Helminth communities of *Nectomys* squamipes naturally infected by the exotic trematode *Schistosoma mansoni* in southeastern Brazil

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Abstract

The water rat Nectomys squamipes is endemic in Brazil and found naturally infected with Schistosoma mansoni. Helminth communities, their prevalences, intensity of infection and abundance in N. squamipes in an endemic area of schistosomiasis in the state of Rio de Janeiro, Brazil were studied. Four species of nematodes (Physaloptera bispiculata, Syphacia venteli, Hassalstrongylus epsilon and Litomosoides chagasfilhoi) were recovered in 85.3%, two trematodes (Schistosoma mansoni and Echinostoma paraensei) in 38.8% and one cestode species (Raillietina sp.) in 1.7% of rats examined. Rats were infected with up to five helminth species each, and these were highly aggregated in distribution. For *H. epsilon* and *S.* venteli, intensities and abundances were higher in adult male and subadult female hosts, respectively. Hassaltrongylus epsilon, P. bispiculata, S. venteli and S. mansoni were classified as dominant species, L. chagasfilhoi and E. paraensei as codominant and Raillietina sp. as subordinated. No significant correlation was found in the intensity of infecton between each pair of helminth species. Schistosoma mansoni was not related to any other helminth species according to their infection rates, although S. mansoni was well established in the natural helminth comunity of the water rat.

Introduction

Schistosomiasis caused by *Schistosoma mansoni* is considered an important and widespread human disease in Brazil. However, control programmes have largely neglected the role of wild rodents in the dynamics of *Schistosoma mansoni* transmission (WHO, 1993) and additional information on *S. mansoni* in rodents is

required, especially with regard to the epidemiology of the host–parasite relationship.

A long-term study focusing on the role of the semiaquatic water rat *Nectomys squamipes* in the dynamic transmission of *S. mansoni* has been carried out in the municipality of Sumidouro, Rio de Janeiro state, Brazil, an endemic area of schistosomiasis. This study indicated that *N. squamipes* could maintain and potentially increase the transmission of this parasite to humans, and may spread the parasite, establishing new infection foci (D'Andrea *et al.*, 2000). The evidence acumulated from water rat collection in different Brazilian ecosystems has

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demonstrated heterogeneity in prevalence rates (Rey, 1993; Chieffi *et al.*, 1994). This variability could result from interaction between species within the helminth community in each ecosystem studied (Lello *et al.*, 2004).

The helminth community ecology of *N. squamipes* has not hitherto been evaluated, especially in regions where the exotic species *S. mansoni* is present. Studies relating to helminths of the water rat are restricted to species descriptions (Gomes & Vicente, 1984). Under laboratory conditions, substantial antagonistic and synergistic interactions between *S. mansoni* and *Echinostoma revolutum* have been described in mice (Christensen *et al.*, 1981) and between *S. mansoni* and *E. paraensei* in *N. squamipes*, the natural host of both trematodes in Brazil (Maldonado Jr *et al.*, 2001a).

The present study aims to investigate helminth communities of *N. squamipes* in an endemic area of schistosomiasis, where this rodent is found naturally infected with *S. mansoni*. The prevalence, intensity of infection and abundance of each helminth are investigated and the influence of *S. mansoni* on the helminth fauna of the water rat evaluated.

Materials and methods

Study site

The study was conducted in the Pamparrão and Porteira Verde valleys, Sumidouro municipality, state of Rio de Janeiro, Brazil (22°02′46″S; 42°41′ 21″W), every other month from April 1997 to April 1999. The landscape is composed of small rural properties with vegetable plantations, pastures and a few small Atlantic Forest fragments. The climate is humid-mesotermic (Nimer, 1979) and the rainfall seasonal. The mean temperature during the period of study was $24.3 \pm 2.4^{\circ}$ C and the rainfall was $121.7 \pm 126.1 \text{ mm}^3$ (data obtained from National Institute of Meteorology of Rio de Janeiro, Brazil).

Collection of rats and parasites

Water rats were collected along watercourses and flooded areas by live traps set at the intervals of 13 m between traps. The age of rats was estimated according to the growth curve obtained for *N. squamipes* in the laboratory (D'Andrea *et al.*, 1996) and three age groups were categorized as described by Gentile *et al.* (2000), namely juveniles with a body mass less than 110 g in both sexes, young adults with a body mass more than 110 g and less than190 g in males and less than 215 g in females, and adults with a body mass more than 190 g in males and 215 g in females. Rat abundances were estimated as the number of animals captured under a constant trapping regime (total number of traps per trapping period).

