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HELMINTH COMMUNITY STRUCTURE OF TWO SIGMODONTINE RODENTS IN SERRA DOS ÓRGÃOS NATIONAL PARK, STATE OF RIO DE JANEIRO, BRAZIL

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Abstract: The fauna and community structure of the helminths of two sympatric sigmodontine rodent hosts, *Akodon montensis* (Thomas, 1913) and *Oligoryzomys nigripes* (Olfers, 1818) (Rodentia, Cricetidae) were studied in two areas of an Atlantic Forest reserve, the Serra dos Órgãos National Park in Petrópolis and Teresópolis municipalities, state of Rio de Janeiro, Brazil. During the study, 127 rodents were collected, among which 63 were parasitized (approximately 50%). The helminths recovered from *A. montensis* were the nematodes *Protospirura numidica criceticola*, *Stilestrongylus aculeata*, *Stilestrongylus eta*, *Stilestrongylus lanfrediae* and *Trichofreitasia lenti*; the trematode *Canaania obesa* and the cestode *Rodentolepis akodontis*. *Oligoryzomys nigripes* was infected by *Avellaria* sp., *Guerrerostrongylus zetta*, *T. lenti* and *S. lanfrediae*. Complete host specificity was observed in all helminth species only in Petrópolis; although *T. lenti* and *S. lanfrediae* were shared between host species in Teresópolis. *Stilestrongylus aculeata*, *S. eta* and *S. lanfrediae* had the greatest abundance, i.e. considering all hosts, and intensity, i.e. considering only infected hosts, in the study. *Stilestrongylus lanfrediae* and *G. zetta* were the most prevalent species. *Guerrerostrongylus zetta* and *S. lanfrediae* had higher abundance and prevalence in adult hosts. The latter species also had higher abundance and prevalence in male hosts. *Stilestrongylus aculeata* and *S. eta* had higher prevalence in young female hosts, and *T. lenti*, higher abundance in males and higher prevalence in adult females of *A. montensis*. Only the helminth community of *O. nigripes* in Teresópolis followed a nested pattern of species distribution. All the other helminth communities in *A. montensis* and *O. nigripes* had random patterns of species distribution. The results suggest the existence of intrinsic characteristics between hosts and parasites as well as different patterns of associations in those interactions with the environment.

Keywords: *Akodon montensis*; Atlantic Forest; host-parasite interaction; *Oligoryzomys nigripes*; parasitism.

INTRODUCTION

Parasites are highly diverse organisms and important components of ecosystems (Combes 2001, Poulin 2007). They can change their hosts' physiology and population dynamics, mediate other interactions such as competition and predation, and influence the species diversity in an ecosystem through the cascade effect (Thomas *et al.* 2005). Thus, the study of parasite populations and communities are important for understanding several local and regional ecological processes, considering infracommunities (communities within an individual host) and component communities (communities including the entire local host population) (Poulin 2007).

The occurrence and abundance of parasites and their distribution patterns vary according to several host attributes, such as phylogenetic history, gender, age, behaviour, body mass, immune response to infection and also in response to temporal and spatial variations in the host populations (Behnke *et al.* 1999). Characteristics of the environment also influence the parasites occurrence, such as weather, seasonality and habitat (Simões *et al.* 2010, Castro *et al.* 2017). Moreover, an increase in host diversity may reflect an increase in parasite diversity in the environment (Poulin 2014).

Helminths are a group of parasites considered good indicators of environmental changes; as such, they are excellent models for studies of host-parasite interactions in ecology. However, there is a large gap concerning surveys of helminth faunas of wild mammals and studies of helminth community structures. Sigmodontine rodents comprise one of the groups of Neotropical mammals that present the greatest species diversity (Patton *et al.* 2015). In addition, many rodents are reservoirs of pathogens of medical and veterinary importance and may share several parasites with humans and other mammals (Han *et al.* 2016). Although there are several studies reporting the helminth fauna of Brazilian rodents, compiled in Pinto *et al.* (2011), few studies have investigated their communities' structures and the influence of ecological aspects on the population parameters of the helminths (Maldonado Jr. *et al.* 2006, Püttker *et al.* 2008, Simões *et al.* 2010, 2011).

The Serra dos Órgãos National Park (hereafter PARNASO) is one of the most important forest remnants of the Atlantic Forest biome in the state of Rio de Janeiro, southeastern Brazil. The aim of the present study was to describe the helminth species composition and to analyse the helminth community structure of two sympatric sigmodontine rodents, *Akodon montensis* (Thomas, 1913) and *Oligoryzomys nigripes* (Olfers, 1818) (Rodentia, Cricetidae), in areas of mountain forest in PARNASO, Petrópolis and Teresópolis municipalities, state of Rio de Janeiro, Brazil. We also investigated the influence of host gender, host age and area (Petrópolis and Teresópolis municipalities) on the abundance and prevalence of the helminths. Data from the helminth fauna of PARNASO-Teresópolis was previously published by Simões *et al.* (2011) and included in the community analysis. This study is part of a comprehensive project on biodiversity that aims to survey the Atlantic Forest fauna in preserved areas, including taxonomic, evolutionary, ecological and parasitological aspects.

MATERIAL AND METHODS

Study sites

PARNASO is a preserved forest with an area of 20,024 ha comprising the municipalities of Teresópolis, Petrópolis, Magé and Guapimirim, state of Rio de Janeiro, Brazil. The study area presents a continuous, dense, ombrophilous vegetation of Mountain Atlantic Forest. The climate of the region is highland mesothermic (Cwb), according to Köppen's classification, with mild temperatures, rainy summers and a dry season between June and August (Ayoade 1986). Samplings were taken in different localities and years: Bonfim (22º27'38.8" S, 43º05'35.3" W, *datum* WGS84), Barragem do Caxambú (22°30'19.2" S, 43º07'12.3" W, *datum* WGS84), and Uricanal (22º29'41.9" S, 43º07'31.0" W, *datum* WGS84) in the municipality of Petropólis in late spring 2014 (rainy season) and winter 2015 (dry season), and PARNASO head unit in municipality of Teresópolis (22°27'17.17" S, 42°59'59.10" W, *datum* WGS84) in winter 2004 (dry season) and late summer 2005 (rainy season).

