

Diet, digestive tract gross anatomy and morphometry of *Akodon cursor* Winge (Sigmodontinae): relations between nutritional content, diet composition and digestive organs

Ricardo Finotti*, Mariana Moraes Santos and Rui Cerqueira

Departamento de Ecologia, Instituto de Biologia – UFRJ, Ilha do Fundão, RJ, Caixa Postal 68044, CEP 21944-970, Brazil, e-mail: finotti@biologia.ufrj.br

* Corresponding author

Abstract

Individuals of *Akodon cursor* were collected at fragments from the Atlantic Forest of Brazil and laboratory food preference experiments were performed. A preference index for each food item and the proportions of organic nutrients (glucids, protein, lipids and fibers) on the diet were calculated. Food items were grouped into fruits, seeds, roots, animal matter, arthropods, tubers and leaves, and their mass and proportions consumed were also calculated. Macroscopic digestive tract morphology was briefly described and the length of digestive organs was measured. Relations between the organic nutrient mass consumption, food type mass consumption and the digestive tract organ relative length were analyzed using Akaike's information criteria. Fruits, seeds and roots made the most abundant food categories of the diet of *A. cursor* and presented the majority of preferred food items. Arthropods and seeds are related to protein consumption. Animal items are not considered preferred but were eventually chosen and are important for protein supply. Fruits and roots are the major source of glucids. *Akodon cursor* has simple macroscopic digestive organ morphology. Relations were found between lipids consumption and small intestine and caecum length. *Akodon cursor* is an omnivorous species and different food items are important for its nutritional supply even those that are considered non-preferred.

Keywords: Akaike's information criterion (AIC); *Akodon cursor*; digestive tract; food preference; nutrients content.

Introduction

Diet is one of the most important components of an animal life and several methods are used to investigate it, field methods being the most common (Southwood and Hendersen 2000). These methods are important as they can be used to determine the temporal and spatial variation on consumed diet items. However, food items are rather variable in nature and nutrient content is difficult to ascertain, and in addition

resources availability can be somewhat variable among seasons during the year (Ceotto et al. 2009). As a consequence, these methods limit comparisons among species (Campos et al. 2001, Astúa de Moraes et al. 2003). Otherwise, in laboratory experimental approaches such as alimentary preference experiments, where resources are standardized by the use of commercial food items available all year long, resources availability can be controlled and nutrients and fibers proportions can be more easily and precisely established, enabling the comparison between species in standardized conditions (Périsse et al. 1989). This method has been considered as experimentally simple and efficient to study nutrient requirements of small mammals (Jones et al. 2003).

Alimentary preference is the result of physiological, behavioral and ecological mechanisms. These mechanisms are responsible for an optimal ingestion of energy and for the selection of a nutritional balanced diet (Louw 1993, Penry 1993, Koteja 1996, Corp et al. 1997, Owl and Batzli 1998). Laboratory preference experiments eliminate external factors (e.g., ecological) related to food choice, being the proportion of food types consumed and the nutrients proportion ingested derived from it, and more related to the physiological and behavioral constraints of the species (Zuwang 1987, Shettleworth et al. 1993, Astúa de Moraes 1998, Augner et al. 1998).

Although commercial food items are not found at the species' natural habitat, it is reasonable to state that chemical characteristics and properties of food types are, in most of cases, similar (Astúa de Moraes et al. 2003). Although it may seem meaningless to offer such items, some studies have shown that offering unfamiliar food items does not prevent animals from choosing a balanced nutritional diet (Louw 1993). Other studies show that there is a close relationship between the proportion of nutrients consumed in alimentary preference experiments and food categories that a species consumes in the field (Périsse et al. 1988, Astúa de Moraes et al. 2003). Comparisons between diet characteristics in the laboratory and in the field showed similar results (Santori et al. 1997).

The alimentary preference approach also allows the relation between diet nutritional characteristics and digestive organ size and morphology. Although individual digestive organs present phenotypic flexibility due to diet quality and energetic content (Naya et al. 2008), the relation between nutrients and food types proportions and the digestive tract morphology and morphometry, considering a large number of individuals, can give important clues to understanding a species' diet and the structural gut changes that can be related to it (Santori et al. 2004).

Akodon cursor Winge (Sigmodontinae) has terrestrial habits and a wide geographical distribution, occurring in a variety of habitats in the Atlantic Forest Morphoclimatic Domain (Geise et al. 2005). The species has a rather large range of diet which together with the generality of its habitat preference may explain its wide distribution in the Atlantic Forest (Cerqueira et al. 2003). Species of the genus *Akodon* are generally considered omnivores (Graipel et al. 2003), but some studies have shown that there is interspecific variation on the proportions of food types consumed. For example, individuals of *Akodon montensis* consume a higher proportion of vegetal matter (Talamoni et al. 2008) and are considered important seed predators in Araucaria forests (Vieira et al. 2006), whereas *Akodon azarae* and *Akodon molinae* present a higher proportion of insects in its diet (Ellis et al. 1998, Campos et al. 2001, Suarez and Bonaventura 2001). *Akodon cursor* seems to have a high degree of insectivory when compared with other sigmodontinae rodents that occur at Atlantic Forest formations (Finotti 2003) or other small mammal species (Carvalho et al. 1999), but due to the low number of studies done with this species' diet, no conclusions can be drawn.

Intraspecific and morphometric analyses related to the diet characteristics are also lacking for this species. Vorontzov (1967) and Carleton (1973) examined the morphology of stomachs of several species of sigmodontinae rodents, including *Akodon cursor*. However, there are no detailed descriptions of other parts of the digestive tract (especially the caecum) and although the authors made some general inferences on the functional significance of digestive tract organs based on the anatomy of Sigmodontinae species, they were not tested.

