Variation in the helminth community structure of three sympatric sigmodontine rodents from the coastal Atlantic Forest of Rio de Janeiro, Brazil

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Abstract

One hundred and eighty specimens of sigmodontine rodents living in sympatric conditions were collected in the Atlantic Forest in the state of Rio de Janeiro, Brazil (25 *Akodon cursor*, 98 *Akodon montensis* and 57 *Oligoryzomys nigripes*) to examine whether the helminth structure and component communities can be characterized among these three closely related rodents. The parasite species richness was 9 in *A. cursor*, 12 in *A. montensis* and 12 in *O. nigripes*. Five species were common to the three rodent species, and eight were common to *A. cursor* and *A. montensis*. The trichostrongylids – *Stilestrongylus eta* in *A. cursor*, *S. aculeata* in *A. montensis* and *S. lanfrediae* in *O. nigripes* – were the species with highest dominance frequency and determined the characterization of individual community structures. The prevalence and abundance of concurrent helminth species among rodents were significantly different. Canonical multivariate analysis demonstrated a similar helminth community structure between *A. cursor* and *A. montensis* but a high discrepancy between *Akodon* spp. *and O. nigripes*. Thus, the data indicated that small rodents such as *A. cursor*, *A. montenis* and *O. nigripes* that are sympatric and phylogenetically related have a different community structure, but similar component community, suggesting the role of helminth specificity and the hosts' habitats as determinants in structuring their helminth communities.

Introduction

Rodents are important members of the mammalian fauna in South America, comprising approximately 45% of the species (Reig, 1986). On this continent, all species of muroid rodents are cricetids, ranked under the subfamily Sigmodontinae. Studies of sigmodontine rodents are significant for public health because these animals can be reservoirs of hantaviruses, *Trypanosoma cruzi* and *Schistosoma mansoni* (Suzuki *et al.*, 2004; Maldonado *et al.*, 2006; Padula *et al.*, 2007; Vaz *et al.*, 2007).

The genus *Akodon* Meyer, 1833 is broadly dispersed in the Neotropics, with over 45 species distributed throughout South America in a variety of habitats

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(Emmons & Feer, 1997). *Akodon montensis* Thomas, 1913 and *A. cursor* Winge, 1887 are cursorial rodents and have diurnal behaviour (Emmons & Feer, 1997; Eisenberg & Redford, 1999; Graipel *et al.*, 2003). *Akodon cursor* is one of the most common species in forest and forest–grassland ecotones (Eisenberg & Redford, 1999). *Oligoryzomys nigripes* Olfers, 1818 is a scansorial rodent common to the Atlantic Forest and it can also live in open areas under deforested conditions, along river edges, and in secondary brush. Additionally, this rodent can be an agricultural pest in rice fields and storage barns (Püttker *et al.*, 2008). It feeds on insects, seeds, fruits and some vegetation (Bonvicino *et al.*, 2002; Mattevi & Andrades-Miranda, 2006). The three species live in sympatric conditions in the Atlantic Forest (Gentile & Fernandez, 1999), which has been suffering great anthropogenic pressure, with the consequent loss of biodiversity (Myers *et al.*, 2000).

Several studies have focused on the characteristics of the helminth communities of small rodents in European and African ecosystems (Fuentes *et al.*, 2000; Behnke *et al.*, 2004, 2008a, b). In contrast, few reports have focused on the helminth fauna of small Brazilian mammals (Travassos, 1927; Travassos & Freitas, 1941; Gomes *et al.*, 2003; Durette-Desset *et al.*, 2006). Past studies have evaluated the structure of the helminth communities in a zoonotic context (Maldonado *et al.*, 2006) or under anthropogenic pressure (Simões *et al.*, 2009). To date, only a few taxonomic records of helminth parasites in *A. cursor*, *A. montensis* and *O. nigripes* are known (Moraes Neto *et al.*, 1996; Notarnicola & Navone, 2002; Robles & Navone, 2007a; Souza *et al.*, 2009a, b).

In an ecological context, host specificity can be defined as the number and identity of host species that are used by a parasite population. Parasites that are highly host-specific will occur in a single host species, whereas generalist parasites will be dispersed unequally among individual hosts from several different species (Morand *et al.*, 2006). From an evolutionary perspective, host specificity reflects the parasite's historical associations with hosts (Brooks & McLennan, 1993), which contribute to shape the helminth community structure. Sympatric hosts with short phylogenetic and geographic distances support likeness between their parasite communities (Poulin & Morand, 1999; Poulin, 2007), although little is known about the community structure of South American rodents.

In this paper, we characterize the component community structure of helminths among three closely related rodents (*A. cursor*, *A. montensis* and *O. nigripes*) living in sympatric conditions in an area of the coastal Atlantic Forest of Rio de Janeiro, Brazil.

Materials and methods

Location and collection of rodents

The study was carried out in Serra dos Órgãos and its surroundings (22°24′36″S, 42°58′48″W), Rio de Janeiro state, Brazil. Serra dos Órgãos is a mountain chain covered by pluvial montane Atlantic Forest, which runs through many municipalities, all of which have mild, humid mesothermal climates (Nimer, 1989). The average altitude is 871 m, average annual temperature of the region is 21°C and mean annual rainfall is 1671.6 mm.

