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DIETARY AND DIGESTIVE CONSTRAINTS ON BASAL ENERGY METABOLISM IN A SMALL HERBIVOROUS RODENT¹

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Abstract. McNab (1986, 1988) has hypothesized that mammals using food with low energy content should exhibit basal metabolic rates (BMR) lower than those expected on the basis of their body mass (m_b). That is, those species that exploit food with low energy content and/or high cost of digestion tend to have low, mass-independent metabolic rates. To date there is not an experimental test of this pattern. The aim of this work was to examine experimentally the effect of diet quality on BMR, digestive efficiency, and the relationship between digestion and energy expenditure in a small herbivorous mammal. We used as a model the herbivorous caviomorph burrowing rodent *Octodon degus* (m_b , nearly 200 g), an inhabitant of semi-arid and mediterranean communities of northern and central Chile.

Individuals maintained during 27 wk with a diet high in dietary fiber showed significantly lower BMRs (28%) than those feeding on low fiber. Daily food intake and ingestion rates (energy and dry matter) of individuals under a high-fiber diet were significantly higher than animals maintained with a low-fiber diet. The same pattern was obtained for total feces production and rate of feces production. The total intake and rate of ingestion of proteins were not significantly different between treatments. However, a significantly higher amount of protein was excreted by the individuals exposed to a high-fiber diet. Apparent digestibility of dry matter, energy, and protein were consistently lower in individuals maintained with high fiber. However, nonsignificant differences were observed between gut contents in the two treatments ($P > .58$), but a significantly higher digesta turnover rate was observed in animals exposed to a high-fiber diet ($P < .05$). A significant correlation was found between digestibility and the basal metabolic rate of individuals ($r_s = 0.781$, $P < .01$), suggesting that elevated digestibilities on high-quality diets allow increased basal rates of metabolism. We suggest that, although small mammals like *degus* may select sparsely distributed plants of high quality in their habitat, their capability to drop their metabolic demands may help them meet their nutritional and energy requirements when nutritional conditions in the environment deteriorate.

Key words: basal metabolic rate; Chile; diet quality; digestive physiological ecology; herbivory; *Octodon degus*; small mammals.

INTRODUCTION

The efficiency of energy intake, processing, allocation, and expenditure is critical to the survival and ecological success of vertebrates (Karasov 1986, Kenagy 1987, Bozinovic 1992a). Nutrient turnover is directly related to the energy metabolism and the amount of food transported throughout the digestive tract. On the other hand, food quality and digestibility can affect the rate of metabolism (Batzli 1985).

McNab (1986, 1988) hypothesized that scaling of basal rate of metabolism (BMR) to body mass (m_b) is sensitive to ecological factors in mammals, such as dietary habits. Some of the mass-independent variation of the allometry between BMR and m_b cuts across phylogenetic relationships, and appears to be mainly

related to food habits (but see Hayssen and Lacy 1985, Elgar and Harvey 1987). McNab (1980) also postulated that under unlimited food availability, higher BMRs are correlated with augmented production rates. This hypothesis was experimentally supported by Derting (1989) at an intraspecific level in juvenile cotton rats.

Species that exploit food with low energy content and/or high cost of digestion appear to have low, mass-independent metabolic rates. Surprisingly, few studies have been conducted to test these generalizations. Results of the experimental effect of food quality on the level of metabolism in small mammals are, so far, contradictory. In fact, Choshniak and Yahav (1987) documented in the Levant vole (*Microtus guentieri*) a significant decrease in metabolic rate when exposed to low-quality diets. However, in the desert gerbil (*Meriones crassus*), no significant effect of experimental diet quality on the magnitude of the rate of oxygen consumption was detected. On the other hand, water voles (*Arvicola terrestris*) exposed to decreased food

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quality (higher dietary cellulose) increased their food intake and metabolic rate (Woodall 1989).

Theoretically, small mammals should show decreased energy expenditures and increased gut turnover time. This is because BMR scales with m_b to the 0.75 power (Kleiber 1961, Peters 1983, Calder 1984), whereas gut capacity (GC) scales isometrically with m_b (Parra 1978, Calder 1984, Batzli 1985, Hume 1989). Consequently the turnover of gut contents (T) should scale as the ratio of gut contents and metabolic rate, namely to body mass to the 0.25 power ($T = GC/BMR = m_b^{0.25}$). This equation predicts that smaller mammals retain food in the digestive tract for a shorter time than large ones (Demment and Van Soest 1985).

Small mammals have similar relative tract size but larger relative metabolic rate and faster gut turnover time. Brown and Nicoletto (1991) hypothesized that these physiological and allometric constraints force smaller mammals to select higher quality foods and to restrict their foraging to habitats where suitable food is available in sufficient supply (see also Batzli 1985).

