUDY ANIMALS

The animals chosen bracket the range of body size found in the genus *Neotoma*, all of which consume a relatively low quality, bulky, herbivorous diet (e.g. Vorhies & Taylor 1940; Escherich 1981; Thompson 1982; F. A. Smith, unpublished observation) and share a common gastrointestinal morphology (Carleton 1980; F. A. Smith, unpublished observation). Fibre digestion abilities have previously been demonstrated for two of the three species (Justice & Smith 1992).

Adult woodrats were trapped during summer and autumn of 1988, and had been in captivity for 2–6 months by the initiation of the experiment. The largest species, *Neotoma cinerea* (150–500+ g), the Bushy-Tailed Woodrat, was trapped near Truckee and Silver Lake in the Sierra Nevada Mountain Range, California. *Neotoma albigula*, the White-Throated Woodrat (120–275 g), was obtained from the Sonoran Desert, approximately an hour east of Mesa, Arizona. Desert Woodrats, *N. lepida* (80–150 g), were trapped in the Mojave desert near Joshua Tree National Monument, California. During captivity, animals were fed a pelleted horse food (Bar-K) supplemented with occasional apple slices; both water and mineral block were provided *ad libitum*. Lights were set on a 12L/12D cycle and ambient temperature was maintained at approximately 20 °C.

The experimental diet was composed of 40.4% plant fibre. To minimize food sorting, it was constructed from alfalfa cubes ground through a 2-mm screen and combined with a 10% cornstarch binder. The mixture was then mechanically compressed into a round 'wafer' and dried overnight at 50 °C. Before distributing, the diet was allowed to equilibrate to laboratory temperature and humidity for 24 h. Sections removed from every fourth wafer were retained for moisture correction and analysis. Each wafer was partitioned among several different woodrats to average the effects of any irregularities in the formulation.

Animals were offered the experimental diet for a 6-day acclimation period before the actual digestion trial began. Both input and output of dry matter were then monitored for an additional 6 days. Woodrats were weighed every 2 days during the entire pretrial and experimental period. The total collection technique assumes that animals maintain body mass; thus four animals that gained >10% of body mass were eliminated from statistical analyses. Additionally, one

N. cinerea that maintained mass was later removed because calculated intake levels were only half the species average, suggesting an error in data entry (Grubb's test for outliers, $P < 0.005$).

SAMPLE ANALYSIS

Discarded food (orts) and faecal pellets (output) were oven dried at 50 °C, stored overnight and weighed. Apparent dry matter and cell wall digestibilities were calculated as [intake (g) – output (g)]/intake (g), with values corrected for moisture content. Aliquots were chemically analysed for fibre content following the neutral detergent method of Goering & Van Soest (1970), as modified by Robertson & Van Soest (1981). Discarded food was analysed separately to determine the degree of sorting performed by the individual animals and to correct for actual consumption of plant fibre. All chemical analyses were conducted in triplicate and mean values for each individual were used in statistical procedures.

Results

DIGESTION TRIAL

Results are reported in Table 1. Two-way analysis of covariance was conducted on each digestive variable to examine the effects of species and sex on performance after removal of body mass (Table 2). In general, transformation of the data was not required because they did not violate assumptions of normality or homoscedasticity. Sex had no significant effect on any factor and no interactions between species and sex were detected ($P > 0.2$, Table 2). Accordingly, one-way ANCOVAs were conducted on the pooled data to increase sample sizes.

Species effects were found for two factors relating to food sorting, with both the fibre content and production of orts (discarded food) differing significantly (Table 2). A multiple range test indicated that this was the result of greater discrimination on the part of *N. lepida* and *N. albigula*, which discarded more fibre than did *N. cinerea*, the largest species (Scheffe procedure, $P < 0.05$).

The variation in fibre digestion ability found among species stems largely from much lower values for *N. albigula*, and, consequently, lower realized dry matter digestibility (Table 2). The effect was not observed in previous empirical work (Justice & Smith 1992) and it is unclear whether it can be attributed to habitat specialization or some unknown physiological feature.

