

# Fiber use and digestion in the herbivorous rodent *Octodon degus*: an analysis using chemical reactor theory

Uso de fibra y digestión en el roedor herbívoro *Octodon degus*: un análisis usando teoría de reactores químicos

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## ABSTRACT

Small herbivorous mammals compensate for high fiber food by "fine-tuned" responses involving increases in gut volume and hence increases in food turnover time and in the amount of energy obtained from fiber. By using models from chemical engineering adapted to digestion — *i.e.* chemical reactor theory — we attempt to understand the mechanisms of fiber hydrolysis and energy use as a function of the digestive design of *Octodon degus* a small herbivorous rodent. These objectives were conducted taking into account the biotic environment, and specifically seasonal changes in the intake of food differing in quality and fiber content. We postulated that during the environmental nutritional bottlenecks occurring in the dry season, *O. degus* may operate according to the principles of foraging and digestion theories. This small herbivorous seems to compensate for the low digestibility of high fiber food by increasing gut volume contents and hence increasing food turnover time. A significant quantity of its daily energy requirements is obtained from the digestion of fiber from plants, as observed from the pattern of fiber disappearance or reaction rate along the gut. The digestion and reaction rate of high dietary fiber food may involve the acid conditions of the stomach acting in concert with microbial cecum fermentation.

**Key words:** Foraging, digestion, small herbivore, reactor theory, *Octodon degus*

## RESUMEN

Los micromamíferos herbívoros que ingieren alimento con alto contenido de fibra compensan con respuestas finas que incluyen incrementos en el volumen del tracto digestivo, tiempo de retención del alimento y consecuentemente en la cantidad de energía obtenida del alimento rico en fibra. Usando modelos de ingeniería química aplicados a la digestión, — *i.e.* teoría de reactores químicos, intentamos comprender los mecanismos de obtención de energía a partir de fibras en función del diseño digestivo de un herbívoro pequeño (*Octodon degus*). Esto, en relación al ambiente biótico, y específicamente frente a los cambios estacionales en la ingesta de alimento con diferente calidad y contenido de fibras. Durante los cuellos de botella nutricionales de la estación seca, *O. degus* operaría según los principios de las teorías de forrajeo y digestión. Observamos que frente a la ingesta de alimento con alto contenido de fibra, este micromamífero compensa con un aumento en la cantidad de alimento transportado en el tracto digestivo y en el tiempo de retención del mismo. Basado en los patrones de tasa de reacción de fibra a lo largo del tracto digestivo, observamos que esta especie obtiene una significativa cantidad de energía de la digestión de las plantas ricas en fibra. La digestión y tasa de reacción de alimento rico en fibra se debería a las condiciones ácidas del estómago actuando junto a la fermentación bacteriana a nivel del ciego.

**Palabras claves:** Forrajeo, digestión, herbívoros pequeños, teoría de reactores, *Octodon degus*.

## INTRODUCTION

Complex polysaccharides such as cellulose, hemicellulose and lignin (fiber) are important plant structural constituents often reducing digestibility for vertebrate herbivores (Howe & Westley 1987). Since fiber-rich plant material is difficult to digest for small herbivorous endotherms, the success of energy transformation into maintenance, somatic and reproductive tissue probably depends on the interaction among plant chemical composition, food selection, food intake, and efficiency with

which food is digested and nutrients and energy are transformed and allocated (Milton 1979).

Using as a model the herbivorous caviomorph Octodontid rodent *Octodon degus*, (henceforth *degus*) an inhabitant of semi-arid and Mediterranean environments of northern and central Chile, Bozinovic (in press) demonstrated that when given a choice, *degus* minimized fiber (neutral detergent fiber = NDF) intake showing pronounced preferences for food containing low fiber. Because low fiber items are not available in the field during the dry season,

this author postulated that observations of degus feeding on grass containing a high percentage (nearly 60%) of NDF during summer time, compared to 37%-NDF during fall and winter, is more likely the consequence of necessity, than of choice.