However, recently Foley and Cork (1992) analyzed how far small herbivorous mammals can bend these allometric constraints. Some species of small mammals compensate for low-quality diets (fibrous diets) by a combination of digestive mechanisms that include: rapid turnover time of fibrous food, changes in gut capacity, and increased nutrient uptake by the small intestine (see Myrcha 1964, 1965, Sibly 1981, Gross et al. 1985, Karasov 1986, Green and Millar 1987, Bozinovic et al. 1988, 1990, Karasov and Diamond 1988, Bozinovic and Iturri 1991, Hammond and Wunder 1991, Foley and Cork 1992).

The aim of this work was to examine experimentally the effect of diet quality on the basal metabolic rate, digestive efficiency and the relationship between digestive performance and energy expenditure in small herbivorous mammals. We used as a model the herbivorous, caviomorph, burrowing rodent *Octodon degus* (degus), an inhabitant of semi-arid and mediterranean communities of northern and central Chile. *Octodon degus* is the most broadly distributed rodent of the genus *Octodon*. Degus live in open scrubs subjected to summer droughts. Geographical and seasonal dietary differences in the relative proportions of shrub, grass foliage, and seed occur between localities. At most localities degus feed primarily on shrub foliage, seeds, and conductive tissue. In mediterranean environments they feed on forb and grass foliage and seeds. Thus, this species experiences spatial and temporal changes in the availability of water, fiber, and nutrients in its food (Meserve 1981, Meserve et al. 1983, 1984). However, when *O. degus* is experimentally exposed to new or mature leaves of different species of the Chilean matorral shrubs (*Colliguaya odorifera*, *Kageneckia oblonga*, and *Quillaja saponaria*), it prefers new rather than mature leaves and does not discriminate between different shrub species (Simonetti and Montenegro 1981).

Because food quality requirements are determined partly by metabolic rate (Brown and Nicoletto 1991), we can predict that, when *O. degus* is exposed to low-quality food in its habitat (temporal nutritional bottleneck, sensu Karasov 1989), a decrease in the rate of metabolism should occur. However, as Justice and Smith (1992) pointed out, small mammalian herbivores may compensate for a dilution of food energy (high dietary fiber) by changes in rates of intake, to maintain a constant intake of digestible metabolizable energy. Here we examine how a small herbivorous endotherm copes with possible constraints imposed by an energy-poor, high-fiber diet, and the consequences (if any) of these constraints on its basal rate of metabolism.

MATERIAL AND METHODS

Animal capture and care

Rodents (initial mean body mass [m_b] = 200.8 ± 24.5 g [mean ± 1 SD]) were captured in the central Chile matorral at Quebrada de la Plata (70°50' W, 33°31' S) with medium-sized Sherman live traps (5.1 × 6.4 × 16.5 cm). The locality has the typical climate of the Chilean mediterranean region, with hot dry summers and cold rainy winters (di Castri and Hajek 1976). After capture, the animals (six females and six males—i.e., six animals per group) were maintained during 27 wk in an outdoor laboratory with natural photoperiod and ambient temperature in two large enclosures (115 × 65 × 80 cm) with water ad libitum. Animals were randomly assigned to two dietary groups of commercial food pellets. Group I was maintained with a high quality of food pellet (diet I = low-fiber) and group II with a low quality of food pellet (diet II = high fiber). Both pellets were analyzed at the Institute of Nutrition and Food Technology, Universidad de Chile, following the Proximal Chemical Analysis Methods (Horwitz 1980). Chemical composition of the diet I pellets was: dry matter = 91.67%, proteins (N × 6.25) = 22.85%, lipids = 7.81%, ash = 7.15%, neutral detergent fiber = 6.16%, non-nitrogenous elements = 47.70%, total energy content = 21.20 ± 0.40 kJ/g (mean ± 1 SD, $n = 5$). The chemical composition of diet II pellets was: dry matter = 89.7%, proteins (N × 6.25) = 18.59%, lipids = 4.53%, ash = 9.86%, neutral detergent fiber = 15.54%, non-nitrogenous elements = 41.18%, total energy content = 19.17 ± 0.51 kJ/g ($n = 5$).

Basal metabolic rate

The basal rate of metabolism (BMR) was individually recorded by measurements of oxygen consumption in metabolic chambers at 30°C, a temperature within the thermoneutral zone of this species (Rosenmann 1977), using a computerized, closed, automatic system based on the design of Morrison (1951). CO₂ and H₂O in the metabolic chamber were absorbed with BaOH and CaCl₂, respectively. Ambient temperature was controlled in a thermoregulated bath. Because *Oc-*

TABLE 1. Effect of two experimental diets on the basal metabolic rate in *Octodon degus* ($\bar{X} \pm 1$ SD). BMR = basal metabolic rate, m_b = body mass.