Although *N. lepida* did lose significantly more mass during the experimental regime than either *N. cinerea* or *N. albigula* (Table 2), the difference constituted just 2.0% of total body mass.

Table 1. Experimental results. Samples sizes are given below species name. Means \pm 1 SD

Variable	<i>N. lepida</i> (14)	<i>N. albigula</i> (10)	<i>N. cinerea</i> (12)	Average (36)
Body mass (g)	110 \pm 19.3	196 \pm 46.1	240 \pm 62.1	176 \pm 70.5
Change in mass (g)	-2 \pm 1.6	0.7 \pm 2.6	-1 \pm 4.1	1 \pm 6.7
Orts (g day ⁻¹)	2.2 \pm 2.4	1.4 \pm 0.5	4.3 \pm 3.3	2.8 \pm 2.7
Intake (g day ⁻¹)	10.6 \pm 1.48	14.9 \pm 2.77	15.3 \pm 3.19	13.4 \pm 3.32
Scats (g day ⁻¹)	4.2 \pm 0.81	6.3 \pm 1.19	6.0 \pm 1.31	5.4 \pm 1.46
Fibre in scats (%)	69.5 \pm 1.65	69.7 \pm 1.53	68.7 \pm 1.16	69.3 \pm 1.53
Fibre in orts (%)	43.3 \pm 1.69	43.0 \pm 1.13	41.7 \pm 1.27	42.7 \pm 1.58
Fibre eaten (%)	39.8 \pm 0.60	40.2 \pm 0.12	40.0 \pm 0.62	40.0 \pm 0.54
Dry matter digestibility	59.9 \pm 1.41	57.9 \pm 1.74	60.3 \pm 2.89	59.5 \pm 2.06
Total fibre digested (%)	29.8 \pm 2.64	26.9 \pm 3.52	32.0 \pm 4.30	29.8 \pm 3.51
Digestible energy from fibre (kcal day ⁻¹)	19.7 \pm 1.49	18.6 \pm 1.99	21.1 \pm 1.87	19.9 \pm 1.77

Table 2. Results of two-way analysis of covariance. Values given are the significance levels of each dependent variable (species and sex) after removal of the mass covariate. ^aSignificant at the $P < 0.05$ level in a one-way analysis of covariance (with sexes pooled)

Variable	Mass	Species	Sex	Sex \times Spp
Mass change (g)	0.589	0.077 ^a	0.980	0.613
Ort Production (g day ⁻¹)	0.677	0.101 ^a	0.707	0.357
Intake (g day ⁻¹)	<0.001	0.305	0.699	0.366
Scats (g day ⁻¹)	<0.001	0.079	0.506	0.422
Fibre in scats (%)	0.771	0.165	0.402	0.375
Fibre in orts (%)	0.180	0.274 ^a	0.309	0.449
Fibre eaten (%)	0.194	0.417	0.468	0.364
Dry matter digestibility (%)	0.739	0.047	0.317	0.956
Total fibre digested (%)	0.416	0.033	0.620	0.822
Digestible energy from fibre (%)	0.274	0.045	0.837	0.627

It should be noted that overall, the woodrats in the present study digested ~30% of the total fibre in the experimental diet. A distinction is made here between total and available fibre because as much as 49% of alfalfa fibre binds so tightly within the cell-wall matrix that it is essentially refractory even to the most cellulolytic microflora (Van Soest 1982). The animals thus fermented approximately 57% of the potentially available fibre — a value that constitutes a significant energetic benefit (~20% digestible energy; Table 1).

FOOD SORTING

The selective feeding observed by Justice & Smith (1992) led to significantly lower fibre consumption for smaller animals. This occurred despite homogenization and compression of the experimental diet to discourage sorting, and emphasizes the importance of analysing discarded food particles. Accordingly, in this study, neutral detergent analysis was conducted on ort samples, permitting calculation of actual fibre intake. The fibre content of discarded food particles differed significantly among species, with the two smaller species rejecting more fibrous particles (Table 2). The logarithmic regression of dietary fibre intake with body mass, however, proved to be of marginal significance ($P \sim 0.057$, Table 3).