Collection and examination of rodents

Samplings were taken in six linear transects with

15 trapping points in Petrópolis and four transects with 20 trapping points in Teresópolis using Tomahawk (40.64 cm x 12.70 cm x 12.70 cm) and Sherman traps (7.62 cm x 9.53 cm x 30.48 cm) on the ground and in the understorey. All these transect were 300 m long. These traps were baited with a mixture of peanut butter, banana, oats and bacon. In Petrópolis, pitfall traps were used in four additional transects with 20 trapping points and 200 m long. The rodents were euthanized and necropsied, and their bionomic data were recorded (*i.e.*, age, gender, reproductive activity, body mass and external measurements). Host ages were based on body mass (grams), dividing individuals into two classes: juvenile (< 28 g for *A. montensis* and < 18 g for *O. nigripes*) and adult (≥ 28 g for *A. montensis* and ≥ 18 g for *O. nigripes*) (adapted from Teixeira *et al.* 2014). Rodents were identified by external and cranial morphology and by cytogenetics analysis (diploid number) (Bonvicino *et al.* 2008).

Animals were captured under authorization of the Brazilian Institute of Environment and Renewable Natural Resources, licence numbers 061/2003, 064/2004, 129/2004 and 068/2005 and Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBIO, license number 45839- 1). All procedures followed the guidelines for capture, handling and care of animals of the Ethical Committee on Animal Use of the Oswaldo Cruz Foundation (CEUA license numbers P-0083-01 and LW – 39/14). Biosafety techniques and personal safety equipment were used during all procedures involving animal handling and biological sampling.

The viscera, thoracic and abdominal cavities, stomach, lungs, liver, pelvis and musculature of the rodents were examined for helminths. Nematodes, trematodes and cestodes recovered were washed in saline solution (NaCl 0.85%) and fixed in AFA (2 parts 100% acetic acid, 5 parts 0.4% formol and 93 parts 70% ethanol). Nematodes were cleared in lactophenol, and trematodes and cestodes were stained with chlorhydric carmine. Helminths were identified under a Zeiss Standard 20 light microscope (Zeiss, Jena, Germany). Taxonomic identification was carried out following Travassos (1937), Yamaguti (1961), Khalil *et al.* (1994), Vicente *et al.* (1997) and Bray *et al.* (2008). Voucher specimens of the rodents were deposited at scientific collection of the Department of Vertebrates of the National Museum of Rio de Janeiro, and those of helminths were deposited at the Helminthological Collection of the Oswaldo Cruz Institute (CHIOC numbers 38556, 38557, 38558, 38559, 38560, 38561, 38562 and 38563).

Data analysis

Parasitological parameters were calculated for each species of helminth according to Bush *et al.* (1997). Overall species richness of the helminths was considered as the number of species found, and the mean species richness of the helminths was the number of helminth species in each infracommunity divided by the number of analysed infracommunities. Estimated species richness was calculated using the Jackknife 1 method for each host species, considering the two areas together. Species diversity was estimated using the Shannon Index (*H'*) and equitability using the Pielou index (*J*) for each host species and each area. The Jaccard qualitative index was used to investigate the similarity in the helminth species composition between hosts, between areas, and overall.

Mean abundance was considered as the total number of individuals of a helminth species divided by the number of analysed rodents. Mean intensity was calculated as the total number of individuals of a helminth species divided by the number of rodents infected with this species. Prevalence of each helminth species was calculated as the proportion of the infected rodents for a given helminth species in relation to the total number of analysed rodents.

The influence of host gender, host age, sampling area (Teresópolis and Petrópolis) and host species (only for the helminth species shared between the two rodent species) on the abundance and prevalence were tested using generalized linear models (GLM). Models containing all possible combinations of the variables were tested (global model: Host Gender + Host Age + Area + Host Species). The best models were chosen using the corrected Akaike information criterion (AICc), in which the plausible models presented ΔAICc ≤ 2. The modelling significance was evaluated comparing each plausible model with the null model using analysis of variance (ANOVA). The GLM analysis for abundance followed a Gaussian distribution and for prevalence, a binomial distribution. These tests were only performed for the helminth species whose overall prevalence was higher than 10% and/or for species with sufficient data for the analysis.

Nested subset analyses were used to examine whether the distribution patterns of the helminth species in their communities of each host followed a nested pattern (Patterson & Atmar 1986), considering a matrix of species presence or absence in each infracommunity. This analysis was performed for the infracommunities of *A. montensis* and *O. nigripes* separately using the nestedness measure of overlap and decreasing fills metric (NODF) (Almeida-Neto *et al.* 2008). The observed pattern was compared with the null model by generating 1000 random matrices. This analysis was carried out for each area separately (PARNASO-Petrópolis and PARNASO-Teresópolis) and for both areas gathered. Importance indices of helminth species were calculated according to Thul *et al.* (1985) for each host component community. Each helminth species was classified in the community as dominant species (I ≥ 1.0), co-dominant (0.01 ≤ I < 1.0) or subordinate (0 < I < 0.01).

All analyses were performed with RStudio software version 1.0.136, considering a 5% significance level. For the ANOVA tests, we used the stats package (R Core Team 2017); for GLM, Jackknife 1 method, Shannon–Wiener and Equitability diversity indices, the vegan package (Oksanen *et al.* 2017); and for nestedness, the bipartite package (Dormann *et al.* 2008).

RESULTS

Overall, 127 hosts were collected: 8 *A. montensis* and 14 *O. nigripes* in Teresópolis and 62 *A. montensis* and 43 *O. nigripes* in Petrópolis. Considering the two areas, 63 rodents were parasitized by one or more species of helminths, with 26 specimens of *A. montensis* and 37 of *O. nigripes* infected. A total of 2606 specimens of helminths were collected: 70 from *A. montensis* and 972 from *O. nigripes* in Teresópolis and 679 from *A. montensis* and 885 from *O. nigripes* in Petrópolis.

Host specificity was observed for all helminth species only in Petrópolis, with six helminth species recovered from *A. montensis* and two from *O. nigripes* (Tables 1 and 2). Helminths recovered from *A. montensis,* considering both areas, were the nematodes *Protospirura numidica criceticola* (Quentin, Karimi & Rodrigues De Almeida, 1968) (Spirurida, Spiruridae), *Stilestrongylus aculeata* (Travassos, 1918), *Stilestrongylus eta* (Travassos, 1937), *Stilestrongylus lanfrediae* Souza, Digiani, Simões, Luque, Rodrigues-Silva & Maldonado Jr., 2009 and *Trichofreitasia lenti* Sutton & Durette-Desset, 1991 (Rhabditida, Heligmonellidae); the trematode *Canaania obesa* (Travassos, 1944) (Digenea, Dicrocoeliidae) and the cestode *Rodentolepis akodontis* (Rêgo, 1967) (Cyclophyllidea, Hymenolepididae). Four helminth species were recovered from *O. nigripes*, the nematodes *Avellaria* sp. (Rhabditida, Viannaiinae), *Guerrerostrongylus zetta* (Travassos, 1937) Sutton & Durette-Desset, 1991 (Rhabditida, Heligmonellidae), *S. lanfrediae* and *T. lenti*.