	High fiber	Low fiber	P
Number of animals	6	6	
Body mass (g)	206.4 \pm 24.0	229.2 \pm 26.7	>.208
Basal rate of metabolism (J · g ⁻¹ · h ⁻¹)			
at time = 0 wk	17.15 \pm 3.03	16.55 \pm 1.41	>.900
at time = 27 wk	9.48 \pm 1.61	13.12 \pm 0.61	<.020
BMR/29.87 $m_b^{-0.201}$ (%)	92.77 \pm 11.11	130.10 \pm 5.92	<.040

odon degus is a diurnal rodent, each measurement was conducted during 2–3 h in post-absorptive individuals during the resting phase of their activity cycle (night-time between 2100 and 0100) following the same methodology reported in Bozinovic (1992b). Body mass \pm 0.1 g was recorded before and after each measurement of oxygen consumption. Oxygen consumption values were obtained from the average of the two minimal periods of each run lasting \approx 5 min. Animals were measured within the 1st wk after capture (time = 0) and after 27 wk of treatment with both diets. BMR was estimated from the mean values of oxygen consumption. Observed BMR (in joules per gram per hour) was compared against the standard BMR values predicted for small burrowing grazers (McNab 1988)—i.e., BMR = 29.87 $m_b^{-0.201}$.

Nutritional analysis

During nutritional experiments, individuals were kept in metabolic cages with metal trays underneath to collect feces and channel urine into 25-mL test tubes. Water was provided ad libitum. At week 27, and during three consecutive days, we conducted feeding trials offering the same amount of food, and collecting feces and remaining food. Each day the collected feces and rejected food were weighed and stored, after drying at 60°C. Energy content was determined in a Parr 1261 computerized calorimeter. Two replicates were expressed ash-free, and considered reliable when the difference between two measurements was <1%. Total protein in food and feces was determined in our laboratory using a simplification of the protein assay method of Lowry (Peterson 1977). Apparent digestibility, defined as the percentage of matter, energy, or nutrients consumed that is absorbed by the body, was calculated for dry matter, energy, and proteins, as: $[(Q_i - Q_e)/Q_i] \times 100\%$, where Q_i = daily rate of food intake, and Q_e = daily rate of feces production. Digestibility is termed “apparent” because this method underestimates digestive efficiency by the contribution of metabolic wastes, nonabsorbed secretions of the digestive system, and microorganisms. All values of ingestion and egestion were expressed ash-free.

Gut turnover time (T), defined as the time (in hours) required to process the gut volume resulting from the ingestion of one unit of food, was calculated according to Penry and Jumars (1987) using the relationship T

= GC/ Q_i , where GC = total mass content of the gut (in grams), and Q_i = food intake or mass flow rate (in grams per hour), (see Van Soest 1982, Hammond and Wunder 1991). To measure Q_i and GC, two groups of five animals previously acclimated with both experimental diets during 28 wk were maintained during 6 d to conduct feeding trials offering the same amount of food, and collecting the feces and remaining food; with these data we calculated Q_i . After these experiments the animals were killed at same time and day by cervical dislocation and the gut was dissected. From the difference of the wet mass of the total digestive tract, with and without contents, we calculated the mass contents of the gut. The masses of tissues, previously dried with laboratory towels, were measured to within \pm 0.0001 g on an AND analytical balance (A and D Company Limited, Tokyo, Japan); see Bozinovic et al. (1990), Hammond and Wunder (1991) for methodological details.

Statistical analyses

The significance of the effect of diet quality on the basal metabolic rate and nutritional variables was assessed by nonparametric statistics. Comparisons of two samples were conducted by rank tests (Wilcoxon rank-sum test) and correlations by Spearman rank correlations (Steel and Torrie 1985). Results are given as means \pm 1 SD.

RESULTS

Basal metabolic rate

Body mass (m_b) did not differ significantly between groups ($Z = 1.258$, $P > .208$; Table 1). The basal rate of metabolism was practically the same at time 0 between the two groups ($Z = 0.0001$, $P > .900$; Table 1). The treatments after 27 wk, however, resulted in significantly different BMRs among groups ($Z = 2.097$, $P < .04$; Table 1). As predicted, individuals maintained on higher dietary fiber showed significantly lower BMRs than those feeding on high-quality food. Thus, the metabolic rate was 28% higher under the low-fiber condition.