Twenty-five specimens of *A. cursor*, 98 of *A. montensis* and 57 of *O. nigripes* were collected during 2004–2005 using two live traps: the Tomahawk® trap (model 201; $16 \times 5 \times 5$ inches ($40.6 \times 12.5 \times 12.5$ cm), Wisconsin, USA) and the Sherman® trap (model XLK; $3 \times 3.75 \times 12$ inches ($7.6 \times 9.5 \times 30.5$ cm), Florida, USA). The captured rodents were transported to a base camp for euthanasia and necropsy. All animal procedures followed the guidelines for capture, handling and care of mammals of the American Society of Mammalogy and the bio-security procedures of the Brazilian Health Ministry. The animals were collected under the permission of the Brazilian government's Institute for Wildlife and Natural Resources (IBAMA numbers 012/2004 and 068/2005). Bio-security techniques and individual safety equipment were used during all procedures involving animals or biological samples (Lemos & D'Andrea, 2006). The captured rodents were identified according to Bonvicino *et al.* (2008).

Parasitological procedures

Nematodes, trematodes and cestodes collected from the lungs, bile ducts, stomach, small intestine, caecum, thoracic and abdominal cavity were washed in saline solution (NaCl 0.85%) and fixed in AFA (acetic acid 2%, formaldehyde 3% and ethanol 95%). The nematodes were cleared in lactophenol, and the trematodes and cestodes were stained with chlorhydric carmine and studied using a Zeiss Standard 20 light microscope. General identification of helminth parasites was according to Travassos (1937), Yamaguti (1961), Khalil *et al.* (1994), Vicente *et al.* (1997), Gibson *et al.* (2002) and Jones *et al.* (2005).

Data analysis

To analyse the helminth community structure, we considered prevalence, mean intensity of infection and mean abundance of each species by taking into account all captured rodents and using procedures described by Bush *et al.* (1997). Component community refers to all infrapopulations of parasites associated with some subset of a host species (Bush *et al.*, 1997). The prevalence and confidence limits were calculated according to Rósza *et al.* (2000). Statistical analyses were performed only for those parasite species with higher than 10% prevalence. Chi-squared analyses were used to test significant differences in the prevalence of parasites among the three species of rodents. Analysis of variance (ANOVA) on $\log(x + 1)$ transformed data was used for comparison of parasite abundance, and statistical significance was tested by comparing the *F*-test statistic (Zar, 1999). The variance-to-mean ratio of parasite abundance (index of dispersion) and discrepancy index (Poulin, 1993), computed using the software Quantitative Parasitology 3.0 (a free statistical toolset for parasitologists), were employed to detect distribution patterns of the helminth infrapopulation (Rósza *et al.*, 2000).

The following community descriptors were calculated at the parasite infracommunity level: (1) number of parasite individuals (total abundance), (2) species richness, (3)

Brillouin's diversity index ($\log_{10}$), (4) evenness associated with Brillouin's diversity index, (5) Berger–Parker dominance index and frequency of dominance (percentage of infracommunities in which either parasite species was numerically dominant). In addition, two measures of similarity, the Jaccard qualitative and the Sørensen quantitative indices, were calculated among parasite infracommunities between host rodent species (Magurran, 1988). The level of statistical significance was taken to be $P < 0.05$.

To determine whether helminth abundance can be used to identify the host helminth community, canonical multivariate analysis (CMA) was performed using helminth burdens as explanatory variables (previous $\log(n + 1)$ transformation of abundance data for each helminth species). This analysis was performed following the recommendations of Wilkinson (1990) using the SYSTAT® statistical software.

Results

Component community

Eighteen helminth parasite species were collected in the three hosts studied: 9 in *A. cursor*, 12 in *A. montensis* and 12 in *O. nigripes* (table 1). The rodents *A. cursor* and *A. montensis* are new host records for the nematodes *Stilestrongylus lanfrediae* and *Syphacia carlitosi*, while *A. montensis* is a new host record for the nematodes *Trichofreitasia lenti* and *Protospirura numidica* and the trematode *Echinostoma luisrey*. *Oligoryzomys nigripes* is a new host record for the nematode *T. lenti*, the cestode *Rodentolepis akodontis* and the trematode *Canaania obesa*. Five species were common to all the rodent species, and eight were common to *A. cursor* and *A. montensis*. Nematodes were the dominant species and the highest species number, with nine species in *A. montensis*, eight in *O. nigripes* and seven in *A. cursor*, representing 88.6%, 99.4% and 94.5% of all parasite specimens collected, respectively.

Infracommunities

One hundred and sixty-one rodents were parasitized by one or more helminth species (18 *A. cursor*, 87 *A. montensis* and 56 *O. nigripes*), and 19 were negative for parasites (7 *A. cursor*, 11 *A. montensis* and 1 *O. nigripes*). A total of 5197 individual parasites were collected: 420 in *A. cursor*, 2155 in *A. montensis* and 2622 in *O. nigripes*, with mean total abundances of 16.8 ± 6.81 (0–160), 21.9 ± 2.93 (0–146) and 46 ± 8.43 (0–271), respectively. Four trichostrongylid nematode species contributed to the high abundance in the helminth community. All helminth species had an aggregated distribution pattern, and overall they showed discrepancy index values higher than 0.7 (table 2). The prevalence and abundance comparison of common helminth species to *A. cursor*, *A. montensis* and *O. nigripes* revealed significant differences for the following species: *C. obesa*, *R. akodontis*, *S. lanfrediae*, *Stilestrongylus aculeata* and *Stilestrongylus eta* (table 3). The trichostrongylids, *S. eta* in *A. cursor*, *S. aculeata* in *A. montensis* and *S. lanfrediae* in *O. nigripes*, were the species with the highest frequency of dominance (table 4).