Oligoryzomys nigripes presented higher mean richness in relation to *A. montensis*, whether considering Teresópolis (1.92 and 1.62, respectively), Petrópolis (0.69 and 0.45, respectively) or both areas together (1 and 0.58, respectively). The estimated species richness of helminths was 8.5 ± 0.5 (± SE) for *A. montensis* and 5 ± 1 (± SE) for *O. nigripes*, considering the two areas simultaneously. Teresópolis was the area with the greater helminth diversity and equitability, either for *A. montensis* (Teresópolis: H' = 1.13 and J = 0.70; Petrópolis: H' = 0.72 and J = 0.40) or for *O. nigripes* (Teresópolis: H' = 0.75 and J = 0.54; Petrópolis: H' = 0.21 and J = 0.31). The Jaccard indices indicated that helminth species composition were more similar within each host when compared between areas (0.57 for *A. montensis* and 0.50 for *O. nigripes*) than between host species within areas (0.28 in Teresópolis; 0 in Petrópolis). Low similarity was also observed for the helminth species composition between the two rodents, considering both areas (0.22).

Intensity was higher for the three species of the genus *Stilestrongylus*, *S. aculeata* and *S. eta* in *A. montensis* (Table 1) and *S. lanfrediae* in *O. nigripes* (Table 2). The helminth intensity was higher in adult male hosts collected in Teresópolis for most species, except for *S. eta* that presented higher intensity in young female hosts in Petrópolis, *P. n. criceticola,* with higher intensity in females , and *S. aculeata* and *S. eta,* with higher values in Petrópolis (Tables 1 and 2).

The most abundant helminth species were *S. aculeata* for *A. montensis* (Table 1) and *S. lanfrediae*

Table 1. Mean abundance and mean intensity of the helminths followed by standard deviation, and helminth prevalence (%) with 95% confidence limits of *Akodon montensis* (Rodentia, Cricetidae) in the Serra dos Órgãos National Park, Teresópolis and Petrópolis municipalities, state of Rio de Janeiro, Brazil.

Parameters	Helminth species						
	Stilestrongylus aculeata	*Stilestrongylus eta*	*Stilestrongylus lanfrediae*	*Protospirura n. criceticola*	*Trichofreitasia lenti*	*Canaania obesa*	*Rodentolepis akodontis*
Abundance	7.54 ± 32.03	2.07 ± 13.63	0.01 ± 0.11	0.11 ± 0.55	0.62 ± 2.36	0.22 ± 1.33	0.10 ± 0.45
Male hosts	6.30 ± 34.38	0.13 ± 0.83	0.01 ± 0.13	0.05 ± 0.30	0.77 ± 2.68	0.30 ± 1.52	0.07 ± 0.43
Female hosts	11.41 ± 23.72	8.11 ± 27.35	0	0.29 ± 0.98	0.17 ± 0.52	0	0.17 ± 0.52
Juvenile hosts	10.12 ± 20.77	5.66 ± 23.14	0	0	0.16 ± 0.81	0	0.12 ± 0.44
Adult hosts	6.19 ± 36.71	0.19 ± 0.85	0.02 ± 0.14	0.17 ± 0.67	0.86 ± 2.83	0.34 ± 1.63	0.08 ± 0.46
Petrópolis	8.27 ± 33.97	2.19 ± 14.47	0	0.06 ± 0.30	0.04 ± 0.21	0.25 ± 1.41	0.11 ± 0.48
Teresópolis	1.87 ± 3.94	1.12 ± 2.23	0.12 ± 0.35	0.50 ± 1.41	5.12 ± 5.33	0	0
Intensity	27.78 ± 66.68	24.16 ± 43.87	1	2.00 ± 1.41	4.40 ± 4.92	5.33 ± 4.50	1.75 ± 0.95
Male hosts	47.71 ± 89.11	3.50 ± 3.53	1	1.50 ± 0.70	5.12 ± 5.30	5.33 ± 4.50	2.00 ± 1.41
Female hosts	32.33 ± 31.45	34.50 ± 52.69	0	2.50 ± 2.12	1.50 ± 0.70	0	1.5 ± 0.70
Juvenile hosts	30.37 ± 26.73	45.33 ± 58.85	0	0	4	0	1.50 ± 0.70
Adult hosts	57.00 ± 107.44	3.00 ± 2.00	1	2.00 ± 1.41	4.44 ± 5.22	5.33 ± 4.50	2 ± 1.41
Petrópolis	46.64 ± 71.23	34.00 ± 53.10	0	1.33 ± 0.57	1 ± 0	5.33 ± 4.50	1.75 ± 0.95
Teresópolis	7.50 ± 4.94	4.50 ± 2.12	1	4	5.85 ± 5.30	0	0
Prevalence	18.6 (10.3-29.7)	8.6 (3.2-17.7)	1.4 (0-7.7)	5.7 (1.6-14.0)	14.3 (7.1-24.7)	4.3 (0.9-12)	5.7 (1.6-14.0)
Male hosts	13.2 (5.5-25.3)	3.8 (0.5-13.0)	1.9 (0-10.1)	3.8 (0.5-13.0)	15.1 (6.7-27.6)	5.7 (1.2-15.7)	3.8 (0.5-13.0)
Female hosts	35.3 (14.2-61.0)	23.5 (6.8-49.9)	0	11.8 (1.5-36.4)	11.8 (1.5-36.4)	0	11.8 (1.5-36.4)
Juvenile hosts	33.3 (15.6-55.3)	12.5 (2.7-32.4)	0	0	4.2 (0.1-21.1)	0	8.3 (1.0-27.0)
Adult hosts	10.9 (3.6-23.6)	6.5 (1.4-17.9)	2.2 (0.1-11.5)	8.7 (2.4-20.8)	19.6 (9.4-33.9)	6.5 (1.4-17.9)	4.3 (0.5-14.8)
Petrópolis	17.7 (9.2-29.5)	6.5 (1.8-15.7)	0	4.8 (1-13.5)	4.8 (1-13.5)	4.8 (1-1.35)	6.5 (1.8-15.7)
Teresópolis	25.0 (16.2-33.7)	25.0 (20.0-29.9)	12.5 (11.7-13.2)	12.5 (9.3-15.6)	87.5 (75.6-163.1)	0	0

Table 2. Mean abundance and mean intensity of the helminths followed by standard deviation, and helminth prevalence (%) with 95% confidence limits of *Oligoryzomys nigripes* (Rodentia, Cricetidae) in the Serra dos Órgãos National Park, Teresópolis and Petrópolis municipalities, state of Rio de Janeiro, Brazil.