During environmental nutritional bottlenecks, small herbivorous endotherms may operate according to the principles of foraging theory and digestion (Sibly 1981). Degus seems to compensate for the low digestibility of high fiber food by increasing gut volume content, because of changes in rates of food intake, and hence increasing in food turnover time. These digestive responses allow them to increase the amount of energy obtained from fiber (c.a. 40% of their daily energy expenditure), and to satisfy their maintenance energy costs during temporal exposures to different levels of fiber food (Veloso & Bozinovic 1993, Bozinovic in press). During the dry season, however, high fiber food does not provide enough energy for productive events, but allows survival until the next breeding season.

In short, small herbivorous mammals compensate for high fiber food by "fine-tuned" responses involving increases in gut volume and hence increases in food turnover time and in the amount of energy obtained from fiber (see Myrcha 1964, 1965, Sibly 1981, Gross *et al.* 1985, Green & Millar 1987, Karasov 1986, Karasov & Diamond 1988, Bozinovic *et al.* 1990, Bozinovic & Iturri 1991, Hammond & Wunder 1991, Foley & Cork 1992, Justice & Smith 1992, Derting & Bogue 1993). However, the particular digestive traits that determine such rate of fiber utilization are unknown. By using models from chemical engineering adapted to digestion, *i.e.* chemical reactor theory (see Penry & Jumars 1987, Martinez del Rio *et al.*, 1994), we attempt to understand the digestive mechanisms of fiber use as a function of the gut design of this small herbivorous. These objectives will be conducted within the framework of the biotic environment and specifically to seasonal changes in the intake of food differing in quality and fiber contents.

According to Penry & Jumars (1987), three types of reactor can be analogous to digestive organs, — batch reactors, continuous-flow stirred tank reactors (CSTR) and plug-flow reactors (PFR). In a batch reactor, reactants and reagents are mixed in a tank, and the concentration of reactants and products changes as a function of reaction time. In a CSTR model, reactants and reagents flow constantly in and out maintaining a constant concentration and a constant rate of reaction, being product and reaction rate functions that depend on the flow rate. Finally, in a PFR a steady state of gradient in the concentration of reagents, reactants, products and reaction rates occurs along the length of the reactor with a continuous constant flow. Theoretical models of optimal digestive design based on reactor theory and chemical composition of food have been applied in mammals (Alexander 1991, Hume & Sakagushi 1991, Martinez del Rio *et al.* 1994), birds (Martinez del Rio & Karasov 1990) and fishes (Horn & Messer 1992).

Using models of reactor theory applied to digestion and food quality, in this paper we examine how a small herbivorous endotherm copes with possible constraints imposed by two diets with contrasting fiber content. We conducted feeding trials offering two items with different fiber (cellulose) concentrations to determine the digestive mechanisms by which this small herbivorous is able to process fiber and obtain energy.

#### MATERIAL AND METHODS

Ten rodents of about one year old and an initial mean body mass ( $m_b$ ) of  $180.2 \pm 35.2$  g (mean  $\pm$  SD) were obtained from our colony. Animals were randomly assigned to two dietary groups. Powdered diets were prepared with the addition of cellulose (Sigma Chemical Co.) to commercial rabbit. Diets were analyzed for neutral detergent fiber (NDF or simply fiber, see Bjorndal & Bolten 1993). Protein content of the diets was also measured using a simplification of the method of Lowry (Peterson 1977).

Both groups (five animals each) were maintained with 35% and 57% of fiber respectively. The caloric content and chemical composition of the experimental diets are shown in Table 1. The pH values of both experimental diets were practically the same: 5.81 for the 57%-NDF and 5.80 for the 35%-NDF diets. Animals were maintained during five days in an outdoor laboratory with natural photoperiod and ambient temperature in two large enclosures (115 by 65 by 80 cm) with water and their experimental diets *ad libitum*, before the feeding trials were conducted.

During feeding trials, individuals were kept in individual metabolic cages with metal trays underneath to avoid contact with feces and urine. Water was provided *ad libitum*, photoperiod was L:D = 12:12 and ambient temperature was maintained at approximately 20 °C. During eight consecutive days, we conducted feeding trials offering the same amount of food, and collecting feces and orts. Each day, the rejected foods were weighed and stored after drying at 60 °C until constant weight to determine food intake.