Here, we present the results of laboratory food preference experiments and an evaluation of the nutritional contents of the food consumed. *Akodon cursor* digestive tract morphology is described and its morphometry is related to its diet nutritional contents and food categories consumed.

Materials and methods

We used adult animals from two localities of the Atlantic Forest at Rio de Janeiro State, locality of Guapimirim (22°32'14"S and 42°58'55"W) and locality of Varre e Sai (20°55'55"S and 41°52'08"W). The age of vaginal opening in females and the appearance of scrotal testes in males was registered and used as indicators of age of puberty (Araípe et al. 2006). Young individuals and pregnant or nursing females,

i.e., those who had nestling before, during or after the experiment, were excluded from the analysis as they may present different nutritional needs related to differences in metabolism and physiological state. The experiments were conducted in a maximum of 4 days after the arrival of individuals to the laboratory and were initiated during the day in a way that animals were included in the experiment during the night.

Temperature at the laboratory varied between 19°C and 24°C and relative humidity varied between 65% and 82%.

Food preference experiments

Food preference was determined through a laboratory experiment developed in the Laboratory of Vertebrados – UFRJ (Périsse et al. 1989). The experiments consisted in offering 27 food items (Table 1) of animal and vegetable origins to test the food preference, with water *ad libitum*. Each individual was put inside a plastic cage (0.49×0.34×0.16 m) with food, where it remained for 18–24 h. Each animal and the food items were previously weighed. At the end of the experiment, individuals were removed from the cages and weighed again if there was evidence of food consumption (tooth marks and/or fragments). If not, the food item was considered not consumed. The mass consumption of each food item was estimated as the difference between the amount of food offered and the amount that was weighed at the end of the experiment. We calculated a preference index as:

$$P = Fd / Fr,$$

where P=preference index, d=total consumed of a given food item, Σd =the total consumed of all items, r=resource, the quantity of each item offered, Σr =the sum of all offered food items, $Fd = d \times 100 / \Sigma d$, and $Fr = r \times 100 / \Sigma r$.

Fd is the frequency of each item consumed and Fr the frequency of the item offered (resource). Items with a preference index >1–50% or more of the individuals in the experiment were considered preferred (Périsse et al. 1989).

We also estimated the proportion of organic nutrients of each food item [lipids (fats), proteins, fibers (structural carbohydrates) and glucids (non-structural carbohydrates)] using food chemical composition tables (Franco 1987, Mendez et al. 1995). The total food mass consumption and organic nutrients consumed were calculated, and the proportion of each organic nutrient consumed (organic nutrient mass consumption/total nutrient mass consumption) was calculated. The food items were grouped into the following food types: fruit,

Table 1 Food items used in the food preference experiments.

Food type	Food items
Fruits	Banana, orange, gumbo, tomato, grapes, apple and chayote
Roots and tubers	Carrot, manioc, beetroot, yam and potato
Leaves	Lettuce, cabbage and spring onion
Animal items	Ox meat (muscle), quail egg, chicken (muscle), fish (muscle), Ox tripe, Ox kidney and eggs
Arthropod	Shrimp
Seeds	Coconut pieces, peanuts, corn, chick peas and sunflower seeds

leaves, seeds, roots, tubers, vertebrate animal matter (meats and egg) and arthropods (Table 1). The mass summation of the items belonging to each one of these categories was considered the category consumption for each individual. Then a mean, median and the standard deviation for each category was calculated for the species. We also calculated the mass proportions of each food category in the diet (food category mass consumption/total food mass consumption).

Digestive tract

Animals were sacrificed, weighed and their body measurements were taken just after they left the preference experiment. To extract the digestive tube we made a cut from just below the external to the end of the abdomen. The esophagus was ignored as it serves only as a passage for the food to the stomach and no digestive processes occur there. The other organs were carefully cleaned and their lengths were measured with a millimeter board, just after death. The organs measured included: the small intestine, caecum, gross intestine and stomach region (corpus and antrum) lengths. We calculated the mean and variance of the absolute measure of each organ, as well as the relative proportion of each organ (organ length divided by the sum of all organs lengths). We described the macromorphological characteristics of each digestive tract organ. Anatomical terms on stomach morphology are those established by Carleton (1973) and for the other organs we used the nomenclature of Grassé (1973) and Vorontzov (1967).

Digestive organs' length differences between sexes were tested using the Mann-Whitney (U) test.

To test the necessity for adjustments to the body size, absolute measures of body length and each digestive organ length regression analyses were made between these variables. The variables were log-transformed; body length was used as the independent measure and the each digestive organ length as the dependent measure.

Relation between food type mass, digestive organs and organic nutrients

We analyzed the relations between food type consumption and organic nutrient consumption, as well as the relation between digestive organ length and organic nutrient consumption. For this, an information-theoretic measure approach, Akaike's information criterion (AIC) (Burnham and Anderson 2002) was used. We constructed models using food type consumption (g) as independent variables and organic nutrient mass consumption (g) as dependent variables and using digestive organ length (mm) as independent variables and organic nutrient mass consumption (g) as dependent variables.

Stomach total length was not used in this analysis, only the length of its regions (antrum and corpus). As these regions are made up of different tissues, we considered that they may have different functions on food and nutrient digestion, as previously hypothesized by other authors (Vorontzov 1967, Carleton 1973).

We first built a general model where all independent variables were used and related to each dependent variable. For

the other models, independent variables and their combinations were chosen based on a previous hypothesis. For the relations between food types and organic nutrients, independent variables (food types) were selected based on their importance on organic nutrient consumption. The hypotheses for this were based on the nutritional proportion analysis of food types, and information from the literature as well (Louw 1993, Schmidt-Nielsen 1996). To understand the importance of food type on protein and lipid consumption, only seeds, arthropods and animal matter were included in the model. Roots, fruits and seeds were used in the glucids consumption models and seeds, roots, fruits and leaves were used in the fiber consumption models. Tubers and roots were grouped because these two food types have very similar nutritional contents and tubers were consumed in a very low proportion.