Parameters	Helminth species			
	Avellaria sp.	*Guerrerostrongylus zetta*	*Stilestrongylus lanfrediae*	*Trichofreitasia lenti*
Abundance	0.29 ± 2.25	7.33 ± 25.04	24.91 ± 41.15	0.03 ± 0.18
Male hosts	0.39 ± 2.59	8.53 ± 28.53	28.04 ± 42.42	0.02 ± 0.15
Female hosts	0	3.64 ± 7.22	15.28 ± 36.74	0.07 ± 0.26
Juvenile hosts	0	1 ± 4.38	11.40 ± 20.96	0
Adult hosts	0.53 ± 3.00	12.28 ± 32.57	29.66 ± 43.47	0.06 ± 0.24
Petrópolis	0	1.16 ± 3.77	19.41 ± 35.21	0
Teresópolis	1.21 ± 4.54	26.28 ± 46.30	41.78 ± 53.71	0.14 ± 0.36
Intensity	17	20.90 ± 39.38	41.76 ± 46.36	1
Male hosts	17	22.93 ± 43.90	43.07 ± 46.13	1
Female hosts	0	12.75 ± 8.46	35.66 ± 51.36	1
Juvenile hosts	0	6.25 ± 10.50	23.75 ± 25.27	0
Adult hosts	17	24.56 ± 43.25	51.59 ± 52.50	1
Petrópolis	0	5.55 ± 6.87	39.76 ± 41.88	0
Teresópolis	17	33.45 ± 50.23	45.00 ± 54.48	1
Prevalence	1.7 (0-3.6)	35.0 (14.2-55.8)	59.6 (25.4-93.8)	3.5 (3.3-6.8)
Male hosts	2.3 (0-4.8)	37.2 (9.9-64.4)	65.1 (24.5-105.6)	2.3 (2.1-2.4)
Female hosts	0	28.6 (8.4-58.1)	42.9 (17.7-71.1)	7.1 (0.2-33.9)
Juvenile hosts	0	16.0 (10.4-21.5)	48.8 (21.7-74.2)	0
Adult hosts	3.1 (0.1-16.2)	50.0 (31.9-68.1)	68.8 (50.0-83.9)	6.2 (0.8-20.8)
Petrópolis	0	20.9 (17.3-24.5)	48.8 (15.1-82.5)	0
Teresópolis	7.1 (0.4-14.7)	78.6 (0.9-156.1)	92.8 (2.8-182.8)	14.3 (13.6-14.8)

for *O. nigripes* (Table 2). The GLM analysis showed that *G. zetta* had higher abundance and prevalence values in adult hosts, collected in Teresópolis (Tables 2 and 3). For *S. aculeata* and *S. eta* prevalence, the plausible models were observed in relation to host gender, host age, and area, so that young female hosts collected in Teresópolis had higher prevalence (Tables 1 and 3). *Stilestrongylus eta* abundance was also higher for young females (Tables 1 and 3). The abundance of *S. aculeata* was not influenced by any of the analysed variables, as the null model was the only plausible in the GLM analysis (Table 3). *Stilestrongylus lanfrediae* had higher abundance and prevalence values in adult male specimens of *O. nigripes*, collected in Teresópolis (Tables 2 and 3). *Trichofreitasia lenti* had higher abundance in male specimens of *A. montensis* collected in Teresópolis, and higher prevalence in adult females also in Teresópolis (Tables 1, 2 and 3). *Avellaria* sp. and *C. obesa* only occurred in adult male hosts collected in Teresópolis and Petrópolis, respectively. *Protospirura n. criceticola* was only found in adult hosts, and *R. akodontis* in hosts collected in Petrópolis (Table 1).

Stilestrongylus lanfrediae and *G. zetta* were dominants in the component community of *O. nigripes*, either considering each area separately or together (Table 4). However, considering both areas together, the helminth *T. lenti* recovered from *O. nigripes* was the only subordinate species (Table 4). In the rodent *A. montensis*, the helminths *S. aculeata* and *S. eta* were considered dominant species, either

Table 3. Generalized Linear Models (GLM) for abundance and occurrence of the most prevalent helminth species recovered from *Akodon montensis* and/or *Oligoryzomys nigripes* (Rodentia, Cricetidae) in the Serra dos Órgãos National Park, Teresópolis and Petrópolis municipalities, state of Rio de Janeiro, Brazil. ΔAICc = difference between the model with smallest AICc (corrected version of Akaike information criterion) and each model; Weight = Akaike weights, K = number of parameters of the model. Except for the null model, only models with ΔAICc ≤ 2 were shown.

Helminth species	Models	Δ AICc	Weight	K
Abundance				
Guerrerostrongylus zetta	Area	0	0.500	3
	Age+Area	1.37	0.252	4
	Null	9.76	0.004	2
Stilestrongylus aculeata	Null	0	0.380	2
Stilestrongylus eta	Gender	0	0.323	3
	Age+Gender	0.79	0.217	4
	Null	2.44	0.095	2
Stilestrongylus lanfrediae	Age+Host species+Area	0	0.283	5
	Age+Host species	0.75	0.195	4
	Host species+Area	1.06	0.167	4
	Age+Gender+Host species+Area	1.95	0.107	6
	Null	24.88	0	2
Trichofreitasia lenti	Host species+Area	0	0.517	4
	Gender+Host species+Area	1.85	0.205	5
	Null	28.66	0	2
Prevalence				
Guerrerostrongylus zetta	Age+Area	0	0.489	3
	Area	1.30	0.256	2
	Null	14.35	0	1
Stilestrongylus aculeata	Age+Gender	0	0.250	3
	Age	0.07	0.241	2
	Gender	1.34	0.128	2
	Age+Area	1.34	0.127	3
	Age+Gender+Area	1.36	0.127	4
	Null	2.96	0.057	1
Stilestrongylus eta	Gender+Area	0	0.320	3
	Gender	0.38	0.265	2
	Age+Gender+Area	1.54	0.148	4
	Null	3.63	0.052	1
Stilestrongylus lanfrediae	Host species+Area	0	0.337	3
	Gender+Host species+Area	0.54	0.258	4
	Age+Host species+Area	0.57	0.253	4
	Age+Gender+Host species+Area	1.68	0.146	5
	Null	71.72	0	1
Trichofreitasia lenti	Age+Host species+Area	0	0.378	4
	Host species+Area	0.15	0.350	3
	Age+Gender+Host species+Area	1.90	0.146	5
	Null	33.81	0	1

in each area or for the overall data set (Table 4). Moreover, the helminths *T. lenti* and *P. n. criceticola* from Teresópolis hosts and *T. lenti* in both areas were dominants in *A. montensis*. All other helminth species were co-dominants (Table 4).