After these measurements animals were killed at the same time of day by cervical dislocation and the gut was dissected. The digesta dry mass of each organ (stomach, anterior, medium and posterior small intestine, and caecum) was measured on an

analytical balance (AND ± 0.0001 g, see Bozinovic *et al.* (1990) and Hammond & Wunder (1991) for methodological details). Digesta dry samples were analyzed to determine NDF reaction rate (RNDF) in each portion of the digestive tract. Because the amount of digesta mass in different sections of the digestive tract was not sufficient for chemical analysis, pooled samples were analyzed. Thus, we obtained one value of RNDF by digestive section by treatment. To calculate RNDF in each digestive chamber standardized by a linear dimension (cm), the following equation was used (Alexander 1991), this formula show the amount of material degraded in each section of the digestive tract:

$$RNDF = -V_o [C_o - C_i] \text{ (mg NDF/cm h)}$$

where:

$V_o$  = flow rate of food (mg/cm h)

$C_o$  = NDF concentration of the material entering the reactor(mg/g)

$C_i$  = NDF concentration of the material leaving the reactor (mg/g)

To evaluate the effect of acidity as a mechanism for hydrolysis of dietary fiber (Horn & Messer 1992), the pH was measured in two sections of the stomach (cardiac and pyloric), the anterior, medium and posterior small intestine; and in two sections of the caecum, by using an Orion Research pHmeter SA-210 and an Orion microelectrode model 81-63. The significance of the effect of treatments was assessed by a Wilcoxon Mann Whitney test for a two-tailed hypothesis, and corrected for a small sample size (Siegel & Castellan 1988). Results are given as means ± 1 SD.

TABLE 1

Composition (%) and caloric contents (KJ/g) of the experimental diets ( $\bar{X} \pm SD$ ).  
Composición (%) y contenido calórico (KJ/g) de las dietas experimentales ( $\bar{X} \pm DS$ )

Composition	Low-Fiber (35%-NDF)	Medium-Fiber (57%-NDF)
Organic matter (%)	92.3 ± 2.8	95.2 ± 2.6
Neutral detergent		
Fiber (%)	35.0 ± 2.1	57.0 ± 3.0
Protein (%)	19.4 ± 0.3	8.5 ± 0.6
Caloric content		
(KJ/g)	16.96 ± 0.02	16.66 ± 0.01
pH	5.80 ± 0.01	5.81 ± 0.01

RESULTS

Body mass did not differ significantly between both groups (W = 23, P = 0.54, Table 2). Food ingestion rates (dry-matter) of individuals under both dietary treatments were also not significantly different (W = 23, P = 0.54, Table 2)

Total mass digesta contents of individuals maintained with a 57%-NDF was signi-

ificantly higher than in the group feeding on lower dietary fiber contents ( $W = 15$ ,  $P < 0.01$ , Table 2). A significantly higher amount of digesta mass in the ceacum of individuals maintained with higher levels of dietary fiber accounts for this difference ( $W = 15$ ,  $P < 0.01$ , Table 2). Digesta mass contents of the stomach and small intestine were not significantly different between both groups (see Table 2 for details).

Figure 1 shows the reaction rate of NDF. In individuals feeding the 35%-NDF diet, R<sub>NDF</sub> value was higher at the stomach level than in other digestive chambers. On the other hand, in animals maintained with 57%-NDF diet, R<sub>NDF</sub> was higher at the stomach and ceacum level than in other organs. R<sub>NDF</sub> was higher at the stomach level in the group maintained with 35%-NDF diet than in the 57%-NDF group, however, the R<sub>NDF</sub> of individuals feeding 57%-NDF was higher in the ceacum, being almost nil in the lower fiber group (Fig. 1)

The pH values of individuals from both treatments are shown in Table 3. In all cases stomach pH was acid, whilst small intestine and ceacum pH were neutral. In animals maintained with 35%-NDF, values of pH from cardiac and pyloric sections of the stomach were higher than in individuals feeding the 57%-NDF diet.