At 27 wk, the observed BMR of group II (low-quality food) did not differ statistically from the predicted BMR value based on m_b ($Z = 0.839$, $P > .402$ —i.e., 92.77% of expected BMR). However, the individuals maintained on high-quality food (low fiber) showed a sig-

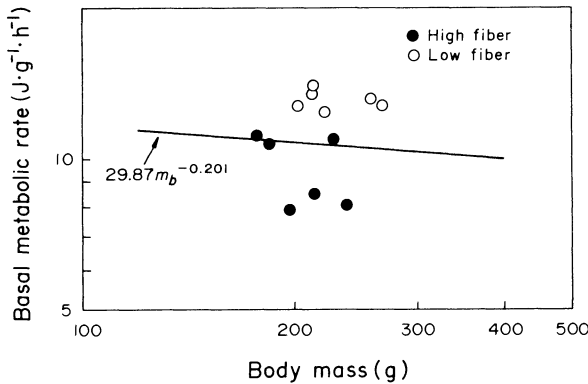


FIG. 1. Relationship between basal metabolic rate and body mass in individuals of *Octodon degus* maintained with two experimental diets at a site in central Chile. The line represents the expected basal metabolic rate for burrowing grazer rodents based on body mass (McNab 1988). Each point represents one individual.

nificantly higher-than-expected BMR ($Z = 2.097$, $P < .036$ —i.e., 130.10% of expected BMR, Fig. 1).

Food intake and excretion

Daily total food intake and ingestion rates (energy and dry matter) of individuals under a high-fiber diet were significantly higher than for animals maintained on a low-fiber diet (Z varies between 2.002 and 2.322, whilst the highest P value was $< .045$; Table 2). In general, total food intake and rate of ingestion were nearly 30% higher when animals were exposed to a high-fiber diet (Table 2). The same pattern was obtained for total feces production and rate of feces production; in all cases individuals from the group II exhibited a significantly high production of feces ($Z = 2.802$ for all cases; Table 2).

The total intake and rate of ingestion of protein were not significantly different between treatments ($Z = 0.319$ in both cases, $P > .749$; Table 2). However, a significantly higher amount of protein ($Z = 2.673$ for mg/d, and $Z = 2.025$ for $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$; Table 2) was excreted by the individuals exposed to a high-fiber diet (a 56.4 to 60.0% increased excretion). Thus, consumption of high-fiber diets by individuals results in the excretion of large amounts of feces (i.e., low digestibility, see below). For the nitrogen and protein budget, an intake of higher dietary concentration of fiber may increase endogenous fecal protein losses (Table 2).

Apparent digestibility

Comparing between diets, dry matter, energy, and protein apparent digestibility were consistently lower in individuals maintained with high fiber ($Z = 2.802$, 2.807, and 2.452 respectively; Table 2). Apparent digestibility varied as a function of individual variability and diet quality, between 62.7% and 92.3%. A mean reduction of 17.2% in digestibility was observed in all cases (dry matter, energy, and proteins) when animals were fed low-quality diets. By correlating individual digestibility with individual basal metabolic rate, a significant correlation between the two variables was observed ($r_s = 0.781$, $P < .01$; Fig. 2), suggesting that elevation of digestibilities by the effect of diet type may consequently produce increased basal rates of energy metabolism.

Gut mass contents and turnover time

Comparing among dietary groups, gut mass content was not significantly different between treatments—i.e., 34.89 ± 9.67 g under the high-fiber condition and 37.37 ± 3.99 g in animals fed with the low-fiber diet ($Z = 0.539$, $P > .589$). However, when we compared

TABLE 2. Intake and digestive efficiency of two experimental diets by *Octodon degus* ($\bar{X} \pm 1$ SD). Number of animals and body mass as in Table 1.

	High fiber	Low fiber	P
Intake			
(g/d)	17.00 ± 2.93	12.00 ± 1.69	$< .020$
($\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	3.50 ± 0.90	2.20 ± 0.40	$< .020$
(kJ/d)	325.86 ± 56.17	254.28 ± 35.89	$< .045$
($\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	67.11 ± 16.70	46.81 ± 8.87	$< .020$
Protein (mg/d)	384.85 ± 66.29	403.88 ± 62.73	$> .749$
Protein ($\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	0.08 ± 0.02	0.07 ± 0.01	$> .749$
Feces			
(g/d)	5.12 ± 1.68	1.44 ± 0.48	$< .005$
($\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	1.10 ± 0.40	0.30 ± 0.10	$< .005$
(kJ/d)	94.67 ± 30.78	24.23 ± 8.38	$< .005$
($\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	19.76 ± 8.04	4.47 ± 1.76	$< .005$
Protein (mg/d)	101.10 ± 39.69	44.05 ± 17.07	$< .028$
Protein ($\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	0.02 ± 0.01	0.008 ± 0.004	$< .043$
Apparent digestibility			
Dry matter (%)	70.60 ± 5.99	88.27 ± 2.39	$< .005$
Energy (%)	71.63 ± 5.93	90.68 ± 1.92	$< .005$
Proteins (%)	74.59 ± 6.68	89.32 ± 2.99	$< .001$