Animals were euthanized using a CO_2 chamber. Organs were removed and placed in Petri dishes with saline 0.9% solution and the thoracic and peritoneal cavities examined for helminths. The species recovered from each organ were counted and fixed according to Amato (1985). Nematodes were fixed with alcoholformalin-acetic acid (AFA) at 60°C and cleared in lactophenol. Trematodes were fixed with AFA at room temperature under the pressure of a cover slip. Ten specimens of trematode species were stained with chlorhydric carmine, dehydrated in a graded alcohol series, cleared in methylsalycilate and mounted in Canada balsam. Species were identified by comparison with paratypes deposited at the Oswaldo Cruz Collection (CHIOC). Protocol experiments were performed according to the Ethical Commission of Animal Use of the Fundação Oswaldo Cruz. The collection of rats was carried out strictly in accordance with the rules and conditions of the licence from the Brazilian Authority for Environment and Natural Resources (IBAMA).

Data analyses

Distribution patterns of each helminth were determined by an index of dispersion calculated as the variance to mean ratio of parasite abundance (Ludwig & Reynolds, 1988).

For helminth community analysis, the prevalence, intensity and abundance of infection for each species were calculated according to Bush *et al.* (1997). These parameters were also compared in relation to host gender and age and prevalences were analysed by logistic regression. Intensities and abundance were compared in relation to host gender and age together only for *H. epsilon* and *S. venteli.* For other species only host gender was compared due to the lack of sufficient data.

The co-occurence of helminths was investigated through Pearson correlation coefficients or Spearman coefficients when data were not normally distributed and the intensities for each helminth pair were considered only in rats infected with both species of the pair (Zar, 1999).

The helminth community structure was classified according to Thul *et al.* (1985) as follows: dominant species characterized by I > 1.0; co-dominant species contributing significantly to the community, though to a lesser degree than dominant species (0.01 < I < 1.0); subordinate species occurring infrequently and although they may develop and reproduce, they do no contribute significantly to the community (0 < I < 0.01); unsuccessful pioneer species that gain access to the host but do not mature or reproduce and they contribute little to the community and are characteristic of another host (I = 0).

The importance value, I, was calculated for each helminth species as follows:

$$I_j = M_j \times [(A_j \times B_j) \div \sum_i (A_i \times B_i)] \times 100$$

where A = number of individual parasites of a particular species, B = number of hosts infected with parasites of species 'x', and M is a mature factor equal to 1.0 if at least one mature individual of species 'x' is found and equal to 0 otherwise (Thul *et al.*, 1985).

Helminth richness was considered as the number of species. Diversity was calculated using the Shannon index, which represents the most abundant species (Ludwig & Reynolds, 1988). Helminth richness and diversity was calculated relative to host gender, age class and for the entire host population.

Helminth prevalences were calculated for each species for each trapping session. The prevalences of *S. mansoni* were correlated with the prevalences of other helminths to evaluate the possible relationship between *S. mansoni* and the natural helminth fauna of *N. squamipes*.

Statistical significance levels of 0.05 were accepted in all tests and a Bonferroni correction was used for multiple comparisons.

Results

One hundred and sixteen individuals of the wild water rat *Nectomys squamipes* were examined which produced a sex ratio biased toward males ($x^2 = 6.40$, P = 0.014, 77M: 39F). The rats harboured from 1 to 5 concurrent helminths species and the overall infection rate was 87% (89.6% for males and 82% for females). There was no difference in the overall infection rate between sexes ($x^2 = 0.09$, P = 0.76).

Seven species of helminths were recovered, four species of which were nematodes with an overall prevalence of 85.3%. Physaloptera bispiculata (Seurat) occurred in the stomach and represented 1.8% of overall worm burdens. Hassalstrongylus epsilon (Travassos) occurred in the duodenum representing 13.8%, with Syphacia venteli (Travassos) occurring in the caecum and large intestine, representing 76.1% of worms. Litomosoides chagasfilhoi (Moraes Neto et al.) was found in the abdominal cavity and represented 1.0% of all nematodes found. This is the first occurrence of L. chagasfilhoi in N. squamipes. Two trematode species were found in 38.8% of rats, 6.9% being Schistosoma mansoni (Sambon) localized in the mesenteric and portal veins and 3% were Echinostoma paraensei (Lie & Basch) from the small intestine, mainly in the duodenum. One cestode species, Raillietina sp., was found in the small

intestine of 1.7% of rats, representing 0.05% of all worms recovered.