Models using digestive organs as independent variables were based on hypotheses based on their physiological role according to the literature (Vorontzov 1967, Carleton 1973, Low 1993, Schmidt-Nielsen 1996). Antrum, corpus, caecum and small intestine lengths were related to protein consumption. Small intestine and caecum lengths were used for relations with lipids and glucids consumption and corpus and caecum were used for models on fiber consumption. The gross intestine was only included in the global model (all organs) because it is important in water absorption but has no *a priori* known importance on organic nutrient digestion.

To establish a goodness comparative model criterion, a null model was constructed. The null model is one where all correlations with independent variables are zero, variation on this model are from the mean and variances of the data itself, with no relation with the independent variables. This model was used as reference for other models goodness-of-fit. Models that had higher AIC values compared to the null model were ruled out as possible explanations.

Results

Food preference experiment

A total of 73 individuals (48 males and 25 females) were captured on forest fragments at the locality of Guapimirim (22°32'14"S and 42°58'55"W) and 11 individuals (6 males and 5 females) were captured at a forest fragment at the locality of Varre e Sai (20°55'55"S and 41°52'08"W). Individuals did not increase body mass at the end of the experiment (initial body mass=50.15±14.75 g, final body mass=51.65±14.30 g, $t=0.99$, $df=84$, $p=0.32$). No gender differences were found ($t=0.78$, $df=84$, $p=0.25$).

Fruits were the most consumed food type in the diet, followed by seeds, roots, arthropods, tubers, animal items and leaves. All the items present high variance (Table 2).

Among the 27 offered food items, only 7 had preference index equal or higher than 1 and thus were considered preferred. With regard to the fruit category, grapes, oranges and bananas were the preferred items; for the seed category, chick peas and coconuts were not preferred; manioc was the only root preferred; and shrimp (arthropod) was also preferred. All food items were consumed for at least one individual (Table 3).

Table 2 Mean weight, standard deviation (SD) and proportion of each food category consumed in the preference experiment (n=84).

Food categories	Mean mass (g)/SD	Proportion (%)
Fruits	21.30/10.94	37.37
Seeds	5.64/2.38	28.71
Roots	5.17/4.69	12.94
Arthropods	2.19/2.79	6.1
Animal items	1.93/3.63	6.38
Tubers	2.36/4.16	5.91
Leaves	1.32/2.44	5.41

Glucids corresponded to a mean proportion of 60.37% (± 11.08) of the total nutrient consumption, followed by proteins (16.07% ± 6.57), lipids (12.03% ± 11.95) and fibers (11.83% ± 2.93). Mean glucids mass consumed was 6.46g (± 2.24), proteins was 1.72 g (± 0.84), lipids was 1.26 g (1.19) and fibers was 1.26 g (± 0.49).

Digestive tract

A total of 13 individuals, 11 from the Guapimirim locality and two from the Varre e Sai locality (8 males and 5 females), were used for morphological and morphometric analysis of the digestive tract.

The stomach shows a monogastric form. It is very plastic, relative measures varying according to the food volume present inside it. The antrum makes the major portion of the stomach, showing fine muscular bands (Figure 1 and Table 4). It is also much more variable in length than the corpus (Table 4). The corpus is spacious, with a broad fornix ventricularis and a less variable length. Distribution of cornified and glandular linings coincides closely with the basic stomach divisions: cornified epithelium is found in the corpus, whereas glandular epithelium is limited mainly to the antrum. The bordering fold crosses the lesser curvature at the apex of the incisura angularis and the greater curvature at a locus opposite the incisura angularis. (Figure 1). At this region, microvilli can be found, extending to the beginning of the small intestine.

The small intestine is the longer linear portion of the digestive tube. It is a cylindrical tube with no identifiable macroscopic structural differentiation or modification at this portion.

The caecum has a coma form, being narrow at the superior portion, smooth and without haustra of the colon or muscular taenia (Figure 2). The ileocecal valve has a very simple structure at this junction with the small intestine. At the junction with the gross intestine there are several folds, forming a straight and tubular route to the gross intestine and extending towards it. These folders suffer an enlargement at the gross intestine initial portion until the middle portion, where it disappears (Figure 3).

Table 3 Mean, median, maximum (max), minimum (min), standard deviation (SD) and preference index (PI) of each food item consumed in the preference experiment.

Food items	Mean (g)	Median (g)	Max (g)	Min (g)	SD	PI
Gambo	0.58	0	6	0	1.07	0.23
Apple	2.22	1.9	12.18	0	2.32	0.71
Chayote	1.25	0	12.86	0	2.28	0.16
Tomato	1.10	0	10.72	0	2.05	0.16
Grapes	3.49	2	18.04	0	4.05	1.43
Orange	6.7	4.93	57.31	0	7.91	1.64
Banana	6.00	4.81	53.68	0	7.40	1.23
Chick peas	0.15	0	2.65	0	0.50	0.25
Corn	1.06	0.68	5.14	0	1.23	1.46
Peanuts	0.70	0	4.03	0	1.21	1.67
Sunflower seeds	0.43	0.35	2.43	0	0.49	2.71
Coconut	3.30	3.32	7.38	0	1.59	0.87
Manioc	3.50	2.76	17.43	0	3.40	1.56
Carrot	0.63	0	12.5	0	1.77	0.08
Yam	1.23	0	14.66	0	2.56	0.25
Beet root	1.04	0	6.78	0	1.80	0.15
Cabbage	0.64	0	6.16	0	1.46	0.6
Lettuce	0.60	0	6.34	0	1.46	0.44
Spring onion	0.08	0	1.36	0	0.31	0.40
Ox meat	0.25	0	4.1	0	0.89	0
Shrimp	2.19	0.65	13.88	0	2.79	1.06
Quail egg	0.01	0	0.5	0	0.05	0
Chicken	0.50	0	8.21	0	1.61	0.17
Fish	0.56	0	4.33	0	1.25	0.27
Ox tripe	0.51	0	7.33	0	1.45	0.05
Ox kidney	0.11	0	4.83	0	0.62	0.13
Potato	1.13	0	7.26	0	2.74	0.21

Preferred food items are those with $PI \geq 1.00$ (n=84).