REPEATABILITY OF SAMPLE ANALYSES

Variation in fibre digestion abilities among individual woodrats was greater than expected and suggested the possibility of irregularities in experimental technique. Errors could have occurred on several levels; in the collection and calculation of intake and output (scat production) values, for example, and also in the chemical analyses. To address the former issue, intake was regressed against output, and yielded an $r^2 = 0.949$, with $P < 0.0001$. Chemical analyses were run in triplicate and thus it was also possible to examine the variation between samples for each individual. Nested one-way ANOVAS were conducted to partition the variation for both scat and ort samples. Over 99.8% of the variation in the scat analyses was attributable to differences between individuals, with the remainder (0.2%) owing to sample technique. The

discarded food was more difficult to homogenize than the scats but nonetheless, the majority of the variation (66.1%) was between individuals with only 33.9% among samples. Thus, the high amount of variation found between animals is a real effect of potential ecological significance and not an artefact of methodology or sampling technique.

DIGESTIVE SCALING

In Fig. 1, the path coefficients between the dependent and independent variables (p_{yx}) are equivalent to the standardized partial regression coefficients (β_{yx}) and were calculated from

$$\beta = \mathbf{R}^{-1} \mathbf{r} \quad \text{eqn 1}$$

where \mathbf{R} represents the correlation matrix of independent (predictor) variables, and \mathbf{r} is the column vector of the correlations between the dependent and independent variables (Sokal & Rohlf 1981; Pedhazur 1982; Table 3). Because the paths from x_1 to x_2 and x_1 to x_3 are dependent only on a single cause and the residual error terms, they simplify to the zero-order correlations r_{12} and r_{13} . Thus, decomposition of the overall correlation between body mass and fibre digested is relatively straightforward and yields the following equation:

$$r_{1y} = p_{y1} + p_{21}p_{y2} + p_{31}p_{y3} \quad \text{eqn 2}$$

where p_{y1} represents the direct path from mass to fibre digested, $p_{21}p_{y2}$ the indirect path through fibre content of the diet and $p_{31}p_{y3}$ the indirect path through intake level. The pairwise relationships between the independent variables are illustrated in Fig. 2 and regressions of the dependent variable on the three independent variables are shown in Fig. 3. Replacing the path coefficients with calculated values (Table 3) yields:

$$r_{1y} = 0.761 - 0.094 - 0.563 = 0.105. \quad \text{eqn 3}$$

Discussion

The low correlation found between body mass and fibre digested results from the summation of all connecting paths between the two variables (Wright 1921). Decomposition of the correlation reveals a strong direct effect of body mass, which is opposed by a large indirect effect through intake, and a weaker compound path through fibre content of the diet (Fig. 1). The indirect compound path through intake influences digestibility more strongly than does diet selection. It should be remembered, however, that the experimental diet was explicitly formulated to minimize sorting behaviour and this was apparently largely successful in preventing differential fibre

Table 3. Correlation matrix used in path analysis. Values above diagonal are correlation coefficients, those below are calculated path coefficients (see text)

Variable	x_1	x_2	x_3	Y
x_1 Body mass	----	0.281	0.844	0.105
x_2 Fibre in diet	0.281	----	0.058	-0.120
x_3 Intake	0.844	0.058	----	-0.024
Y Fibre digested	0.761	-0.334	-0.667	----