The overall helminth diversity was 1.72. Males of *N. squamipes* showed a higher helminth diversity than females (2.46 and 1.85 respectively). The diversity in adults was greater than in sub-adults and young individuals, being 2.84, 1.64 and 1.42, respectively. All helminth species were highly aggregated within the *N. squamipes* population: namely *H. epsilon* 78.6; *P. bispiculalta* 16.8; *S. venteli* 1563.8; *L. chagasfilhoi* 67 + 1; *S. mansoni* 215.7; *E. paraensei* 16.1; *Raillietina* sp. 13.1.

The highest prevalences, intensities and abundances of infection were observed for *S. venteli* followed by *H. epsilon* and *S. mansoni*. The lowest values were observed for *Railletina* sp. followed by *E. paraensei* (tables 1 and 2).

The prevalence of *H. epsilon* was significantly different in relation to gender (P = 0.044), where male hosts had higher prevalences than female hosts. *Physaloptera bispiculata* presented significant differences in prevalences relative to host age (P = 0.037), where young hosts had higher prevalences. No other helminth species showed any significant differences in prevalence relative to host age and gender.

Significant differences between host gender and age in intensity and abundance were observed for *H. epsilon* ($x^2 = 74.79$, P < 0.001; $x^2 = 40.9$, P < 0.001, respectively) and *S. venteli* ($x^2 = 440.2$, P < 0.001; $x^2 = 59.1$, P < 0.001, respectively. In *H. epsilon* the intensity and abundance were larger for adult male hosts whereas in *S. venteli* these values were larger in females. No other helminth showed differences in abundances and intensities relative to host gender.

Analyses of helminth communities indicated that no species was considered an unsuccessful pioneer.

Table 1. The prev	alence (P), intensi	ity (I) and abundanc	e (A) of nematode	species in Nectomy	<i>s squamipes,</i> rel	lative to host gend	ler and age.

	Ha	ssalstrongy epsilon	lus		hysalopten bispiculata	1	Syphacia venteli			Litomosoides chagasfilhoi		
Host gender/age	Р	Ι	А	Р	Ι	А	Р	Ι	А	Р	Ι	А
Males	73.3	49.2	36.5	48.0	9.6	4.6	49.3	326.1	163.0	8.0	28.2	2.3
Females	48.8	22.5	27.3	30.2	12.6	3.9	44.2	488.6	217.9	11.6	20.8	2.5
Juvenile	50.0	48.4	27.0	10.0	27.0	3.0	50.0	570.0	316.7	0	0	0
Sub-adults	50.0	46.5	23.9	31.6	8.8	2.9	39.5	610.5	247.5	7.9	8.7	0.7
Adults	73.2	52.4	39.0	49.3	10.7	5.3	49.3	266.1	131.6	11.3	30.9	3.5
Total	6.3	52.0	33.2	40.5	10.8	4.4	52.6	347.8	362.7	9.5	24.8	2.3

Table 2. The prevalence (P), intensity (I) and abundance (A) of trematode and cestode species in *Nectomys squamipes*, relative to host gender and age.

	Schis	stosoma ma	nsoni	Echin	ostoma para	aensei	Raillietina sp.		
Host gender/age	Р	Ι	А	Р	Ι	А	Р	Ι	А
Males	42.7	50.9	22.0	9.3	7.3	0.7	0	0	0
Females	20.9	33.8	7.2	4.6	13.5	0.6	4.6	7.5	0.4
Iuvenile	10.0	15.0	1.7	0	0	0	0	0	0
Sub-adults	23.7	30.2	7.4	2.6	17.0	0.5	2.6	1.0	0.03
Adults	43.7	53.1	23.5	11.3	7.6	0.9	1.4	14.0	0.2
Total	34.5	48.3	16.7	7.8	8.7	0.7	1.7	7.5	0.13

Hassalstrongylus epsilon, P. bispiculata, S. venteli and *S. mansoni* were considered as dominants (I = 16.9, 1.4, 76.8, 4.6, respectively), with *L. chagasfilhoi* and *E. paraensei* as co-dominants (I = 0.18, 0.04, respectively) and *Raillietina* sp. as subordinated (I = 0.0018).

No significant correlation was found in the overall intensities of infection between helminth species, and no interactions between each pair of helminth species were found. Due to low sample sizes, it was not possible to test the interaction between *S. mansoni* and *L. chagasfilhoi*, *S. mansoni* and *E. paraensei* and *Raillietina* sp. and the other helminth species (table 3).