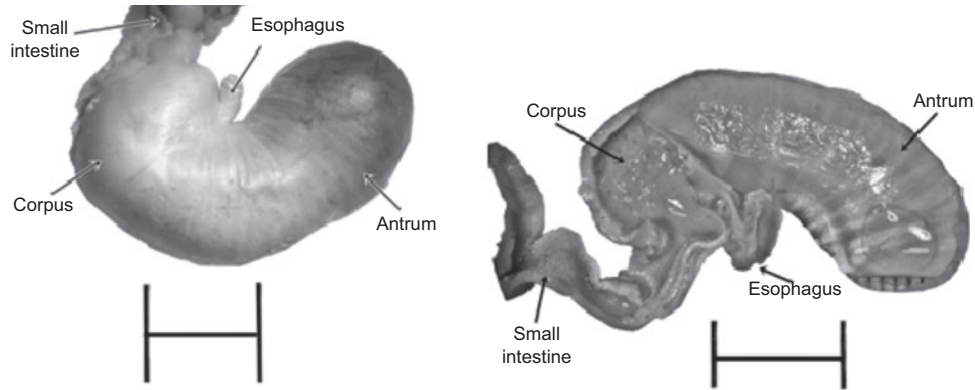


Figure 1 External and internal views of stomach portions. Line represents 1 cm.

The gross intestine is a cylindrical smooth tube, wider and shorter compared with the small intestine. It is formed by muscular crossbands throughout all its length. Depending on the food volume content, the muscular bands can be very close and grouped or may expand and become less obvious forming pouches (Figure 4).

No differences were found between the sexes for each digestive organ: antrum: $U=5.5$, $p=0.13$; corpus and small intestine: $U=10$, $p=0.52$; caecum: $U=6.5$, $p=0.31$; gross intestine: $U=9.0$, $p=0.40$ (for all comparisons $n=13$, 8 males and 5 females).

Significant correlations were found between body length and antrum region length ($n=13$, $R^2=0.19$, $p=0.27$) and with gross intestine length ($n=13$, $R^2=0.16$, $p=0.04$). The other organ length presented no significant relation to body length (corpus: $n=13$, $R^2=0.02$, $p=0.48$, small intestine: $n=13$, $R^2=0.09$, $p=0.09$ and caecum: $n=13$, $R^2=0.4$, $p=0.33$). Thus, the relations between digestive tract organs, food categories and nutrient content were made using their relative measures.

Relation between food type mass, organic nutrients mass and digestive organs

With the exception of the models that relate proteins and glucids with food types (Tables 5 and 6) and the models relating lipids with digestive organ length (Table 7), the null model evidence ratios of all models were three to four times higher, when compared with the second best model. Consequently,

there is very poor evidence for them and they were not considered in our study.

The best model for glucids consumption was the first, which combines roots and fruits. This model has w_i five times greater than the second model, and such findings indicate that roots and fruits are the main source of these organic nutrients (Table 6).

None of the models for consumed proteins mass can be considered as the best (Table 5). Evidence ratios are low, varying from 1.04 to 2.40 when the highest w_i is compared with the others. Although we can state that, concerning the three food types analyzed, evidence suggests that seeds and arthropods are slightly more important food types than animal matter with regard to protein consumption for this species.

Concerning the digestive organs, the best model was that between lipids mass consumption and small intestine and caecum length (Table 7), although the evidence ratios are not very high in comparison with the null model (small intestine: 1.39 and caecum: 1.38). With such evidence ratios, these relations should be considered as weak evidence in this regard.

Table 4 Absolute and relative measures of the digestive tract ($n=13$).

Digestive tract organs	Length (mm) \pm SD	Relative measure (%)
Stomach	31 \pm 7.19	3.26
Antrum region	21.77 \pm 7.3	2.29
Corpus region	13.04 \pm 2.72	1.37
Small intestine	743.61 \pm 162.45	78.12
Caecum	39.46 \pm 13.54	4.15
Gross intestine	102.85 \pm 31.21	10.81
Total length	951.73 \pm 179.73	100.00

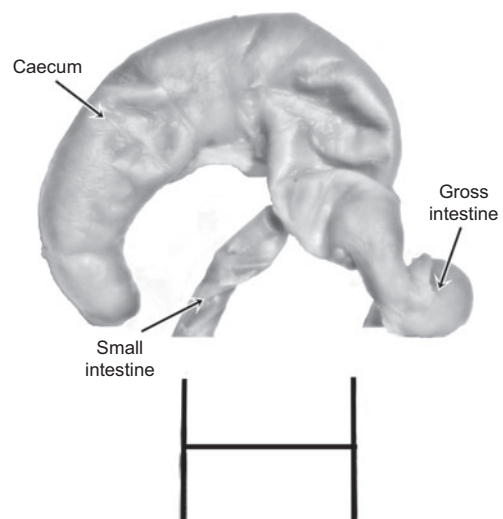


Figure 2 External view of the caecum. Lines represent 1 cm.