#### DISCUSSION

Chemical reactor theory applied to digestion can be used to analyze the design of the digestive tract as a function of food type, or to analyze the optimal chemical dietary composition as a function of a particular digestive design (Penry & Jumars 1987). In this paper, the first approach was conducted.

Alexander (1991) pointed out that the optimal digestive design of mammals feeding on food with a high concentration

TABLE 2

Body mass, intake and digesta mass contents in individuals maintained with two experimental diets. Asterisks (\*) represent significant differences ( $P < 0.05$ ) after the WilcoxonMann-Whitney test.

Masa corporal, ingesta y contenido del tracto digestivo de los individuos mantenidos con las dos dietas experimentales. Los asteriscos (\*) representan las diferencias significativas ( $P < 0.05$ ) obtenidas con la prueba de Wilcoxon Mann-Whitney.

Characteristics	Low-Fiber (35%-NDF)	Medium-Fiber (57%-NDF)
Number of individuals	5	5
Body mass (g)	196.1 ± 15.9	204.9 ± 8.1
Intake (g dry-matter/h)	0.88 ± 0.08	0.80 ± 0.13
Digesta Mass Contents (g)		
Stomach	0.68 ± 0.21	0.71 ± 0.42
Small Intestine		
Anterior	0.03 ± 0.01	0.03 ± 0.01
Medium	0.06 ± 0.02	0.09 ± 0.03
Posterior	0.12 ± 0.02	0.15 ± 0.05
Ceacum	1.04 ± 0.21	2.69 ± 0.38*
Total	1.93 ± 0.32	3.69 ± 0.51*

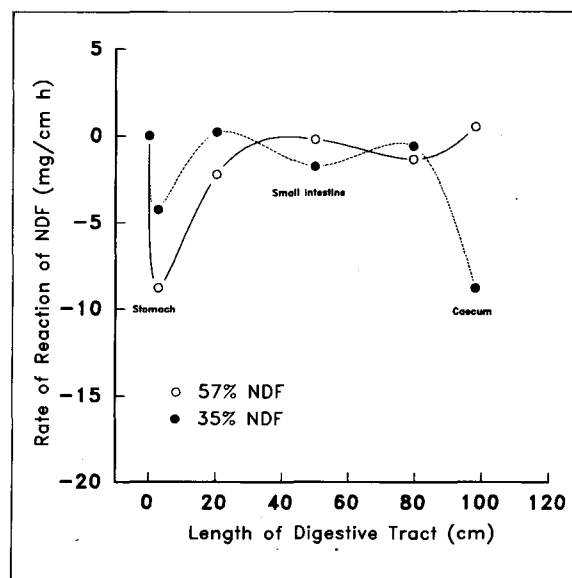


Fig. 1: Relationships between the rate of reaction of two different diets as a function of the length of the digestive tract of *Octodon degus*. 35%-NDF = diet prepared with a 35% of cellulose and measured as neutral detergent fiber; 57%-NDF = experimental diet with a 57% of neutral detergent fiber.

Relación entre la tasa de reacción de dos dietas artificiales a lo largo del tracto digestivo de *Octodon degus*. 35%-NDF = dieta preparada con 35% de celulosa y medida como fibra detergente neutro; 57%-NDF = dieta experimental con un 57% de fibra detergente neutro.

of material refractory to digestion, is a combination of two CSTR reactors. On the other hand, the expected optimal digestive design for mammals feeding on an intermediate diet quality is a PFR in series with a CSTR. For ceacum fermenters as *O. degus*, Hume (1989) postulated a digestive configuration containing a PFR (small intestine) followed in series by a modified CSTR (ceacum). Apparently, and based in our results, this design may be functionally modified by the chemical composition of the food.