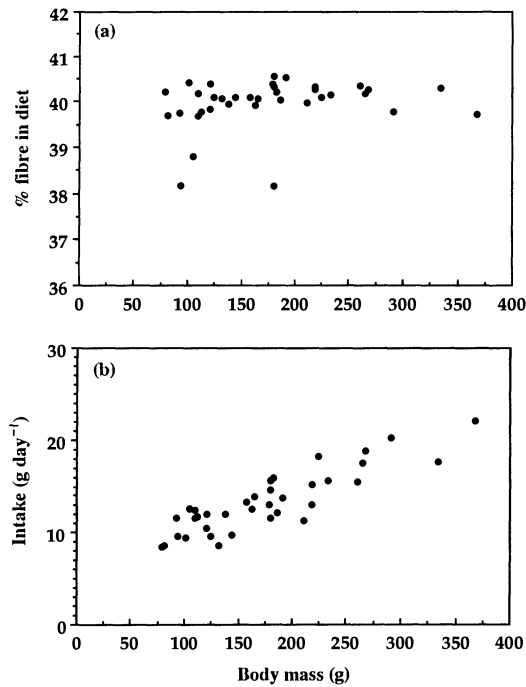


Fig. 2. Scatterplot of (a) % fibre in the diet (x_2) and (b) intake (x_3) against body mass (x_1). Logarithmic regressions are as follows: $\ln[\text{diet}] = 3.63(0.337) + 0.01(0.007) \ln[\text{mass}]$, $r^2 = 0.079$, NS; $\ln[\text{intake}] = -0.17(0.316) + 0.54(0.061) \ln[\text{mass}]$, $r^2 = 0.713$, $P < 0.0001$. Values are coefficient ± 1 SD of the estimate.

intakes. The path through x_2 may be of greater relative importance under natural conditions where smaller animals are free to exercise their ability to discriminate on a finer scale. Significance levels were not assigned to any of the paths depicted in Fig. 1; indeed the interpretation of path analysis is generally restricted to qualitative determination of the relative magnitudes of indirect effects in an *a priori* model (Wright 1921, 1934, 1960).

The pairwise relationships between body mass and intake, and between body mass and dietary fibre content, are illustrated in Fig. 3. It is interesting that although a given univariate regression may not be significant taken singly (e.g. Fig. 3c), the overall path contributes substantially because of strong multicollinearity with mass (Fig. 2b). Thus, a relationship that appears to be of no importance in a two-dimensional analysis may actually be a significant component of the more complicated multi-dimensional model. It is of course critical to identify clearly causal relationships at the outset; this observation should not be viewed as justification for inclusion of extraneous variables on an *ad hoc* basis. As in multiple regression, it is assumed that the path diagram represents causal relationships that are linear and additive. Because at least some of the variables yielded allometric regression equations, all data were log trans-

formed, as is routinely done for multiplicative models.

The signs of the path coefficients calculated on the basis of the empirical data match the *a priori* expectations of Justice & Smith (1992). The magnitudes are somewhat more difficult to assess. Results from the digestion trial were compared with the qualitative estimates of the MR/GC ratio and with values generated by the hindgut fermentation model (Table 4). Both suggest scaling effects, but of somewhat different magnitude. For example, although the MR/GC ratio suggests a roughly 27% decrease in digestive abilities between the smallest and largest animals in the study (*N. lepida* and *N. cinerea*, respectively), the value from the Justice-Smith model is approximately 12% [i.e. $1 - (26.7/30.3)$; Table 4]. Fibre digestibilities of *N. cinerea* and *N. albigula* did not differ signif-