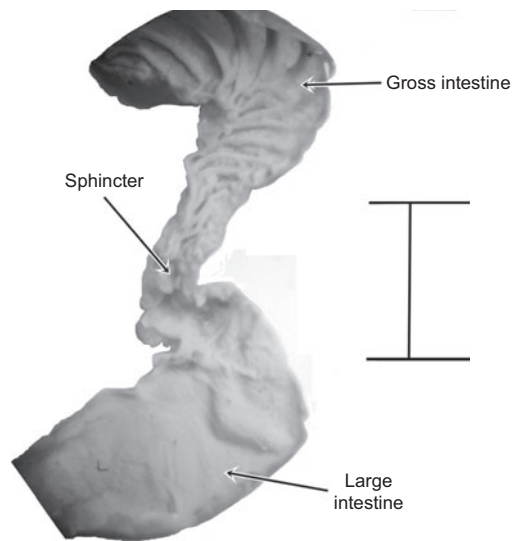


Figure 3 Internal view of the caecum showing the folds extending throughout the gross intestine. Line represents 1 cm.

Discussion

Akodon cursor is generally considered as insectivore-omnivore (Fonseca and Kierluff 1989, Fonseca et al. 1996, Emmons and Feer 1997, Carvalho et al. 1999). Arthropods seems to be an important source for protein supply and can be considered important for diet differentiation of *A. cursor* from that of other species, as described in other laboratory and field studies (Carvalho et al. 1999, Finotti 2003). However, in our study this species presented a very broad diet, with fruits and seeds being the major food types. One can state that these could be the result of fruits and seeds being better represented in the experiment. However, as we discarded the experiment where any item was totally consumed, this is not probable. Fruits and seeds are important for many rodent species (Talamoni et al. 2008) and other small mammal species (Santori et al. 1997, Ceotto et al. 2009). With regard to field studies on rodent diet, these items are frequently underestimated because rodents are seed predators (Vieira et al. 2006)

and can grind seeds to small pieces, not detectable in fecal or stomach content samples (Carvalho et al. 1999, Campos et al. 2001). Thus, it is possible that the importance of these food items in the *A. cursor* diet is being underestimated.

Additionally, in laboratory food experiments where food offer is standardized, food choice is basically reflecting the nutritional needs and/or the energetic demands of the individuals (Périsse et al. 1989, Astúa de Moraes et al. 2003) without the restrictions posed by food accessibility and availability. These studies can contribute to elucidate some aspects about the effects of these restrictions on field diet studies. For example, Castellarini et al. (1998), who carried out field studies and cafeteria experiments with *Calomys venustus* (Rodentia, Muridae), showed that when two different food types, each one more consumed in a different season in the field, are equally offered at the same time in the laboratory, individuals choose the one preferred, concluding that diet seasonal variation is the result of scarcity or competition for a determined food type. Based on field evidence and the results found here, we can state that *Akodon cursor* can be considered omnivorous, similar to other small mammal species (Landry 1970, Graipel et al. 2003, Talamoni et al. 2008). *A priori* traditional species classification in categories such as insectivorous, carnivorous and herbivorous do not make sense for this and other small mammal species (Astúa de Moraes et al. 2003, Finotti 2003).

Analysis of the nutritional content of selected food items can also furnish important information in comparing the diet of *Akodon cursor* with the diet of other species, as species can present differences in quality of food items of a determined food type (seeds, arthropods, fruits). For *A. cursor*, fruits, along with roots, were important glucids (non-structural carbohydrates) sources as selected items of this food type are those with a higher content of sugar (fructose) (Franco 1987). Seeds were important for protein supply and the most preferred seed (sunflower seeds) has a higher protein content compared with other seeds (Franco 1987). Seeds are important water and lipid sources for rodents (Schmidt-Nielsen 1996) and granivory is considered an important strategy of desert rodent species (Mares and Rosenzweig 1978, Murray 1994). To the best of our knowledge, its importance as a protein source has never been demonstrated.

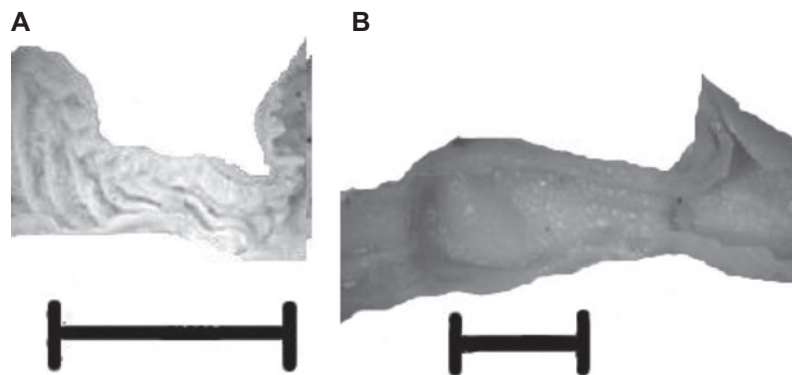


Figure 4 Internal views of the gross intestine. Note the different aspects of muscular bands: (A) empty portion, (B) portion full of digested food. Lines represent 1 cm.

Table 5 Models for proteins mass (g) and food types.