Table 1. Prevalence (P) with 95% confidence limits, mean intensity (MI), and mean abundance (MA) followed by standard error, and site of infection (SI) of helminth parasites of *Akodon cursor*, *Akodon montensis* and *Oligoryzomys nigripes*.

	Akodon cursor			Akodon montensis			Oligoryzomys nigripes			SI
	P (%)	MI	MA	P (%)	MI	MA	P (%)	MI	MA	
TREMATODA										
Canaania obesa	12 (0.03–0.31)	2.7 ± 0.67	0.3 ± 0.19	17.3 (0.10–0.26)	9.2 ± 2.59	1.6 ± 0.56	3.5 (0.004–0.12)	5.0 ± 1.0	0.2 ± 0.13	Small intestine
Echinostoma luisreyi	–	–	–	1 (0.0002–0.06)	2	0.02 ± 0.02	–	–	–	Small intestine
CESTODA										
Rodentolepis akodontis	16 (0.05–0.36)	3.5 ± 1.32	0.60 ± 0.32	25 (0.16–0.34)	1.1 ± 0.09	0.3 ± 0.05	3.5 (0.004–0.12)	1	0.04 ± 0.02	Bile duct
Raillietina sp.	–	–	–	–	–	–	1.8 (0.0004–0.09)	1	0.02 ± 0.02	Small intestine
Taenia taeniaeformis	–	–	–	–	–	–	1.8 (0.0004–0.09)	2	0.04 ± 0.04	Encysted in
NEMATODA										
Stilestrongylus lanfrediae	4.0 (0.001–0.20)	156	6.3 ± 6.24	5.1 (0.02–0.12)	20.2 ± 11.37	1 ± 0.68	89.5 (0.78–0.96)	37.18 ± 7.12	33.26 ± 6.54	Small intestine
Stilestrongylus aculeata	24 (0.09–0.45)	13 ± 4.75	3.1 ± 1.55	50 (0.39–0.60)	21.8 ± 3.43	10.9 ± 2.04	14.3 (0.06–0.26)	3.9 ± 1.91	0.55 ± 0.31	Small intestine
Stilestrongylus eta	32 (0.15–0.54)	16 ± 8.53	5.2 ± 3.03	45 (0.35–0.55)	14.5 ± 2.83	6.5 ± 1.46	5.3 (0.01–0.15)	18.3 ± 5.69	0.96 ± 0.60	Small intestine
Guerrerostrongylus zetta	4 (0.001–0.20)	1	0.04 ± 0.04	–	–	–	21.4 (0.12–0.34)	30.8 ± 15.13	6.61 ± 3.32	Small intestine
Trichofreitasia lenti	–	–	–	7.1 (0.03–0.14)	5.9 ± 2.01	0.4 ± 0.20	5.3 (0.01–0.14)	1.7 ± 0.67	0.09 ± 0.06	Small intestine
Avellaria sp.	–	–	–	–	–	–	1.8 (0.0004–0.09)	17	0.3 ± 0.29	Small intestine
Trichuris sp.	–	–	–	1 (0.0002–0.06)	1	0.01 ± 0.01	–	–	–	Lung
Angiostrongylus sp.	4 (0.001–0.20)	9	0.4 ± 0.36	1 (0.0002–0.06)	1	0.01 ± 0.01	–	–	–	Stomach
Protospirura numidica	–	–	–	2 (0.002–0.07)	3 ± 1.00	0.06 ± 0.05	–	–	–	Caecum
Syphacia carlitosi	12 (0.03–0.31)	6 ± 3.51	0.7 ± 0.53	6.1 (0.02–0.12)	10.3 ± 7.51	0.6 ± 0.49	–	–	–	Caecum
Syphacia kinsellai	–	–	–	–	–	–	25 (0.14–0.38)	16.5 ± 6.45	4.1 ± 1.73	Abdominal cavity
Litomosoides odilae	–	–	–	–	–	–	1.8 (0.0004–0.09)	1	0.02 ± 0.02	Thoracic cavity
Litomosoides silvai	12 (0.03–0.31)	2 ± 1.00	0.2 ± 0.17	2 (0.002–0.07)	26 ± 25.00	0.5 ± 0.52	–	–	–	

Table 2. Distribution of the infracommunity. Values of variance to mean ratio of parasite abundance (ID) and index of discrepancy (D) for helminth parasites of *Akodon* cursor, *Akodon montensis* and *Oligoryzomys nigripes*. Statistical analyses were performed only for those parasite species with higher than 10% prevalence.

Parasites	*Akodon cursor*		*Akodon montensis*		*Oligoryzomys nigripes*	
	ID	D	ID	D	ID	D
Canaania obesa	2.792	0.865	19.482	0.910	–	–
Rodentolepis akodontis	4.625	0.863	1.031	0.773	–	–
Stilestrongylus lanfrediae	–	–	–	–	73.376	0.622
Stilestrongylus aculeata	19.319	0.832	37.314	0.760	–	–
Stilestrongylus eta	44.326	0.827	32.077	0.804	21.281	0.942
Guerrerostrongylus zetta	–	–	–	–	96.604	0.908
Syphacia carlitosi	9.782	0.893	–	–	–	–
Syphacia kinsellai	–	–	–	–	42.103	0.882
Litomosoides silvai	2.875	0.885	–	–	–	–

Mean species richness and mean abundance were lower in *A. cursor* than in *A. montensis* and *O. nigripes*. The mean evenness was higher in *A. montensis* than in the other two host species, and the mean Berger–Parker index value was higher in *O. nigripes* than in *Akodon* spp. (table 4). Additionally, variability among communities of the three rodents was observed when analysed using the Jaccard qualitative and Sørensen quantitative indices (fig. 1a and b) (see standard deviation). The communities were more similar between *A. cursor* and *A. montensis* than *O. nigripes*.