Only the component community of *O. nigripes* in Teresópolis followed a nested pattern of species distribution (NODF = 39.08, $p < 0.01$) (Figure 1). All other component communities analysed followed a random pattern of species distribution, either within areas or overall ($p > 0.05$ in all cases).

Table 4. Importance indices for the helminth communities of *Oligoryzomys nigripes* and *Akodon montensis* (Rodentia, Cricetidae) in the Serra dos Órgãos National Park, Teresópolis and Petrópolis municipalities, state of Rio de Janeiro, Brazil.

Hosts and Helminth species	Index of importance	Classification
Oligoryzomys nigripes		
Petrópolis		
Guerrerostrongylus zetta	2.50	Dominant
Stilestrongylus lanfrediae	97.49	Dominant
Teresópolis		
Avellaria sp.	0.14	Co-dominant
Guerrerostrongylus zetta	34.67	Dominant
Stilestrongylus lanfrediae	65.14	Dominant
Trichofreitasia lenti	0.03	Co-dominant
Teresópolis and Petrópolis		
Avellaria sp.	0.03	Co-dominant
Guerrerostrongylus zetta	14.75	Dominant
Stilestrongylus lanfrediae	85.20	Dominant
Trichofreitasia lenti	< 0.01	Subordinated
Akodon montensis		
Petrópolis		
Canaania obesa	0.76	Co-dominant
Protospirura numidica criceticola	0.19	Co-dominant
Rodentolepis akodontis	0.44	Co-dominant
Stilestrongylus aculeata	89.79	Dominant
Stilestrongylus eta	8.65	Dominant
Trichofreitasia lenti	0.14	Co-dominant
Teresópolis		
Protospirura numidica criceticola	1.17	Dominant
Stilestrongylus aculeata	8.82	Dominant
Stilestrongylus eta	5.29	Dominant
Stilestrongylus lanfrediae	0.29	Co-dominant
Trichofreitasia lenti	84.41	Dominant
Teresópolis and Petrópolis		
Canaania obesa	0.57	Co-dominant
Protospirura numidica criceticola	0.38	Co-dominant
Rodentolepis akodontis	0.33	Co-dominant
Stilestrongylus aculeata	82.86	Dominant
Stilestrongylus eta	10.50	Dominant
Stilestrongylus lanfrediae	0.01	Co-dominant
Trichofreitasia lenti	5.31	Dominant

DISCUSSION

The observed and the estimated indices of helminths species richness indicated larger species richness in *A. montensis* when compared with *O. nigripes*. However, the higher mean species richness observed in *O. nigripes* suggests a greater susceptibility of their infracommunities to infection and reflect coinfection between their helminth species. The strictly terrestrial behaviour

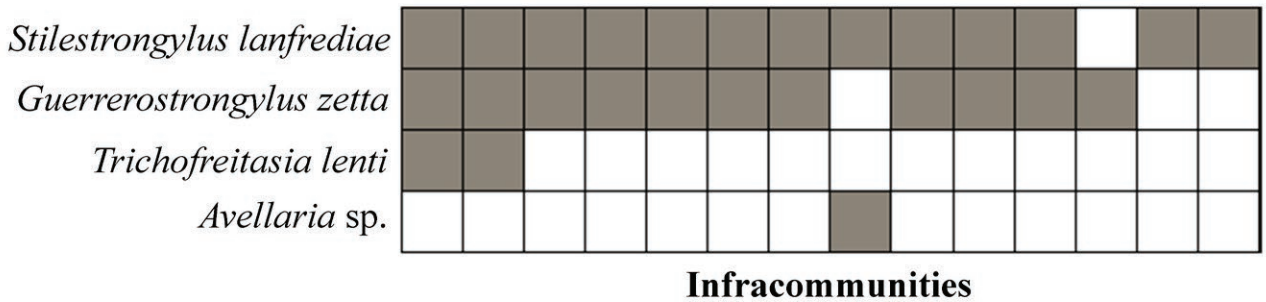

Figure 1. Ordinated matrix for the helminth community of *Oligoryzomys nigripes* (Rodentia, Cricetidae) on the infracommunity level showing a nested pattern of species distribution in the Serra dos Órgãos National Park, Teresópolis, state of Rio de Janeiro, Brazil. The lines correspond to the helminth species and the columns correspond to the host specimens analysed. Filled squares represent species occurrence in an infracommunity.

of *A. montensis* in relation to *O. nigripes*, which has a scansorial habit (Paglia *et al.* 2012), may be a determinant of the greater overall helminth richness in the former host, since it has more direct contact with the soil, especially for helminths with direct life cycle (Callinan & Westcott 1986). Wells *et al.* (2007) showed that the scansorial habit of a Malaysian rodent, *Niviventer cremoriventer* (Rodentia, Muridae), might have contributed to its lower infection by directly transmitted helminths. Moreover, other studies carried out in the Atlantic Forest also recorded higher overall helminth species richness in *A. montensis* in relation to *O. nigripes* (Püttker *et al.* 2008, Kuhnen *et al.* 2012).

Comparing the areas, only in Teresópolis, where helminth species richness in *O. nigripes* was higher than in Petrópolis, we observed species sharing between host species. This may be due to the local characteristics of each area or to temporal differences between Petrópolis and Teresópolis samplings, which where 10 years apart. Teresópolis was the most diverse area, with higher equitability values of helminth species, indicating less dominance of a specific parasite in both hosts. The higher similarity observed between areas within a host than between hosts was expected due to the evolutionary history between parasites and their hosts (Poulin 2007), furthermore, temporal differences have to be considered. In addition, although these hosts are sympatric, differences in their microhabitat use (Dalmagro & Vieira 2005, Cardoso *et al.* 2016) may have favoured the local host specificity in some helminth species.