Proteins	n	K	AIC _c	Δ _i	exp(-0.5×Δ _i)	w _i	r ²
Seeds	84	3	4.21	0	1	0.14	0.19
Arthropods	84	3	4.28	0.07	0.96	0.14	0.20
Seeds and animal matter	84	4	4.39	0.18	0.91	0.13	0.28
Seeds and arthropods	84	4	4.41	0.20	0.90	0.13	0.26
Null	84	2	4.48	0.26	0.88	0.12	0.07
Animal matter	84	3	4.48	0.26	0.88	0.12	0.05
Seeds, arthropods and animal items	84	5	4.63	0.42	0.81	0.11	0.4
Arthropods and animal items	84	4	4.72	0.51	0.78	0.11	0.13
All food types	84	8	5.97	1.75	0.42	0.058	0.46

n, sample size; k, number of parameters; AIC_c, Akaike's information criterion for small sample sizes; Δ_i, difference between the AIC of the best model and that of model i (AIC_i-min AIC); exp(-0.5×Δ_i), estimate of likelihood; w_i, Akaike's weight (estimate of likelihood of the model i divided by the sum of the likelihoods estimate); r², coefficient of determination.

Table 6 Models for glucids mass (non-structural carbohydrates) (g) and food types.

Non-structural carbohydrates	n	K	AIC _c	Δ _i	exp(-0.5×Δ _i)	w _i	r ²
Roots and fruits	84	4	3.48	0	1	0.41	0.18
Null	84	2	6.57	3.10	0.21	0.09	0.00
Seeds	84	3	6.63	3.15	0.21	0.09	0.13
Roots	84	3	6.73	3.25	0.20	0.08	0.16
Seeds and roots	84	4	6.77	3.30	0.19	0.08	0.33
Fruits	84	3	6.81	3.34	0.19	0.08	0.04
Seeds and fruits	84	4	6.92	3.44	0.18	0.07	0.17
Seeds, roots and fruits	84	5	7.12	3.64	0.16	0.07	0.35
All food types	84	8	8.59	5.12	0.08	0.03	0.36

n, sample size; k, number of parameters; AIC_c, Akaike's information criterion for small sample sizes; Δ_i, difference between the AIC of the best model and that of model i (AIC_i-min AIC); exp(-0.5×Δ_i), estimate of likelihood; w_i, Akaike's weight (estimate of likelihood of the model i divided by the sum of the likelihoods estimate); r², coefficient of determination.

Non-preferred food items are also important to understand complete nutritional status of a species. Although no animal items and leaves were considered preferred, they are eventually eaten, indicating that they can function as a supplementary resource, and more precisely animal items are an important protein source.

The digestive tract of *Akodon cursor* did not present clear changes at the macroscopic level. Hume (1982) states that there is a direct relationship between an animal's diet and its digestive morphology. However, other studies indicate that, in some taxa, this relationship is less clear, due to the plasticity and variability of the relative size of different parts of the

digestive tract (Derting and Bogue 1993, McClelland et al. 1999, Sabat and Bozinovic 2000, del Valle et al. 2006). This appears to be the case for *A. cursor*.

Although the models among the small intestine and caecum length and lipids consumption were considered the best, they presented very low evidence ratios compared to the null model. For the small intestine, it is reasonable to expect this relation as fat digestion occurs, mainly, in this organ (Grassé 1973, Schmidt-Nielsen 1996), but for the caecum this function is not expected. The function of the caecum as a fermenting chamber for fiber digestion is well documented for some mammal taxa (Louw 1993). However, for rodents and

Table 7 Models for lipids mass (g) and digestive organs length.

Lipids	n	K	AIC _c	Δ _i	exp(-0.5×Δ _i)	w _i	r ²
Small intestine	12	3	9.10	0	1	0.37	0.11
Caecum	12	3	9.11	0.01	0.99	0.36	0.13
Null	12	2	9.76	0.67	0.72	0.26	0
Small intestine and caecum	12	4	17.00	7.90	0.02	0.01	0.04
All organs	12	7	48.01	38.92	0.00	0.00	0.48

n, sample size; k, number of parameters; AIC_c, Akaike's information criterion for small sample sizes; Δ_i, difference between the AIC of the best model and that of model i (AIC_i-min AIC); exp(-0.5×Δ_i), estimate of likelihood; w_i, Akaike's weight (estimate of likelihood of the model i divided by the sum of the likelihoods estimate); r², coefficient of determination.

marsupials, this remains a controversial point (Santori 1995, Santori et al. 2004). The caecum of *Akodon cursor* shows a very simple structure and is very different from the caecum of animals known as herbivores. As a hypothesis to be tested, we can state that, for this species, it may function as an organ where the digestion of fat, which begins in the small intestine, continues.

It is important to state that these relative lengths better represent the size of some organs as the small and gross intestines. For other organs, such as stomach and caecum, this may not be a good measure. Measures of volume of these organs and studies of different food type digestibility are essential to understand their role in digestion (Crowe and Hume 1997, del Valle et al. 2004, 2006, Santori et al. 2004).

Akodon cursor is basically omnivorous, uses a large range of food items and has an omnivore digestive tract. These results can serve as a basic framework where diet field seasonal and geographical variation can be analyzed. Laboratory approaches that allow the measure of diet items consumed and their nutritional quantities on other species may enhance our understanding of the differences between species with a very strong alimentary niche superposition.

Acknowledgments

We would like thank N.P. Barros and A.M. Marcondes for technical and clerical help, D. Nascimento and N. Cidade for helping with the preference experiments, J. Prevedello for help on AIC calculations and on discussion of AIC results, and Dra. Lena Geise, Dr. Otávio Menezes de Lima Jr. and two anonymous referees for valuable comments and corrections on the manuscript. We also thank Laboratório de Vertebrados (UFRJ) students for the capture of the animals in the field. We received grants from CNPq, FAPERJ and PDA/MMA. Field IBAMA licenses were: October 2005 to September 2006 no. 87/05-RJ, process no. 02022.003257/05-11, October 2006 to September 2007, no. 099/06-RJ, process no. 02022.003257/05-11, January 2008 to July 2009, no. 13861-1 and August 2008 to July 2009, no. 13861-2.