The classification matrix indicates that, overall, 67% of the helminths were correctly classified within a helminth community. Figure 2 indicates that the helminth community is differently structured in *O. nigripes* (Wilks's lambda 0.288; df 38, 318; approximately $F = 7.226$; $P < 0.001$).

Discussion

The structure and composition of helminth communities in sympatric host populations represent communities assembled from a pool of locally available parasite species. This structure and composition can be related to various features of the hosts themselves, host phylogeny relationships and the physicochemical and biological characteristics of the habitat (Poulin, 2007). Thus, short phylogenetic and geographical distances between host species affected the similarities between their parasite communities. CMA corroborated the high helminth community discrimination between *Akodon* spp. and *O. nigripes* and high similarity between *A. cursor* and *A. montensis* communities. This occurs due to the exchange of parasite species over evolutionary time, a process that is facilitated by phylogenetically related species and among geographically adjacent host populations (Poulin & Morand, 1999; Poulin, 2007). Thus, similarity between structure and composition of parasite communities of sympatric and related host species is expected when hosts share a habitat and resources (Poulin & Morand, 1999; Bush *et al.*, 2001; Poulin, 2007). The helminth communities in small rodents worldwide are mainly colonized by nematode species (Kinsella, 1990;

Fuentes *et al.*, 2004). In South America, the Sigmodontinae rodents comprise a large proportion of all small rodent taxa, inhabit a great diversity of ecosystems (Bonvicino *et al.*, 2008) and are infected mainly by nematodes (Gomes *et al.*, 2003; Maldonado *et al.*, 2006; Simões *et al.*, 2009).

The helminth communities of the congeneric species *A. cursor* and *A. montensis* revealed similar characteristics when compared with *O. nigripes*, supporting coevolution speciation and habitat overlap as important determinants of community structure. The *Stilestrongylus* genus was the dominant species for the three rodent hosts; however, the highest dominance index observed in *O. nigripes* can be explained as the outcome of the higher abundance of *S. lanfrediae* when compared to the dominant species *S. aculeata* and *S. eta* infecting *A. montensis* and *A. cursor*, respectively. The *Stilestrongylus* genus includes 23 Neotropical species, of which 22 are parasites of Sigmodontinae rodents (Digiani & Durette-Desset, 2003). This suggests a coevolutionary relationship. The *Stilestrongylus* species found infecting the congeneric *Akodon* species showed similar parasitological parameters when compared to *S. lanfrediae* in *O. nigripes*, reinforcing the hypothesis of a coevolutionary relationship, as suggested by Durette-Desset (1985). In fact, *Stilestrongylus* has been found in hosts with sympatric and possibly syntopic distributions that may be closely phylogenetically and/or ecologically related

Table 3. Values for comparisons of prevalence (χ^2) and abundance (ANOVA *F*), of helminth community component species of *Akodon cursor, Akodon montensis* and *Oligoryzomys nigripes* from the Atlantic Forest, Rio de Janeiro state, Brazil. Degrees of freedom = 2.

Helminths	Prevalence		Abundance	
	χ^2	P	F	P
Canaania obesa	21 666.9	<0.05	3.20	<0.05
Rodentolepis akodontis	11.4	<0.05	5.09	<0.001
Stilestrongylus lanfrediae	128.8	<0.05	129.02	<0.001
Stilestrongylus aculeata	22.1	<0.05	15.32	<0.001
Stilestrongylus eta	26.7	<0.05	10.08	<0.001

Table 4. Characteristics of the helminth parasites infracommunities found in *Akodon cursor*, *Akodon montensis* and *Oligoryzomys nigripes*. *F* = values of *F* in ANOVA (degrees of freedom = 2).

Characteristics	*Akodon cursor* (n = 25)	*Akodon montensis* (n = 98)	*Oligoryzomys nigripes* (n = 57)	*F*
Helminth species richness	9	12	12	NT
Total number of specimens	420	2155	2622	NT
Mean species richness	1.2 ± 1.2	1.6 ± 0.9	1.7 ± 0.8	4.98*
Mean total abundance	16.8 ± 6.81 (0–160)	21.9 ± 2.93 (0–146)	46 ± 8.43 (0–271)	11.86*
Mean Brillouin index	0.15 ± 0.06 (0–1.29)	0.25 ± 0.03 (0–1.11)	0.26 ± 0.4 (0–1.93)	1.38
Mean evenness index	0.01 ± 0.01 (0–0.13)	0.08 ± 0.02 (0–1.15)	0.02 ± 0.01 (0–0.23)	4.54*
Dominant species	*Stilestrongylus eta* 24%	*Stilestrongylus aculeata* 35%	*Stilestrongylus lanfrediae* 72%	–
Mean Berger–Parker index	0.69 ± 0.07 (0.37–0.97)	0.69 ± 0.03 (0.42–0.98)	0.78 ± 0.03 (0.5–0.99)	3.57*

*, $P < 0.05$

(León *et al.*, 2000). The level of specificity showed by the *Stilestrongylus* species suggests its function in partially shaping the community's structure.