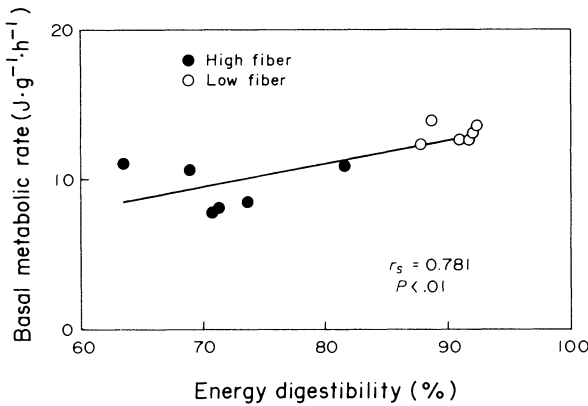


FIG. 2. Relationship between basal metabolic rate and apparent energy digestibility for *Octodon degus* maintained with high and low dietary fiber. Each point represents one individual.

individuals maintained with high and low dietary fiber, gut turnover time or throughput time was 36.5% significantly lower in individuals maintained with high fiber (46.18 ± 17.32 h under high fiber and 72.73 ± 15.39 h under low fiber; $Z = 1.918, P < .050$).

DISCUSSION

Much of the residual variation in basal rate of metabolism (BMR) among mammals is correlated with their ecological physiology of food exploitation and diet quality (McNab 1988). The mechanisms and processes underlying this statistical pattern are not clear but appear to be related to the concomitant effects of body size, quality of diets, energy expenditure, digestive strategies, and habitat conditions. Also, physiological and allometric constraints appear to force small mammals to select a higher quality of food and to restrict their foraging areas where food is abundant enough and suitable. Thus, the general explanation—that there is a digestive constraint on the metabolic rate set by the individual’s capacity to digest and assimilate energy and nutrients from the ingested food—appears to be experimentally supported here.

Diet, metabolic rate and digestive strategies

Octodon degus experienced lower total and mass-independent basal rates when fed an experimental high-fiber diet. We hypothesize that the low availability of energy from this diet and the lower metabolizable energy imposed by lower gut processing rates may limit BMR compared to animals eating a high-quality diet (see Fig. 2). The observed reduction in digestibility with increased dietary fiber may be associated with an increase in gut motility and a decrease in the turnover time of digesta. In fact, the decreased throughput time under a high-fiber dietary treatment is achieved with a high rate of food intake (Table 2). Therefore, less time might be available for digestion, including enzymatic action and nutrient uptake by the small in-

testine, to satisfy and maintain high levels of basal energy metabolism.

Digestibility depends on digestive strategies and design, but primarily on the food type itself (Grodzinski and Wunder 1975, Castro et al. 1989). Bulky food is less digestible than concentrated (low-fiber) food. In fact, Cork and Kenagy (1989) demonstrated that individuals of a mycophagous-forest-dwelling squirrel exhibited an almost minimal digestibility in order to maintain themselves when feeding on fungus. This example illustrates how small mammals may compensate for digestive and energy design constraints by behaviorally maximizing the yield of matter-to-energy in relation of the energy cost of foraging when energy-poor food is abundant in the environment.

Animals with diminished digestibility and increased digesta transit times may compensate with high food intake, as pointed out by Cork and Foley (1991). In other words, diets that have poor nutritional/energy contents have to be consumed in higher amounts to permit normal and/or higher magnitudes of basal rates. However, a high overall intake of fibrous diets to meet metabolic requirements may increase endogenous fecal protein losses and trade off the protein budget (Table 2). Also, the volume of food that can be consumed appears to be structurally constrained by the volume of the alimentary canal. In fact, we obtained no significant change in mass contents of the digestive tract between individuals of the two dietary groups (gut content is significantly correlated with gut volume in herbivores, Demment and Van Soest 1985). Nevertheless, some species of microtine rodents are able to exploit highly fibrous diets, but they possess specialized mechanisms of digesta separation in the hindgut (Batzli 1985), and some are caecotrophic (Kenagy and Hoyt 1980).