Observing Fig. 1, Alexander's model appears to apply, *i.e.* a functional CSTR-PFR in series for the 35%-NDF diet and a CSTR-CSTR also in series for the 57%-NDF diet. Thus, a first CSTR (stomach) in both treatments can be explained because of acid lysis acting on dietary fiber. This mechanism has been documented as an important way of digestion of cell walls by herbivorous fish (Lobel 1981, Horn 1989). According to Horn & Messer (1992), the acid lysis and the autocatalytic reactions are more efficient in CSTR reactors because they operate at high concentrations, *i.e.* when the principal nutrient is the most abundant. Acid lysis operates in discrete and spherical stomach, with high concentrations of nutrients by unit of stomach area. The observed low pH values in the stomach (Table 3) may support this explanation. The different pH values observed in the stomach (cardiac zone, see Table 3) between treatments are probably a consequence of the different buffering chemical capacities of both diets. For the 57%-NDF diet, a second CSTR was observed (see Fig. 1). In this reactor the ingestion and egestion are mixed, allowing the maintenance of a microbial assemblage in such container, increasing the mean retention time of the particles in the reactor, and allowing a higher RNDP, and energy acquisition from high fiber food.

As we mentioned, during the environmental nutritional bottlenecks occurring in the dry season, degus may operate according to the principles of foraging theory (Stephens & Krebs 1986) and digestion theory (Sibly 1981, Penry & Jumars 1987). This small herbivorous seems to compensate for the

low digestibility of high fiber food by increasing gut volume contents and hence an increase in food turnover time. Thus in short, a significant quantity of its daily energy requirements is obtained from the digestion of fiber from plants, as observed from the pattern of NDF disappearance or reaction rate along the gut (Fig. 1). The digestion and reaction rate of high fiber food may involve the acid conditions of the stomach acting in concert with microbial ceacum fermentation.

Thus our observations of degus feeding on high fiber food suggest that feeding on low quality food is rather a necessity than a process of active choice (Bozinovic in press). Nevertheless, these small mammalian herbivores can bend (*sensu* Foley & Cork 1992); their design constraints, and compensate for low quality - high fiber food items by means of combination of physiological and anatomical digestive features that include increased in gut contents, mainly in the ceacum where the

TABLE 3

Values of pH of the digestive tract in individuals maintained with two experimental diets. Asterisks (\*) represent significant differences ( $P < 0.05$ ) after the Wilcoxon Mann-Whitney test.

Valores de pH del tracto digestivo de los individuos mantenidos con las dos dietas experimentales. Los asteriscos (\*) representan las diferencias significativas ( $P < 0.05$ ) obtenidas con la prueba de Wilcoxon Mann-Whitney.

Characteristics	pH	
	Low-Fiber (35%-NDF)	Medium-Fiber (57%-NDF)
Stomach		
Cardiac	5.17 ± 0.93	3.02 ± 0.87*
Pyloric	2.41 ± 0.26	1.75 ± 0.18*
Small Intestine		
Anterior	6.90 ± 0.26	6.82 ± 0.55
Medium	7.36 ± 0.35	7.40 ± 0.19
Posterior	7.91 ± 0.05	7.82 ± 0.26
Ceacum		
I Section	6.57 ± 0.11	6.72 ± 0.54
II Section	6.62 ± 0.21	6.83 ± 0.51

microbial degradation is possible, allowing energy extraction from high fiber food.

Interestingly, during short time intervals and when high quality food is scarce, this phenomenon may operate without increasing food intake, allowing small mammalian herbivores to satisfy their nutritional requirements without compromising their time budget. However, this short-time compensatory response is probably a consequence of microbial fermentation acting on cellulose, producing volatile fatty acids (VFA), and consequently providing energy. However, during long-time exposures to high dietary fiber, animals may fall in a nitrogen deficiency (Mattson 1980), be constrained to increase their food intake and time allocated to foraging behavioral processes.

Finally, a generalist herbivore, may benefit from a physiological plasticity allowing it to cope with different and changing food items in space and time. On the other hand, small mammalian herbivores lacking such plasticity may be constrained in their dietary scope (Penry & Jumars 1987) and being consequently restricted to habitats where their preferred trophic items are available over time.

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