The component community may be influenced by many factors, such as the habitat connection of the host species, the broad geographic distribution and the generalist behaviour of some helminth species. For instance, *Guerrerostrongylus zetta* was collected in this study in *A. cursor* and *O. nigripes* and has been reported in other sigmodontines, including *Nectomys squamipes*, *Euryoryzomys russatus*, *Oligoryzomys subflavus* and in the Cavidae *Galea spixii* (Vicente *et al.*, 1997). Additionally, *Trichofreitasia lenti* has been described infecting *Oryzomys flavescens* and *Akodon simulation* (Sutton & Durette-Desset, 1991; Digiani *et al.*, 2007). Furthermore, *Syphacia carlitosi* was described in *Akodon azarae* and *Syphacia kinsellai* in *O. nigripes*, both in the Chaco ecosystem in Argentina (Robles & Navone, 2007a, b).

The helminth richness value was slightly higher in *O. nigripes* and *A. montensis* than in the other rodents.

This finding agrees with the report of Gomes *et al.* (2003) in *A. cursor* and *O. nigripes* from the Atlantic Forest. Lacher *et al.* (1989) found that *A. montensis* and *O. nigripes* do not interact competitively with each other and *A. montensis* seems to be a greater microhabitat specialist than *O. nigripes*. The presence of nematode species infecting *A. montensis*, such as *Angiostrongylus lenzii*, *Protospirura numidica* and *Echinostoma luisreyi*, could be related to the use of an intermediate host as the alimentary resource, including insects and other invertebrates (Alho, 1982), differing from *O. nigripes*, which preferentially feeds on seeds (Emmons & Feer, 1997). Moreover, the host species that coexist spatially might show differences in feeding strategies, occupy different habitats or present distinct temporal activity patterns (Schoener, 1974; Feliciano *et al.*, 2002), and these differences could be mechanisms to reduce competition (Pimm & Rosenzweig, 1981). The scansorial behaviour of *O. nigripes* determines the share of soil resources with *A. montensis* and *A. cursor* and probably favours the possibility of new infections.

Kennedy *et al.* (1986) outlined factors that influence the diversity of helminth communities, including host
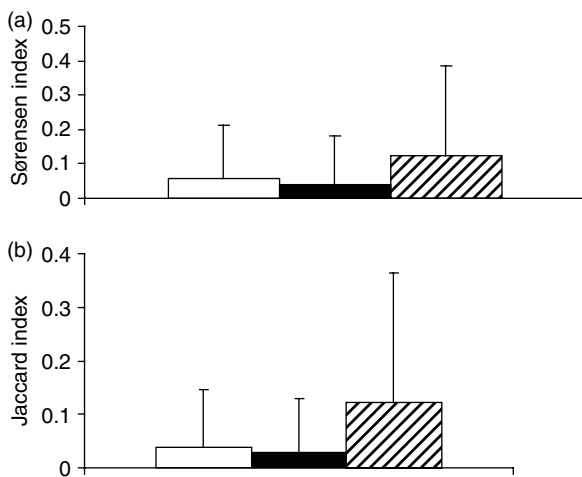

Fig. 1. Similarity indexes in helminth infracommunities of *Akodon montensis*, *Akodon cursor* and *Oligoryzomys*. (a) Quantitative similarity between *A. montensis*, *A. cursor* and *O. nigripes*. (b) Qualitative similarity between *A. montensis*, *A. cusor* and *O. nigripes*. White bars, *A. montensis* and *O. nigripes*; black bars, *A. cursor* and *O. nigripes*; striped bars, *A. cursor* and *A. montensis*.
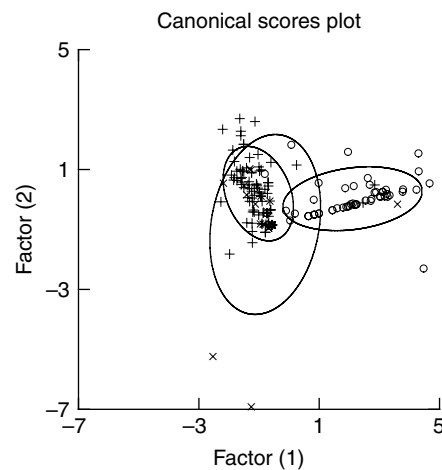

Fig. 2. Results of canonical multivariate analysis showing host discrimination using abundance data for each helminth species; *Oligoryzomys nigripes* (○), *Akodon cursor* (×) and *Akodon montensis* (+).

vagility, host diet, host physiology/anatomy, selective feeding on intermediate hosts, and exposure of hosts to the direct life cycle of helminths. Some of these factors may be applicable to the differences in the helminth community in a sympatric population of wild rodents. The non-significant differences in the Brillouin diversity index for helminth infracommunities may have resulted from the short phylogenetic host distances and low specificity of some of the helminth species.

An aggregated distribution of the parasite population is considered the most frequent pattern for parasites in the wild (Bush *et al.*, 2001; Poulin, 2007). In the present study, two aggregation measures were used: the variance-to-mean ratio and a discrepancy index. The latter is a measure of the disparity between the observed and uniform distributions of the parasite population in host samplings, with values ranging from 0 to 1 (Poulin, 1993). Values obtained from these two indices revealed a high aggregation level, confirming a characteristic typical of parasite populations in wild animals, as has been observed in wild rodents (Fuentes *et al.*, 2004; Brouat *et al.*, 2006).

The trematode *Echinostoma luisreyi* has been primarily described in mice and hamsters under experimental conditions (Maldonado *et al.*, 2003) and the natural vertebrate host is now identified as *A. montensis*.