The response of *degus* to declining digestibility was a significantly ($r_s = -0.944, P < .002$) increased dry-matter intake (Fig. 3), and increased energy intake ($r_s = -0.902, P < .0030$; Fig. 4), to meet their metabolic

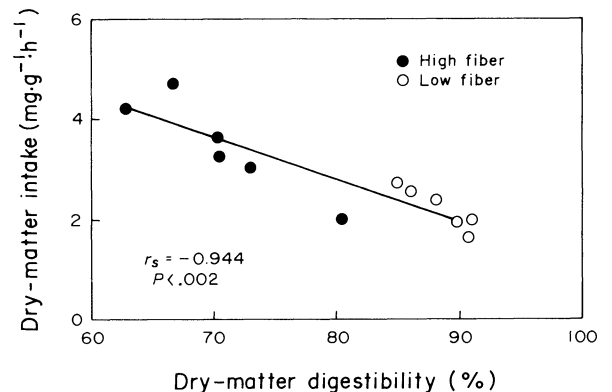


FIG. 3. Intake of dry matter and dry-matter digestibility by *Octodon degus* in relation to diet quality. The line represents the significant correlation between the two variables. Each point represents one individual.

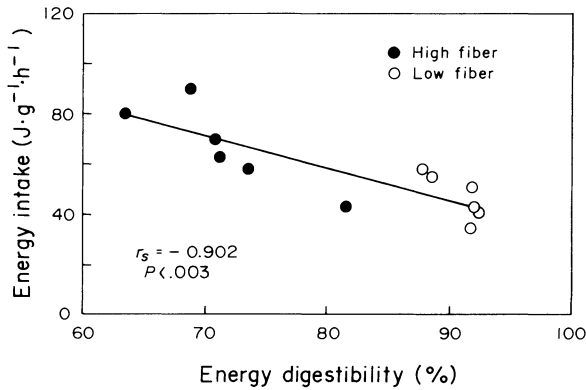


FIG. 4. Intake of energy and energy digestibility by *Octodon degus* in relation to diet quality. The line represents the significant correlation between the two variables. Each point represents one individual.

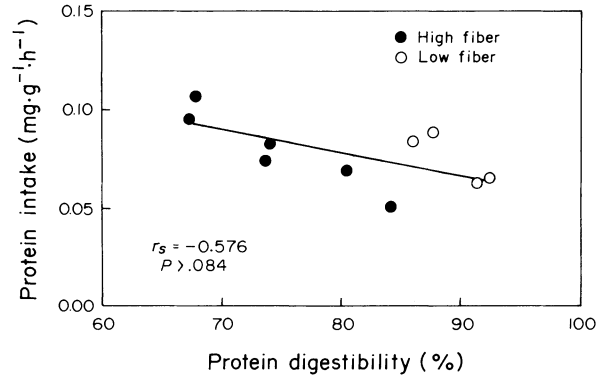


FIG. 5. Intake of protein and protein digestibility by *Octodon degus* in relation to diet quality. Only in four individuals maintained with low-fiber diets did we obtain enough samples of feces for the protein determinations. The line represents the correlation between the two variables.

requirements. However, protein intake was not correlated with protein digestibility ($r_s = -0.576$, $P > .084$; Fig. 5), perhaps as a consequence of an equivalent protein intake between treatments, but a higher fecal loss of proteins under a higher dietary fiber was observed (Table 2). Thus, in general, under our experimental conditions degus increased their food consumption (see Table 2), while basal rate of metabolism, apparent digestibility, and turnover time decreased with increased dietary fiber content.

Physiological responses can range from immediate (to an acute exposure) to acclimation (to chronic exposure) to developmental to genetic (evolutionary) change. The differences in basal metabolism documented by McNab (1986, 1988) were interspecific—i.e., apparent evolutionary adaptation to diet. Even the present study deals with a relatively short-term physiological shift at an interspecific level; this particular case could be used to explain in part the broadly documented statistical correlations between food habits and the mass-independent variations in the magnitude of basal rates of energy metabolism (McNab 1986, 1988 and references therein).

Among other factors related to the level of energy expenditure (e.g., climate, activity levels), the mass-independent level of basal rate of energy metabolism may have been influenced by selective pressures acting on structural and functional adjustments of the digestive tract.