References

- Araripe, L.O., P. Aprigliano, N. Olifiers, P. Borodin and R. Cerqueira. 2006. Comparative analysis of life-history traits in two species of *Calomys* (Rodentia: Sigmodontinae) in captivity. *Mammalia* 70: 2–8.
- Astúa de Moraes, D. 1998. Análise morfométrica do crânio e da mandíbula de marsupiais didelfídeos: implicações ecológicas e funcionais. Dissertação de Mestrado, Curso de Pós-Graduação de Ecologia, Conservação e Manejo de Vida Silvestre – UFMG, Belo Horizonte. pp. 154.
- Astúa de Moraes, D., R.T. Santori, R. Finotti and R. Cerqueira. 2003. Nutritional and fiber contents of laboratory-established diets of neotropical opossums (Didelphimorphia, Didelphidae). In: (M. Jones, C. Dickman and M. Archer, eds.) *Predators with pouches: the biology of carnivorous marsupials*. CSIRO Publishing, Collingwood, Australia. pp. 225–233.
- Augner, M., F.D. Provenza and J.J. Villalba. 1998. A rule of thumb in mammalian herbivores. *Animal Behav.* 56: 337–345.
- Burnham, K.P. and D.R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. Springer Science/Media Inc., New York. pp. 487.
- Campos, C., R. Ojeda, S. Monge and M. Dacar. 2001. Utilization of food resources by small and medium-sized mammals in the Monte Desert biome, Argentina. *Austral Ecol.* 26: 142–149.
- Carleton, M.D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Murioidea), with comments on functional interpretations. *Misc. Publ. Mus. Zool. Univ. Michig.* 146 pp.
- Carvalho, F.M.V., P.S. Pinheiro, F.A.S. Fernandez and J.L. Nessimian. 1999. Diet of small mammals in Atlantic forest fragments in southeastern Brazil. *Rev. Brasil. Zool. Juiz Fora* 1: 91–101.
- Castellarini, F., H.L. Agnelli and J.J. Polop. 1998. Study on the diet and feeding preferences of *Calomys venustus* (Rodentia, Muridae). *Mastozool. Neotrop.* 5: 5–11.
- Ceotto, P., R. Finotti, R. Santori and R. Cerqueira. 2009. Diet variation of the marsupials *Didelphis aurita* and *Philander frenatus* (Didelphimorphia, Didelphidae) in a rural area of Rio de Janeiro state, Brazil. *Mastozool. Neotrop.* 16: 49–58.
- Cerqueira, R., R.T. Santori, R. Gentile and S.M.S. Guapyassu. 2003. Micrographical ecological differences between two populations of *Akodon cursor* (Rodentia, Sigmodontinae) in a Brazilian restinga. *J. Adv. Zool.* 24: 46–52.
- Corp, N., M.L. Gorman and J.R. Speakman. 1997. Apparent absorption and gut morphometry of wood mice, *Apodemus silvicultus*, from two distinct populations with different diets. *Physiol. Zool.* 70: 610–614.
- Crowe, O. and I.D. Hume. 1997. Morphology and function of the gastrointestinal tract of Australian folivorous possums. *Austr. J. Zool.* 45: 357–368.
- del Valle, J.C., C. Busch and A.A.L. Mañanes. 2004. Phenotypic flexibility of digestive morphology and physiology of the South American omnivorous rodent *Akodon azarae* (Rodentia: Sigmodontinae). *Comp. Biochem. Physiol. A* 139: 503–512.
- del Valle, J.C., C. Busch and A.A.L. Mañanes. 2006. Phenotypic plasticity in response to low quality diet in the South American omnivorous rodent *Akodon azarae* (Rodentia: Sigmodontinae). *Comp. Biochem. Physiol. A* 145: 397–405.
- Derting, T.L. and A. Bogue. 1993. Responses of the gut to moderate energy demands in small herbivore (*Microtus pennsylvanicus*). *J. Mammal.* 74: 58–68.
- Ellis, B.A., J.N. Mills, G.E. Glass, K.T. McKee, D.A. Enria and J.E. Childs. 1998. Dietary habits of the common rodents in an agroecosystem in Argentina. *J. Mammal.* 79: 1203–1220.
- Emmons, L.H. and F. Feer. 1997. *Neotropical rainforest mammals: a field guide*, 2nd edn. The University of Chicago Press, Chicago. pp. XVI+307.
- Finotti, R. 2003. *Ecologia alimentar de roedores de Mata Atlântica por meio da análise da preferência alimentar em laboratório*. Dissertação (Mestrado em Ecologia) – Universidade Federal do Rio de Janeiro, Rio de Janeiro. pp. 79.
- Fonseca, G.A.B. and M.C.M. Kierluff. 1989. Biology and natural history of Brazilian Atlantic Forest small mammals. *Bull. Florida State Mus. Biol. Sci.* 34: 99–152.
- Fonseca, G.A.B., G. Herrmann, Y.L.R. Leite, R.A. Mittermeier, A.B. Rylands and J.L. Patton. 1996. Lista Anotada dos Mamíferos do Brasil. *Occas. Pap. Conserv. Biol.* 4: 1–38.
- Franco, G. 1987. *Tabela de composição química dos alimentos*, 8th edn. Atheneu, Rio de Janeiro.
- Geise, L., D.A. Astúa de Moraes and H.S. Silva. 2005. Morphometric differentiation and distributional notes of three species of *Akodon* (Muridae, Sigmodontinae, Akodontini) in the Atlantic Coastal area of Brazil. *Arq. Mus. Nacl. Rio de Janeiro*, 63: 63–74.
- Graipel, M.E., P.R.M. Miller and L. Glock. 2003. Padrão de atividades de *Akodon montensis* e *Oryzomys russatus* na reserva de Volta Velha, Santa Catarina, sul do Brasil. *Mastozool. Neotrop.* 10: 255–260.