As stated by Brouat *et al.* (2006), the species composition of helminth parasites in a host species may be determined not only by host–parasite relationships but also by host–habitat or parasite–habitat relationships. The activity pattern in *A. montensis* is characterized as twilight and in *A. cursor* as nocturnal (Graipel *et al.*, 2003). Both are completely terrestrial and travel in tunnels under the leaf litter and nest in burrows (Emmons & Feer, 1997). *Akodon cursor* is susceptible to habitat disturbances and is more habitat selective (Gentile & D'Andrea, 2000). *Akodon cursor* and *A. montensis* occur in proximity: *A. cursor* occurs from sea level to 800 m, while *A. montensis* is found above 800 m (Geise & Smith, 2001). The study was carried out at an altitude of 871 m, which represents the boundary of *A. cursor's* distribution. In spite of the small sample of *A. cursor* collected, the data showed the habitat effect on the helminth community structure, since it was reported to be infected by other helminths (Gomes *et al.*, 2003). *Oligoryzomys nigripes* is nocturnal and can be caught on the ground as well as in trees. These rodents build ball nests, usually in trees, although they are also reported to burrow under logs (Emmons & Feer, 1997). These findings suggest a key role of host habitat in shaping the community structure.

Acknowledgements

References

Alho, C.J.R. (1982) Brazilian rodents: their habitats and habits. pp. 143–166 *in* Mares, M.A. & Genoways, H.H. (*Eds*) *Mammalian biology in South America*. The Pymatuning Symposia in Ecology, Special Publication Series, Pymatuning Laboratory of Ecology, Pittsburgh, University of Pittsburgh.

Behnke, J.M., Harris, P.D., Bajer, A., Bernard, C.J., Sherif, N., Cliffe, L., Hurst, J., Lamb, M., Rhodes, A., James, M., Clifford, S., Gilbert, F.S. & Zalat, S. (2004) Variation in the community structures in spiny mice (*Acomys dimidiatus*) from four montane wadis in the St Katherine region of the Sinai Peninsula in Egypt. *Parasitology* **129**, 379–398.

Behnke, J.M., Bajer, A., Harris, P.D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C., Kulis-Malkowska, K., Sinski, E., Gilbert, F.S. & Bernard, C.J. (2008a) Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E. Poland. 1. Regional fauna and component community levels. *Parasitology* **135**, 985–997.

Behnke, J.M., Bajer, A., Harris, P.D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C., Kulis-Malkowska, K., Sinski, E., Gilbert, F.S. & Bernard, C.J. (2008b) Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E. Poland. 2. The infracommunity level. *Parasitology* **135**, 999–1018.

Bonvicino, C.R., Lindbergh, S.M. & Maroja, L.S. (2002) Small non-flying mammals in altered and conserved areas of Atlantic Forest and Cerrado: comments on their potential use for monitoring environment. *Brazilian Journal of Biology* **62**, 1–12.

Bonvicino, C.R., Oliveira, J.A. & D'Andrea, P.S. (2008) *Guia dos Roedores do Brasil*. 1st edn. 122 pp. Rio de Janeiro, Organização Panamericana da Saúde.

Brooks, D.R. & McLennan, D.A. (1993) *Parascript: Parasites and the language of evolution*. 429 pp. Washington, Smithsonian Institution Press.

Brouat, C., Kane, M., Diouf, M., Bâ, K., Sall-Dramé, R. & Duplantier, J.M. (2006) Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology* **134**, 437–450.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology in its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **86**, 575–583.

Bush, A.O., Fernandez, J.C., Esch, G.W. & Seed, J.R. (2001) *Parasitism: the diversity and ecology of animal parasites*. 1st edn. 566 pp. Cambridge, Cambridge University Press.

Digiani, M.C. & Durette-Desset, M.C. (2003) Two new species (Nematode, Nippostrongylinae, Helig-monellidae) from a sigmodontine rodent in Argentina. *Acta Parasitology* **48**, 12–18.

Digiani, M.C., Navone, G.T. & Durette-Desset, M.C. (2007) The systematic position of some nippostrongy-linae nematodes (Trichostrongylina: Heligmosomoi-dea) parasitic in Argentinean sigmodontine rodents. *Systematic Parasitology* **67**, 87–92.

Durette-Desset, M.C. (1985) Trichostrongyloid nema-todes and their vertebrate hosts: reconstruction of

the phylogeny of a parasitic group. *Advances in Parasitology* **24**, 239–306.

Durette-Desset, M.C., Goncalves, A.Q. & Pinto, R.M. (2006) Trichostrongylina (Nematoda, Heligmosomoidea) co-parasitos em *Dasyprocta fuliginosa* Wagler (Rodentia, Dasyproctidae) do Brasil, com o restabelecimento do gênero *Avellaria* Freitas and Lent e a descrição de duas novas espécies. *Revista Brasileira de Zoologia* **23**, 509–519.

Eisenberg, J.G. & Redford, K.H. (1999) *Mammals of the Neotropics: The central Neotropicals*. Vol. **3**, 609 pp. London, University Chicago Press.

Emmons, L.H. & Feer, F. (1997) *Neotropical rainforest mammals. A field guide*. 2nd edn. 307 pp. Chicago, University of Chicago Press.

Feliciano, B.R., Fernandez, F.A.S., De Freitas, D. & Figueredo, M.S.L. (2002) Population dynamics of small rodents in a grassland between fragments of Atlantic Forest in southeastern Brazil. *Mammalian Biology* **67**, 301–314.