The species *S. aculeata* was recovered from rodents of the genus *Akodon* in the state of Rio de Janeiro (Gomes *et al.* 2003) and in Argentina (Panisse *et al.* 2017). *Stilestrongylus eta* was recorded in *O. nigripes* (Gomes *et al.* 2003) and in the genus *Akodon* (Durette-Desset & Digiani 2010), both in the state of Rio de Janeiro. The species *P. n. criceticola* was found in several hosts including carnivores (Stein *et al.* 1994) and rodents (Quentin 1971, Grundmann *et al.* 1976, Sutton 1989, Jiménez-Ruiz & Gardner 2003, Miño 2008). *Guerrerostrongylus zetta* was previously reported in different species of rodents from northern to southeastern Brazil, as well as in Argentina (Werk *et al.* 2016). The species *S. lanfrediae* was previously reported in *O. nigripes* in Argentina (Panisse *et al.* 2017). The genus *Avellaria* was originally described in *Cuniculus paca* (Rodentia, Cuniculidae) (reported as *Agouti paca*) in Rio de Janeiro by Freitas & Lent (1934). Simões *et al.* (2010) also recorded a species of this genus, *Avellaria Intermedia* (Nematoda, Viannaiidae) infecting the rodent *Thrichomys pachyurus* (Rodentia, Echimyidae) in Pantanal. The trematode *C. obesa* was originally described from *A. cursor* (Rodentia, Cricetidae) specimens in the Atlantic Forest (Travassos 1944). Maldonado Jr. *et al.* (2010) reported the occurrence of this species in *A. montensis*, *A. cursor*, *O. nigripes* and *Nectomys squamipes* (Rodentia, Cricetidae) in the mountain region of the state of Rio de Janeiro, and suggested that the genus *Akodon* is the most important host of this parasite. The nematode *T. lenti* and the cestode *R. akodontis* were previously found parasitizing *A. montensis* in Argentina (Panisse *et al.* 2017).

Considering the helminth fauna of *A. montensis* described in the literature, several species and genera were previously registered for this host and were not observed either in PARNASO-Petrópolis or in PARNASO-Teresópolis. The helminth species list for this host also includes *Eucoleus* sp., *Trichuris navonae* (Nematoda, Trichuridae), *Platynosomoides* sp. (Platyhelminthes, Dicrocoeliidae) and *Tapironema coronatum* (Nematoda, Cooperiidae) in Argentina (Robles 2011, Panisse *et al.* 2017). For *O. nigripes*, the helminth species list includes *Echinoparyphium scapteromae* (Platyhelminthes, Echinostomatidae), *Litomosoides bonaerensis*, *Litomosoides navonae* (Nematoda, Onchocercidae), *Stilestrongylus flavescens*, *Hassalstrongylus epsilon* (Nematoda, Heligmonellidae) and *T. coronatum* registered in Argentina (Navone *et al.* 2009, Panisse *et al.* 2017), and *Trichuris travassosi* (Nematoda, Trichuridae) registered in the state of Rio Grande do Sul (Gomes *et al.* 1992). However, many of those records suggest regional variations in the composition of the helminth community of these rodent species.

Among the nine helminths species recorded in the present study, three are from the genus *Stilestrongylus*, and presented the highest abundance and intensity in their hosts. This genus was previously reported as a group of common parasites of sigmodontine rodents, suggesting a co-evolutionary process (Digiani & Durette-Desset 2003, Simões *et al.* 2011). Cardoso *et al.* (2016) also observed a higher abundance of *S. aculeata* and *S. eta* in *A. montensis* and *S. lanfrediae* in *O. nigripes* in forest fragments surrounding Parnaso. The genus *Stilestrongylus* is considered the most common helminth taxon in these rodents (Digiani & Durette-Desset 2003).

The highest intensity values for most helminth species in adult male hosts corroborates the pattern most commonly observed in studies of mammalian helminths (Zuk & McKean 1996, Behnke *et al.* 1999, Poulin 2007). The higher prevalence and abundance of *S. lanfrediae* and *G. zetta* in adult male hosts of *O. nigripes*, as well as the higher abundance of *T. lenti* in males of *A. montensis* may be related to the more exploratory behaviour of males of these rodent species (Püttker *et al.* 2006, Owen *et al.* 2010). In addition, adult or older mammal hosts would be more likely to encounter and accumulate parasites raising their infection rates during their lifetime (Behnke *et al.* 1999). However, the highest values for *S. aculeata* prevalence and *S. eta* prevalence and abundance observed in young female hosts suggest a greater susceptibility or exposure of young female animals to this parasite.

The nested pattern of species distribution found for the helminth community of *O. nigripes* in Teresópolis indicates that rare species only occurred in a few rich species infracommunities, considering the component community, and some high prevalent species (such as *G. zetta* and *S. lanfrediae*) occurred in most of the infracommunities. The random pattern observed in the other component communities analysed could be related to intrinsic characteristics between hosts and parasites in each area. The analysis of the metacommunity structure of the helminths including all the sigmodontine rodent species in Petrópolis also indicated a random pattern of helminth species distribution along the host gradient (Cardoso *et al.* 2018). In the previous study carried out in PARNASO-Teresópolis and also in several fragments nearby (Cardoso *et al.* 2016) a weak nested structure was recorded for the helminth community of *A. montensis* and *O. nigripes* with dominance of *S. aculeata* and *S. lanfrediae*.

Studies on the influence of local characteristics and host attributes on parasite populations help to understand the factors associated with their infection processes and life cycles in natural ecosystems (Behnke *et al.* 1999, Castro *et al.* 2017). The sharing of helminth species between host species only in PARNASO-Teresópolis may be due to different local conditions associated with the infection of these parasites in rodents between areas. However, temporal differences can not be excluded. In addition, the occurrence of two species of helminths (*C. obesa* and *R. akodontis*), not registered in PARNASO in the previous studies, reinforces the importance of studies in both regional and temporal scales. The random pattern of species distribution for most helminth communities' structures in *A. montensis* and *O. nigripes* suggests the existence of intrinsic characteristics between hosts and parasites, and may reflect distinct patterns of association with the environment in PARNASO.

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REFERENCES

Almeida-Neto, M., Guimarães, P., Guimarães Jr., P. R., Loyola, R. D., & Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117(8), 1227–1239. DOI: 10.1111/j.0030-1299.2008.16644.x

Ayoade, J. O. 1986. Introdução à climatologia para os trópicos. 1a ed. São Paulo, SP: Editora Difel: p. 332.

Behnke, J. M., Lewis, J. W., Mohd Zain, S. N., & Gilbert, F. S. 1999. Helminth infections in *Apodemus sylvaticus* in southern England: interactive effects of host-age, sex and year on prevalence and abundance of infections. Journal of Helmintholology, 73(1), 31–44. DOI: 10.1017/S0022149X99000049

Bonvicino, C. R., Oliveira, J. A., & D'Andrea, P. S. 2008. Guia dos roedores do Brasil, com chaves para gêneros baseadas em caracteres externos. Rio de Janeiro: Centro Pan-Americano de Febre Aftosa - OPAS/OMS: p. 120.