- Grassé, P.P. 1973. *Traité de Zoologie: Anatomie, Systématique, Biologie. Mammifères Splanchnologie. Tome XVI, Fascicule V, Vol. I.* Masson et C^{ie} Éditeurs, Librairie de l'academie de médecine, Paris, France.
- Hume, I.D. 1982. *Marsupial nutrition.* Cambridge University Press, Cambridge.
- Jones, M., C. Dickman and M. Archer. 2003. Preface. In: (M. Jones, C. Dickman and M. Archer, eds.) *Predators with pouches: the biology of carnivorous marsupials.* CSIRO Publishing, Collingwood, Australia. p. xii–xiv.
- Koteja, P. 1996. Limits to the energy budget in a rodent, *Peromyscus maniculatus*: does gut capacity set the limit? *Physiol. Zool.* 69: 994–1020.
- Landry, S.L., Jr. 1970. The Rodentia as omnivores. *Q. Rev. Biol.* 45: 351–372.
- Louw, G.N. 1993. *Physiological animal ecology.* John Wiley & Sons, New York. pp. 281.
- Mares, M.A. and M.L. Rosenzweig. 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* 59: 235–241.
- McClelland, K.L.M., I.D. Hume and N. Soran. 1999. Responses of the digestive tract of the omnivorous northern brown bandcoot, *Isodon macrourus* (Marsupialia, Peramilidae), to plant-and insect-containing diets. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 69: 411–418.
- Mendez, M.H.M., S.C.N. Derivi, M.C.R. Rodrigues and M.L. Fernandes. 1995. *Tabela de Composição química dos alimentos: amiláceos, cereais e derivados, frutas, hortaliças, Leguminosas, Nozes e Oleaginosas,* 2nd edn. EDUFF, Rio de Janeiro.
- Murray, B. 1994. Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia* 99: 216–225.
- Naya, D.E., F. Bozinovic and W.H. Karasov. 2008. Latitudinal trends in digestive flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am. Natural.* 172: 122–134.
- Owl, M.Y. and G.O. Batzli. 1998. The integrated processing response of voles to fibre content of natural diets. *Funct. Ecol.* 12: 4–13.
- Penry, D.L. 1993. Digestive constraints on diet selection. In: (R.N. Hughes, ed.) *Diet selection: an interdisciplinary approach to foraging behaviour.* Blackwell Scientific Publications, London. pp. 32–55.
- Périssé, M., R. Cerqueira and C.R. Sorensen. 1988. A alimentação na separação de nicho entre *Philander opossum* e *Didelphis aurita* (Polyprotodontia, Didelphidae). *An. Sem. Reg. Ecol. São Carlos S.P. VI:* 283–294.
- Périssé, M., C.R.S.D. Fonseca and R. Cerqueira. 1989. Diet determination for small laboratory-housed mammals. *Can. J. Zool.* 67: 775–778.
- Sabat, P. and F. Bozinovic. 2000. Digestive plasticity and the cost of acclimation to dietary chemistry in the omnivorous leaf-eared mouse *Phyllotis darwini*. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 170: 411–417.
- Santori, R.T. 1995. *Aparato trófico e variação nos hábitos alimentares da Philander opossum e Didelphis aurita* (Didelphimorphia, Didelphidae). Dissertação de Mestrado, Museu Nacional, U.F.R.J.
- Santori, R.T., D. Astúa de Moraes, C.E.V. Grelle and R. Cerqueira. 1997. Natural diet at Restinga forest and laboratory food preferences of the opossum *Philander frenata* in Southeastern Brazil. *Stud. Neotrop. Fauna Environ.* 32: 12–16.
- Santori, R.T., D. Astúa de Moraes and R. Cerqueira. 2004. Comparative gross morphology of the digestive tract in ten Didelphidae marsupial species. *Mammalia* 68: 27–36.
- Schmidt-Nielsen, K. 1996. *Animal physiology – environment and adaptation,* 6th edn. Cambridge University Press, Cambridge. pp. 564.
- Shettleworth, S.J., P.J. Reid and C.M.S. Plowright. 1993. The psychology of diet selection. In: (R.N. Hughes, ed.) *Diet selection: an interdisciplinary approach to foraging behaviour.* Blackwell Scientific Publications, London. pp. 56–77.
- Southwood, T.R.E. and P.R. Hendersen. 2000. *Ecological methods.* Blackwell Scientific, Oxford. pp. 565.
- Suarez, O.V. and S.M. Bonaventura. 2001. Habitat use and diet in sympatric species of rodents of the low Parana delta, Argentina. *Mammalia* 65: 167–175.
- Talamoni, S.A., D. Couto, D.A. Cordeiro and F.M. Diniz. 2008. Diet of some species of Neotropical small mammals. *Mammal. Biol.* 73: 337–341.
- Vieira, E.M., G. Paise and P.H.D. Machado. 2006. Feeding of small rodents on seeds and fruits: a comparative analysis of three species of rodents of the Araucaria forest, southern Brazil. *Acta Theriol.* 51: 311–318.
- Vorontsov, N.N. 1967. *Evollutzia: pishtchevaritelnoi sistemy gryzunov (mysheobraznye)* (Evolution of the digestive system of Muroid rodents). Novosibirsk; Izdatel'stvo "Nauka" Sib. Otd. Akad. Nauk. SSSR (In Russian).
- Zuwang, W. 1987. Some observations of Pocket gopher feeding behaviour. *Acta Theriol. Sin.* 7: 35–45.

Received October 3, 2009; accepted December 30, 2011