Fuentes, M.V., Cerezuela, A.M. & Galan-Punchades, M.T. (2000) A helminthological survey of small mammals (insetivores and rodents) in the Serra Calderona mountains (Valencian Community, Spain). *Research and Reviews in Paratsitololgy* **60**, 25–35.

Fuentes, M.V., Sáez, S., Trelis, V., Galán-Punchades, M.T. & Esteban, J.G. (2004) The helminth community of the wood mouse, *Apodemus sylvaticus*, in the Sierra Espuña, Murcia, Sapin. *Journal of Helminthology* **78**, 219–223.

Geise, L. & Smith, M.F. (2001) Diversification in the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern South America: Mitochondrial DNA sequence analysis. *Journal of Mammalogy* **82**, 92–101.

Gentile, R. & D'Andrea, P.S. (2000) Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study. *Studies on Neotropical Fauna and Environment* **35**, 1–9.

Gentile, R. & Fernandez, F.A.S. (1999) Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. *Mammalia* **63**, 29–40.

Gibson, D.I., Jones, A. & Bray, R.A. (2002) *Keys to the Trematoda*. Vol. 1. 1st edn. 521 pp. London, CABI Publishing and the Natural History Museum.

Gomes, D.C., Cruz, R.P., Vicente, V. & Pinto, R.M. (2003) Nematode parasites of marsupials and small rodents from the Brazilian Atlantic Forest in state of Rio de Janeiro, Brazil. *Revista Brasileira de Zoologia* **20**, 699–707.

Graipel, M.E., Miller, P.R.M. & Glock, L. (2003) Padrão de atividade de *Akodon montensis* e *Oryzomys russatus* na Reserva Volta Velha, Santa Catarina, Sul do Brasil. *Journal of Neotropical Mammalogy* **10**, 255–260.

Jones, A., Bray, R.A. & Gibson, D.I. (2005) *Keys to the Trematoda*. Vol. 2. 1st edn. 768 pp. London, CABI Publishing and the Natural History Museum.

Kennedy, C.R., Bush, A.O. & Aho, J.M. (1986) Patterns in helminth communities: Why are birds and fish different? *Parasitology* **93**, 205–215.

Khalil, L.F., Jones, A. & Bray, R.A. (1994) *Keys to the cestode parasites of vertebrates*. 1st edn. 768 pp. London, CABI Publishing and the Natural History Museum.

Kinsella, J.M. (1990) Comparison of three species of mice, *Apodemus floridays*, *Peromyscus gossypinus*, and *Peromyscus polionotus*, from southern Florida. *Canadian Journal of Zoology* **69**, 3078–3083.

Lacher, J.R., Mares, M.A. & Alho, C.J.R. (1989) The structure of a small mammal community in a central Brazilian savana. pp. 137–162 *in* Eisenberg, J.F. & Redford, K.H. (*Eds*) *Advances in neotropical mammalogy*. Gainesville, Sandhill Crane Press.

Lemos, E.R.S. & D'Andrea, P.S. (2006) Trabalho com animais silvestres. pp. 273–288 *in* Martins, E.V., Martins, A.S., Silva, F.H.A.L., Lopes, M.C.M., Moreno, M.L.V. & Silva, P.C.T. (*Eds*) *Biossegurança, informação e conceitos, textos básicos*. Rio de Janeiro, FIOCRUZ.

León, G., Gardner, S.L. & Falcón-Ordáz, J. (2000) Phylogenetic relationships among species of *Stilestrongylus* Freitas, Lent and Almeida, 1937 (Trichostrongyloidea: Heligmonellidae: Nippostrongylinae), parasites of myomorph rodents (Rodentia: Muridae) in the Neotropics. *Journal of Parasitology* **86**, 1326–1335.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. 192 pp. New Jersey, Princeton University Press.

Maldonado, A. Jr, Vieira, G.O. & Lanfredi, R.M. (2003) *Echinostoma luisreyi* n. sp. (Platyhelminthes: Digenea) by light and scanning electron microscopy. *Journal of Parasitology* **89**, 800–808.

Maldonado, A. Jr, Gentile, R., Fernandes-Moraes, C.C., D'Andrea, P.S., Lanfredi, R.M. & Rey, L. (2006) Helminth communities of *Nectomys squamipes* naturally infected by the exotic trematode *Schistosoma mansoni* in southeastern Brazil. *Journal of Helminthology* **80**, 369–375.

Mattevi, M.S. & Andrades-Miranda, J. (2006) Estudos genéticos nos roedores da tribo Oryzomysi. pp. 107–137 *in* Freitas, T.R.O., Vieira, E., Pacheco, S. & Christoff, A. (*Eds*) *Mamíferos do Brasil: Genética, sistemática, ecologia e conservação*. São Carlos, Editora Sociedade Brasileira de Genética.

Moraes Neto, A.H.A., Lanfredi, V. & De Souza, W. (1996) Emended description of *Litomosoides silvai* (Nematoda: Filarioidea) of *Akodon cursor* (Rodentia: Muridae). *Journal of Parasitology* **82**, 988–991.

Morand, S., Krasnov, B.R. & Poulin, R. (2006) *Micro-mammals and macroparasites from evolutionary ecology to management*. 1st edn. 647 pp. Tokyo, Japan, Springer-Verlag.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Nimer, E. (1989) *Climatologia do Brasil*. 421 pp. Rio de Janeiro, Instituto Brasileiro de Geografia e Estatística/Departamento de Recursos Naturais e Estudos Ambientais.

Notarnicola, J. & Navone, G.T. (2002) A new species, *Litomosoides odilae* n. sp. (Nematoda: Onchocercidae) from *Oligoryzomys nigripes* (Rodentia: Muridae) in the rainforest of Misiones, Argentina. *Journal of Parasitology* **88**, 967–971.