Bray, R. A., Gibson, D. I., & Jones, A. (Eds.). 2008. Keys to the Trematoda, volume 3. London: CAB International and Natural History Museum: p. 848.

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. The Journal of Parasitology, 83(4), 575–583. DOI: 10.2307/3284227

Callinan, A. P. L., & Westcott, J. M. 1986. Vertical distribution of trichostrongylid larvae on herbage and in soil. International Journal for Parasitology, 16(3), 241–244. DOI: 10.1016/0020-7519(86)90050-0

Cardoso, T. S., Simões, R. O., Luque, J. L. F., Maldonado, A., & Gentile, R. 2016. The influence of habitat fragmentation on helminth communities in rodent populations from a Brazilian Mountain Atlantic Forest. Journal of Helminthology, 90(4), 460–468. DOI: 10.1017/S0022149X15000589

Cardoso, T. S., Braga, C. A. C., Macabu, C. E., Simões, R. O., Costa-Neto, S. F., Maldonado-Júnior, A., Gentile, R., & Luque, J. L. 2018. Helminth metacommunity structure of wild rodents in a preserved area of the Atlantic Forest, Southeast Brazil. Revista Brasileira de Parasitologia Veterinária, 27(4), 495–504. DOI: 10.1590/S1984-296120180066

Castro, R. G. B. M., Costa-Neto, S. F., Maldonado Júnior, A., & Gentile, R. 2017. Ecological aspects of nematode parasites of *Didelphis aurita* (Didelphimorphia, Didelphidae) in urban-sylvatic habitats in Rio de Janeiro, Brazil. Oecologia Australis, 21(1), 54–61. DOI: 10.4257/oeco.2017.2101.06

Combes, C. 2001. Parasitism: the ecology and evolution of intimate interactions. 1st ed. Chicago, IL: University of Chicago Press: p. 552.

Dalmagro, A. D., & Vieira, E. M. 2005. Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. Austral Ecology, 30(4), 353–362. DOI: 10.1111/j.1442-9993.2005.01447.x

Digiani, M. C., & Durette-Desset, M. C. 2003. Two new species of Nippostrongylinae (Nematoda, Heligmosomoidea, Heligmonellidae) from a sigmodontine rodent in Argentina. Acta Parasitologica, 48(1), 12–18.

Dormann, C. F., Gruber, B., & Fründ, J. 2008. Introducing the bipartite Package: analysing ecological networks. R news, 8/2, 8–11.

Durette-Desset, M. C., & Digiani, M. C. 2010. Taxonomic revision of the type specimens of Ethiopian Nippostrongylinae (Nematoda) deposited at the Natural History Museum of London. Zootaxa, 2494, 1–28. DOI: 10.5281/zenodo.195700

Freitas, J. F. T., & Lent, H. 1934. Novo nematodeo da sub-familia Heligmosominae Travassos, 1914, parasito de *Agouti paca* (L.): *Avellaria avellari* n. g., n. sp. Memórias do Instituto Oswaldo Cruz, 28(4), 577–583. DOI: 10.1590/S0074-02761934000400003

Gomes, D. C., Lanfredi, R. M., Pinto, R. M., & Souza, W. 1992. Description of *Trichuris travassosi* n. sp. (Nematoda: Trichurinae) from a Brazilian rodent, by light and scanning electron microscopy. Memórias do Instituto Oswaldo Cruz, 87(suppl. 1), 1–10. DOI: 10.1590/S0074-02761992000500004

Gomes, D. C., Cruz, R. P., Vicente, J. J., & 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(4), 699–707. DOI: 10.1590/S0101-81752003000400024

Grundmann, A. W., Warnock, R. G., & Wasson, D. L. 1976. Some mechanisms of natural regulation of parasitic helminth populations. American Midland Naturalist, 95(2), 347–360. DOI: 10.2307/2424399

Han, B. A., Kramer, A. M., & Drake, J. M. 2016. Global patterns of zoonotic disease in mammals. Trends in Parasitology, 32(7), 565–577. DOI: 10.1016/j.pt.2016.04.007

Jiménez-Ruiz, F. A., & Gardner, S. L. 2003. The nematode fauna of long-nosed mice *Oxymycterus* spp. from the Bolivian Yungas. Journal of Parasitology, 89(2), 299–308. DOI:10.1645/0022-3395(2003)089[0299:TNFOLM]2.0.CO;2

Khalil, L. F., Jones, A., & Bray, R. A. 1994.Keys to the cestode parasites of vertebrates. Wallingford: CAB International: p. 768.

Kuhnen, V. V., Graipel, M. E., & Pinto, C. J. C. 2012. Differences in richness and composition of gastrointestinal parasites of small rodents (Cricetidae, Rodentia) in a continental and insular area of the Atlantic Forest in Santa Catarina state, Brazil. Revista Brasileira de Biologia, 72(3), 563–567. DOI: 10.1590/S1519-69842012000300019

Maldonado Jr., A., 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(4), 369–375. DOI: 10.1017/JOH2006366

Maldonado Jr., A., Pinheiro, J., Simões, R. O., & Lanfredi, R. M. 2010. *Canaania obesa* (Platyhelminthes: Dicrocoeliidae): redescription and new hosts records. Zoologia, 27(5), 789–794. DOI: 10.1590/S1984-46702010000500015

Miño, M. H. 2008. Infection pattern of the spirurid nematode *Protospirura numidica* criceticola in the cricetid rodent *Akodon azarae* on poultry farms of central Argentina. Journal of Helminthology, 82(2), 153–158. DOI: 10.1017/S0022149X08912396

Navone, G. T., Notarnicola, J., Nava, S., Robles, M. R., Galliari, C., & Lareschi, M. 2009. Ensamble de artrópodos y helmintos parásitos en roedores sigmodontinos de los humedales del Río de la Plata, Argentina. Mastozoología Neotropical, 16(1), 121–134.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. 2017. vegan: community ecology package. R package version 2.4-2. (Retrieved on February 10, 2017, from http://CRAN.R-project.org/package=vegan).

Owen, R. D., Goodin, D. G., Koch, D. E., Chu, Y.-K., & Jonsson, C. B. 2010. Spatiotemporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosystem. Journal of Mammalogy, 91(2), 467–481. DOI: 10.1644/09-MAMM-A-152.1

Paglia, A. P., Fonseca, G. A. B., Rylands, A. B., Herrmann, G., Aguiar, L. M. S., Chiarello, A. G., Leite, Y. L. R., Costa, L. P., Siciliano, S., Kierulff, M. C. M., Mendes, S. L., Tavares, V. C., Mittermeier, R. A., & Patton, J. L. 2012. Annotated checklist of Brazilian Mammals. Occasional Paper No. 6. 2nd ed. Arlington, VA: Conservation International: p. 76.