However, even digestive capacities would at times constitute a bottleneck on the animal's acquisition of energy and matter (Toloza et al. 1991), and consequently set the level of metabolic rates. Small mammals can alternatively be viewed as organisms that may plastically lower their energy metabolism when the quality and/or availability of food in the environment is limited. Cork (*in press*) hypothesized that individuals may drop their basal rate of energy expenditure in order to use poor-quality food. That is, the basal rate of metabolism is lowered so that the poorer quality diet

(high fiber) can be exploited and utilized by small mammals. Based on allometric considerations, a lower rate of energy metabolism may enhance digestive efficiency by retaining food in the digestive tract, and consequently extract as much energy/nutrients as possible from each unit of food ingested. Also, during nutritional bottlenecks, small mammals may compensate for low-quality food by fine-tuned responses involving increases in gut volume and hence increases in food turnover time (Gross et al. 1985, Green and Millar 1987, Hammond and Wunder 1991, Bozinovic 1993). Nevertheless, although small mammals like degus may select sparsely distributed plants of high quality in their foraging habitat, their ability to drop their energy demands when nutritional conditions in the environment deteriorate may help them meet their nutritional and energy requirements. In short, lowering metabolic rate may also lead to enhanced digestive efficiency and may allow small mammals to maintain their energy/matter budget when food quality is poor in the environment.

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LITERATURE CITED

- Batzli, G. O. 1985. Nutrition. Pages 799–806 in R. H. Tammarin, editor. *Biology of new world Microtus*. Special Publication of the American Society of Mammalogists, Lawrence, Kansas, USA.
- Bozinovic, F. 1992a. Scaling of basal and maximum metabolic rate in rodents and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology* **65**: 921–932.

- . 1992b. Rate of basal metabolism of grazing rodents from different habitats. *Journal of Mammalogy* **73**:379–384.
- . 1993. Nutritional ecophysiology of the Andean mouse *Abrothrix andinus*: energy requirements, food quality and turnover time. *Comparative Biochemistry and Physiology A, Comparative Physiology* **104**:601–604.
- Bozinovic, F., and S. J. Iturri. 1991. Seasonal changes in glucose and tyrosine uptake of *Abrothrix andinus* (Cricetidae) inhabiting the Andes range. *Comparative Biochemistry and Physiology B. Comparative Physiology* **99**:437–440.
- Bozinovic, F., F. F. Novoa, and C. Veloso. 1990. Seasonal changes in energy expenditure and digestive tract of *Abrothrix andinus* (Cricetidae) in the Andes range. *Physiological Zoology* **63**:1216–1231.
- Bozinovic, F., C. Veloso, and M. Rosenmann. 1988. Cambios del tracto digestivo de *Abrothrix andinus* (Cricetidae): efecto de la calidad de dieta y requerimientos de energía. *Revista Chilena de Historia Natural* **61**:245–251.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist* **138**:1478–1512.
- Calder, W. A., III. 1984. Size, function and life history. Harvard University Press, Cambridge, Massachusetts, USA.
- Castro, G. C., N. Stoyan, and J. P. Myers. 1989. Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemistry and Physiology A, Comparative Physiology* **92**:271–278.
- Choshniak, I., and S. Yahav. 1987. Can desert rodents better utilize low quality roughage than their non-desert kindred? *Journal of Arid Environments* **12**:241–246.
- Cork, S. J. *In press*. Digestive constraints on dietary scope in small and moderately-small mammals: how much do we really understand? *In* D. Chivers and P. Langer, editors. *The digestive system in mammals: food, form and function*. Cambridge University Press, Cambridge, England.
- Cork, S. J., and W. J. Foley. 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forest. Pages 133–166 *in* R. T. Palo and C. T. Robbins, editors. *Plant defenses against mammalian herbivory*. CRC Press, Boca Raton, Florida, USA.
- Cork, S. J., and G. J. Kenagy. 1989. Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. *Ecology* **70**:577–586.
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *American Naturalist* **125**:641–672.
- Derting, T. L. 1989. Metabolism and food availability as regulators of production in juvenile cotton rats. *Ecology* **70**:587–595.
- di Castri, F., and E. Hajek. 1976. *Bioclimatología de Chile*. Editorial Universidad Católica, Santiago, Chile.
- Elgar, M. A., and P. H. Harvey. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Functional Ecology* **1**:25–44.
- Foley, W. J., and S. J. Cork. 1992. Use of fibrous diets by small herbivores: how far can the rules be “bent”? *Trends in Ecology and Evolution* **7**:159–162.
- Green, D. A., and J. S. Millar. 1987. Changes in gut dimensions and capacity of *Peromyscus maniculatus* relative to diet quality and energy needs. *Canadian Journal of Zoology* **65**:2159–2162.
- Grodzinski, W., and B. A. Wunder. 1975. Ecological energetics of small mammals. Pages 173–204 *in* F. B. Golley, K. Petruszewicz, and L. Ryszkowski, editors. *Small mammals: their productivity and population dynamics*. Cambridge University Press, Cambridge, England.
- Gross, J. E., Z. Wang, and B. A. Wunder. 1985. Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. *Journal of Mammalogy* **66**:661–667.
- Hammond, K. A., and B. A. Wunder. 1991. The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. *Physiological Zoology* **64**:541–567.
- Hayssen, V., and R. C. Lacy. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comparative Biochemistry and Physiology A, Comparative Physiology* **81**:741–754.
- Horwitz, W. 1980. Official methods of analysis. Association of Official Analytical Chemists. Washington, D.C., USA.
- Hume, I. D. 1989. Optimal digestive strategies in mammalian herbivores. *Physiological Zoology* **62**:1145–1163.
- Justice, K. E., and F. A. Smith. 1992. A model of dietary fiber utilization by small mammalian herbivores, with empirical results for *Neotoma*. *American Naturalist* **139**:398–416.
- Karasov, W. H. 1986. Energetics, physiology and vertebrate ecology. *Trends in Ecology and Evolution* **1**:101–104.
- . 1989. Nutritional bottleneck in a herbivore, the desert wood rat (*Neotoma lepida*). *Physiological Zoology* **62**:1351–1382.
- Karasov, W. H., and J. M. Diamond. 1988. Interplay between physiology and ecology in digestion. *BioScience* **38**:602–611.
- Kenagy, G. J. 1987. Energy allocation for reproduction in the golden-mantled ground squirrel. *Symposia of the Zoological Society of London* **57**:259–273.
- Kenagy, G. J., and D. F. Hoyt. 1980. Reingestion of feces in rodents and its daily rhythmicity. *Oecologia (Berlin)* **44**:403–409.
- Kleiber, M. 1961. *The fire of life*. John Wiley & Sons, New York, New York, USA.
- McNab, B. K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist* **130**:370–398.
- . 1986. The influence of food habits on the energetics of eutherian mammals. *Ecological Monographs* **56**:1–19.
- . 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *The Quarterly Review of Biology* **63**:25–54.
- Meserve, P. L. 1981. Trophic relationship among small mammals in a Chilean semiarid thorn scrub community. *Journal of Mammalogy* **62**:304–314.
- Meserve, P. L., R. E. Martin, and J. Rodriguez. 1983. Feeding ecology of two Chilean caviomorphs in a central mediterranean savanna. *Journal of Mammalogy* **64**:322–325.
- Meserve, P. L., R. E. Martin, and J. Rodriguez. 1984. Comparative ecology of the caviomorph *Octodon degus* in two Chilean mediterranean-type communities. *Revista Chilena de Historia Natural* **57**:79–89.
- Morrison, P. R. 1951. An automatic manometric respirometer. *Review of Scientific Instruments* **22**:264–267.
- Myrcha, A. 1964. Variations in the length and weight of the alimentary tract of *Clethrionomys glareolus* (Schreber, 1780). *Acta Theriologica* **10**:139–148.
- . 1965. Length and weight of the alimentary tract of *Apodemus flavicollis* (Melchior, 1834). *Acta Theriologica* **16**:225–228.
- Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 205–229 *in* G. G. Montgomery, editor. *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- Penry, D. L., and P. A. Jumars. 1987. Modeling animal guts as chemical reactors. *American Naturalist* **129**:69–96.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, England.
- Peterson, G. L. 1977. A simplification of the protein assay method of Lowry *et al.* which is more generally applicable. *Analytical Biochemistry* **83**:346–356.