Padula, P., Martinez, V.P., Bellomo, C.B., Maidana, V., Juan, J.S., Tagliaferri, P., Bargardi, V., Vazquez, C., Colucci, N., Estévez, J. & Almiron, M. (2007) Pathogenic hantaviruses, northeastern Argentina and eastern Paraguay. *Emerging Infectious Diseases* **13**, 1211–1214.

Pimm, S.L. & Rosenzweig, M.L. (1981) Competitors and habitat use. *Oikos* **37**, 1–6.

Poulin, R. (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. *International Journal of Parasitology* **23**, 937–944.

Poulin, R. (2007) *Evolutionary ecology of parasites from individuals to communities*. 2nd edn. 332 pp. Princeton, Princeton University Press.

Poulin, R. & Morand, V. (1999) Geographical distances and the similarity among parasite communities of conspecific host population. *Parasitology* **119**, 369–374.

Püttker, T., Pardini, R., Meyer-Lucht, Y. & Sommer, S. (2008) Responses of five small mammal species to micro-scale variations in vegetation structure in secondary Atlantic Forest remnants, Brazil. *BMC Ecology* **8**, 9.

Reig, O.A. (1986) Diversity patterns and differentiation of High Andean rodents. pp. 404–440 *in* Vuilleumier, F. & Monasteiro, M. (*Eds*) *High altitude tropical biogeography*. New York, Oxford University Press.

Robles, M.R. & Navone, G.T. (2007a) A new species of *Syphacia* (Nematoda: Oxyuridae) from *Oligoryzomys nigripes* (Rodentia: Cricetidae) in Argentina. *Parasitology Research* **101**, 1069–1075.

Robles, M.R. & Navone, G.T. (2007b) A new species of *Syphacia* (Nematoda: Oxyuridae) from *Akodon azarae* (Rodentia: Cricetidae) in Argentina. *Journal of Parasitology* **93**, 383–391.

Rósza, L., Reiczigel, V. & Majoros, G. (2000) Quantifying parasites in samples of hosts. *Journal of Parasitology* **86**, 228–232.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science* **185**, 27–39.

Simões, R.O., Gentile, R., Rademaker, V., D'Andrea, P.S., Herrera, H., Freitas, T., Lanfredi, R. & Maldonado, A. Jr (2009) Variation in the helminth community structure of *Thrichomys pachyurus* (Rodentia: Echimyidae) in two sub-regions of the Brazilian Pantanal: the effects of land use and seasonality. *Journal of Helminthology* in press. doi:10.1017/S0022149X09990629.

Souza, J.G.R., Digiani, M.C., Simões, R.O., Luque, J.L., Rodrigues-Silva, R. & Maldonado, A. Jr (2009a) A new heligmonellid species (Nematoda) from *Oligoryzomys nigripes* (Rodentia: Sigmodontinae) in the Atlantic Forest, Brazil. *Journal of Parasitology* **95**, 734–738.

Souza, J.G.R., Simões, R.O., Thiengo, S.A.R.C., Lima, W., Mota, E., Rodrigues-Silva, R., Lanfredi, R.M. & Maldonado, A. Jr (2009b) A new metastrongilidae species (nematoda): A lungworm from *Akodon montensis* (Rodentia: Sigmodontinae) in Brazil. *Journal of Parasitology* **95**, 1507–1511.

Sutton, C.A. & Durette-Desset, M.C. (1991) Nippostrongylinae (Nematoda: Trichostrongyloidea) parasites d'*Oryzomys flavescens* en Argentine et en Uruguay. *Revue Suisse de Zoologie* **98**, 535–553.

Suzuki, A., Bisordi, I., Levis, S., Garcia, J., Pereira, L.E., Souza, R.P., Sugahara, T.K.N., Pini, N., Enria, D. & Souza, L.T.M. (2004) Identifying rodent hantavirus reservoirs, Brazil. *Emerging Infectious Diseases* **10**, 2127–2134.

Travassos, L. (1927) Nematódeos novos. *Boletim de Biologia* **6**, 52–61.

Travassos, L. (1937) *Revisão da família Trichostrongylidae Leiper, 1912*. 512 pp. Rio de Janeiro, Monografia do Instituto Oswaldo Cruz.

Travassos, L. & Freitas, J.F.T. (1941) Relatório da terceira excursão a zona da Estrada de Ferro Noroeste do Brasil realizada em fevereiro e março de 1940. II Pesquisas helmintológicas. *Memórias do Instituto Oswaldo Cruz* **35**, 610–634.

Vaz, V.C., D'Andrea, P.S. & Jansen, A.M. (2007) Effects of habitat fragmentation on wild mammal infection by *Trypanosoma cruzi*. *Parasitology* **34**, 1785–1793.

Vicente, J.J., Rodrigues, H.O., Gomes, D.C. & Pinto, R.M. (1997) Nematóides do Brasil. Parte V: Nematóides de mamíferos. *Revista Brasileira de Zoologia* **14**, 1–452.

Wilkinson, L. (1990) *SYSTAT: The system for statistics*. 822 pp. Evanston, Illinois, Systat Inc.

Yamaguti, F. (1961) *Sistema Helminthum. Vol II. The nematodes of vertebrates*. 1261 pp. New York, Interscience Publisher.

Zar, J.H. (1999) *Biostatistical Analysis*. 4th edn. 960 pp. New Jersey, Prentice Hall.