Panisse, G., Robles, M. D. R., Digiani, M. C., Notarnicola, J., Galliari, C., & Navone, G. T. 2017. Description of the helminth communities of sympatric rodents (Muroidea: Cricetidae) from the Atlantic Forest in northeastern Argentina. Zootaxa, 4337(2), 243–262. DOI: 10.11646/zootaxa.4337.2.4

Patterson, B. D., & Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society, 28(1-2), 65–82. DOI: 10.1111/j.1095-8312.1986.tb01749.x

Patton, J. L., Pardiñas, U. F. J., & D'Elía, G. 2015. Mammals of South America, Volume 2: rodents. Chicago: The University of Chicago Press: p. 1384.

Pinto, R. M., Knoff, M., Gomes, D. C., & Noronha, D. 2011. Nematodes from mammals in Brazil: an updating. Neotropical Helminthology, 5(2), 139–183.

Poulin, R. 2007. Evolutionary ecology of parasites. 2nd ed. Princeton, NJ: Princeton University Press: p. 360.

Poulin, R. 2014. Parasite biodiversity revisited: frontiers and constraints. International Journal for Parasitology, 44(9), 581–589. DOI: 10.1016/j.ijpara.2014.02.003

Püttker, T., Meyer-Lucht, Y., & Sommer, S. 2006. Movement distances of five rodent and two marsupial species in forest fragments of the coastal Atlantic rainforest, Brazil. Ecotropica, 12(2), 131–139.

Püttker, T., Meyer-Lucht, Y., & Sommer, S. 2008. Effects of fragmentation on parasite burden (nematodes) of generalist and specialist small mammal species in secondary forest fragments of the coastal Atlantic Forest, Brazil. Ecological Research, 23(1), 207–215. DOI: 10.1007/s11284-007-0366-z

Quentin, J.-C. 1971. Morphologie comparée des structures céphaliques et génitales des Oxyures du genre *Syphacia*. Annales de Parasitologie Humaine et Comparee, 46(1), 15–60. DOI: 10.1051/parasite/1971461015

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. (Retrieved on February 10, 2017, from https://www.R-project.org/).

Robles, M. R. 2011. New species of *Trichuris* (Nematoda: Trichuridae) from *Akodon montensis* Thomas, 1913 of the Paranaense forest in Argentina. Journal of Parasitology, 97(2), 319–327. DOI: 10.1645/GE-2434.1

Simões, R., Gentile, R., Rademaker, V., D'Andrea, P., Herrera, H., Freitas, T., Lanfredi, R., & Maldonado Jr., A. 2010. 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, 84(3), 266–275. DOI: 10.1017/S0022149X09990629

Simões, R. O., Souza, J. G. R., Maldonado Jr., A., & Luque, J. L. 2011. Variation in the helminth community structure of three sympatric sigmodontine rodents from the coastal Atlantic Forest of Rio de Janeiro, Brazil. Journal of Helminthology, 85(2), 171–178. DOI: 10.1017/S0022149X10000398

Stein, M., Suriano, D. M., & Novaro, A. J. 1994. Parasite nematodes from *Dusycion griseus* (Gray, 1837), *D. culpaeus* (Molina, 1782) and *Conepatus chinga* (Molina, 1782) (Mammalia:Carnivora) in Neuquen, Argentina. Systematics and ecology. Boletin Chileno de Parasitologia, 49(3-4), 60–65.

Sutton, C. A. 1989. Contribution to the knowledge of Argentina's parasitological fauna. XVII. Spirurida (Nematoda) from Neotropical Cricetidae: *Physaloptera calnuensis* n. sp. and *Protospirura numidica criceticola* Quentin, Karimi and Rodriguez de Almeida. Bulletin du Museum National d'Histoire Naturelle, 11(1), 61–67.

Teixeira, B. R., Loureiro, N., Strecht, L., Gentile, R., Oliveira, R. C., Guterres, A., Fernandes, J., Mattos, L. H. B. V., Raboni, S. M., Rubio, G., Bonvicino, C. R., Duarte dos Santos, C. N., Lemos, E. R. S., & D'Andrea, P. S. 2014. Population ecology of hantavirus rodent hosts in southern Brazil. The American Journal of Tropical Medicine and Hygiene, 91(2), 249–257. DOI: 10.4269/ajtmh.13-0465

Thomas, F., Bonsall, M. B., & Dobson, A. P. 2005. Parasitism, biodiversity, and conservation. In: F. Thomas, F. Renaud & J.-F. Guégan (Eds.), Parasitism and ecosystems. pp. 124–139. New York: Oxford University Press.

Thul, J. E., Forrester, D. J., & Abercrombie, C. L. 1985. Ecology of parasitic helminths of wood ducks, *Aix sponsa*, in the Atlantic flyway. Proceedings of the Helminth Society Washington, 52(2), 297–310.

Travassos, L. 1937. Revisão da família

Trichostrongylidae Leiper 1912. Memórias Do Instituto Oswaldo Cruz, 1, 1–512.

Travassos, L. 1944. Revisão da família Dicrocoeliidiae, Odhner, 1910. Rio de Janeiro: Imprensa Nacional: p. 357.

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(suppl. 1), 1–452. DOI: 10.1590/S0101-81751997000500001

Wells, K., Smales, L. R., Kalko, E. K. V., & Pfeiffer, M. 2007. Impact of rain-forest logging on helminth assemblages in small mammals (Muridae, Tupaiidae) from Borneo. Journal of Tropical Ecology, 23(01), 35–43. DOI: 10.1017/S0266467406003804

Werk, D. F., Gallas, M., Silveira, E. F., & Périco, E. 2016. New locality records for *Guerrerostrongylus zetta* (Travassos, 1937) Sutton; Durette-Desset, 1991 (Nematoda: Heligmonellidae) parasitizing *Oligoryzomys nigripes* (Olfers, 1818) (Rodentia: Sigmodontinae) from southern Brazil. Check List, 12(2), 1861. DOI: 10.15560/12.2.1861

Yamaguti, S. 1961. Systema Helminthum. The nematodes of vertebrates, Vol III. New York: Interscience Publisher: p. 1261.

Zuk, M., & McKean, K. A. 1996. Sex differences in parasite infections: patterns and processes. International Journal for Parasitology, 26(10), 1009–1023. DOI: 10.1016/S0020-7519(96)80001-4

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