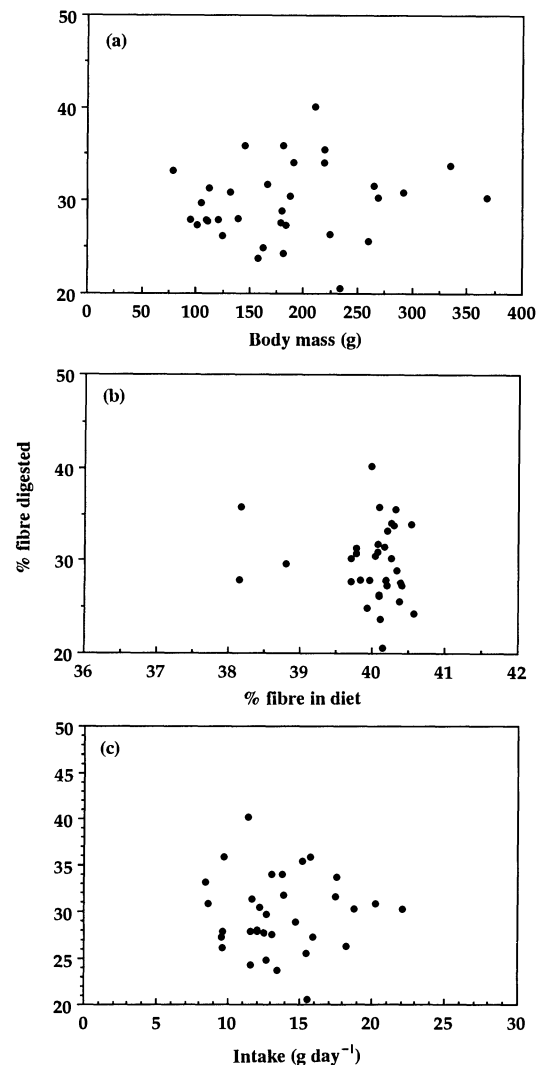


Fig. 3. Scatterplot of % fibre digested (y) vs (a) body mass (x_1), (b) % fibre in the diet (x_2), and (c) intake (x_3). Logarithmic regressions are as follows: $\ln[\text{fibre digested}] = 3.19(0.337) + 0.04(0.065) \ln[\text{mass}]$, $r^2 = 0.011$, NS; $\ln[\text{fibre digested}] = 3.73(0.062) - 0.012(0.018) \ln[\text{fibre in diet}]$, $r^2 = 0.014$, NS; $\ln[\text{fibre digested}] = 2.72(1.056) - 0.041(0.312) \ln[\text{intake}]$, $r^2 = 0.001$, NS.

icantly from predicted values but *N. lepida* did ferment more fibre than predicted (Table 4). Perhaps additional physiological or morphological adaptations have occurred in the smaller animals that are not fully incorporated into the Justice-Smith model.

One motivation for the work described here has been the numerous accounts of body size variation among insular mammals (e.g. Foster 1964; Sondaar 1977; Lawlor 1982). Numerous workers have suggested that observed trends are somehow related to trophic level, with carnivores, ungulates and insectivores decreasing and small herbivorous rodents increasing in size (Foster 1964; Van Valen 1973; Sondaar 1977; Case 1978; Lawlor 1982; Smith 1992). The apparent common evolutionary response of small herbivores to isolation on islands suggested to Smith (1991, 1992) an underlying mechanism. She postulated that large size could be advantageous if it allows more energy and nutrients to be extracted from plant materials (see also Brown & Maurer 1989), and if it is not selected against by predators. Predation has often been implicated as a potential selective agent acting against large size in rodent species (Falconer 1953; Corbet 1961; Kurten 1971; Bourliere 1975; Sondaar 1977; Smith 1991, 1992). For *Neotoma* at least, gigantism only occurs on islands where predators are absent (Smith 1992). Although this study cannot directly address the phenomena of insular gigantism, I have demonstrated that body mass does strongly influence fibre digestion abilities in small herbivores, at least over the mass range tested. It is also true, however, that by moderating the diet selected and reducing the actual amount of fibre entering the fermentation chamber, animals can increase the digestibility of the remaining particles. It might be expected that larger size would be of greatest advantage in habitats where food resources are extremely coarse grained and their ability to discriminate on a fine scale is of little consequence.

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Table 4. Comparisons between mean fibre digestibilities obtained and values predicted by the model of Justice & Smith (1992). For each species, a two-tailed Wilcoxon’s signed-rank test was performed on individual values to determine whether they fell above or below those predicted. MR/GC ratio (in [kcal day⁻¹]/[g kg⁻¹]) is also shown and was calculated at the average mass of each species and standardized against *Neotoma cinerea*

Species	MR/GC	Fibre digestibility (%)		Significance level
		Actual	Predicted	
<i>N. lepida</i>	1.27	29.8	26.7	<i>P</i> <0.01
<i>N. albigula</i>	1.04	26.9	29.4	<i>P</i> ~0.06
<i>N. cinerea</i>	1.00	32.0	30.3	<i>P</i> ~0.10

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