- Rosenmann, M. 1977. Regulación térmica en *Octodon degus*. *Medio Ambiente (Chile)* **3**:127–131.
- Sibly, R. M. 1981. Strategies in digestion and defecation. Pages 109–139 in C. R. Townsend and P. Calow, editors. *Physiological ecology: an evolutionary approach to resource use*. Blackwell Scientific, Oxford, England.
- Simonetti, J. A., and G. Montenegro. 1981. Food preferences by *Octodon degus* (Rodentia Caviomorpha): their role in the Chilean matorral composition. *Oecologia (Berlin)* **51**: 189–190.
- Steel, R. G. D., and J. H. Torrie. 1985. *Bioestadística: principios y aplicaciones*. McGraw-Hill, Bogotá, Colombia.
- Tolosa, E. M., L. Mandy, and J. Diamond. 1991. Nutrient extraction by cold-exposed mice: a test of digestive safety margins. *American Journal of Physiology* **261**:G608–G620.
- Van Soest, P. J. 1982. *Nutritional ecology of the ruminant*. Durham and Downey, Portland, Oregon, USA.
- Woodall, P. F. 1989. The effects of increased dietary cellulose on the anatomy, physiology and behaviour of captive water voles, *Arvicola terrestris* (L.) (Rodentia: Microtinae). *Comparative Biochemistry and Physiology A, Comparative Physiology* **94**:615–621.