Considering the possible co-variation in infection rates between *S. mansoni* and other helminths in the overall *N. squamipes* population, no significant correlation was found. There was no correlation between water rat abundance and the intensity of helminths overall (table 4).

Discussion

Interactions between intestinal helminths may be determined by direct influences of one parasite on another through secretory products, gut physiology, interspecific competition or crowding effects. Furthermore, interactions would be mediated through the host's immune system (Lello *et al.*, 2004).

The water rat Nectomys squamipes, which is widespread in Brazil (Bonvicino, 1994), was highlighted from a parasitological viewpoint when it was found to be involved in the transmission of S. mansoni (Rey, 1993, D'Andrea et al., 2000). Studies on the helminths of N. squamipes were subsequently intensified and its natural helminth fauna was identified. Physaloptera bispiculata was recorded in N. squamipes for the first time by Vaz & Pereira (1935) in Mogi das Cruzes, São Paulo, Syphacia venteli by Travassos (1937) in Angra dos Reis, Rio de Janeiro, Litomosoides chagasfilhoi from Rio Bonito by Moraes-Neto et al. (1997), Hassalstrongylus epsilon by Travassos (1937) in Formosa, Goiás, and Echinostoma paraensei in Sumidouro by Maldonado et al. (2001b). The higher helminth diversity observed in adult hosts was as expected. The heaviest and therefore the oldest rodents would have had the longest exposure and opportunity to accumulate worm burdens. As males forage more than females, and occupy larger home ranges (Gentile et al., 2000), their risk of infection would be expected to be higher than that of females.

Dispersion can be viewed as an extension of the transmission process, and is conditioned by several factors such as longevity, specificity, population density, morbidity, host migration, distribution, free living stage dispersal as well as environmental conditions (Bush *et al.*, 2001). An aggregated distribution is the most frequent pattern observed for parasites in the wild and can indicate social interactions for the purpose of mating, feeding cooperation or defence (Bush *et al.*, 2001). All species exhibited highly aggregated patterns, and *S. mansoni* and *L. chagasfilhoi* may follow the aggregated distribution of their intermediate hosts, *B. glabrata* (Giovanelli *et al.*, 2001) and *Ornithonyssus bacoti* (Renz & Wenk, 1981). *Litomosoides chagasfilhoi* is transmitted by haematophagous arthropods and infection by the *Litomosoides* genus occurs when

	Hassalstrongylus epsilon	Physaloptera bispiculata	Syphacia venteli	Syphacia venteli Litomosoides chagasfilhoi Schistosoma mansoni Echinostoma paraensei	Schistosoma mansoni	Echinostoma paraensei
P. bispiculata S. venteli L. chagasfilhoi S. mansoni E. paraensei Raillietina sD.	n = 35, P = 0.50 R = 0.116 n = 39, P = 0.70 R = -0.062 n = 8, P = 0.56 R = 0.243 n = 30, P = 0.007 R = -0.485 n = 4 n = 2	n = 26, P = 0.59 R = 0.110 n = 6, P = 0.82 R = -0.123 n = 18, P = 0.80 R = -0.062 n = 6, P = 0.80 R = 0.137 n = 0	n = 5, $P = 0.22$ R = 0.667 n = 6, $P = 0.23$ R = 0.577 n = 1 n = 0	n = 3 $n = 0$ $n = 0$	n = 4 n = 1	<i>u</i> = 0

Table 3. Correlation coefficients between helminth intensities in Nectomys squamipes.

n, sample size; P, significance; R, correlation coefficient

Table 4. Prevalence values (%) of each helminth species, relative to the abundance of *Nectomys squamipes* and trapping periods from April 1997 to April 1999.

				I	Helminth specie	es		
Month/year	Number of hosts	Hassalstrongylus epsilon	Physaloptera bispiculata	Syphacia venteli	Litomosoides chagasfilhoi	Schistosoma mansoni	Echinostoma paraensei	<i>Raillietina</i> sp.
1997								
April	16	87.5	31.2	81.2	12.5	43.8	6.7	6.2
July	14	85.7	35.7	64.3	14.3	35.7	7.1	0
September	12	91.7	58.3	66.7	8.7	25.0	16.7	8.3
November	6	83.3	66.7	66.7	0	50.0	0	0
1998								
January	8	37.5	37.5	37.5	12.5	12.5	0	0
March	4	0	50.0	100	0	50.0	50.0	0
May	6	83.3	66.7	33.3	16.7	50.0	16.7	0
July	5	100	0	40.0	0	40.0	0	0
September	2	100	50.0	50.0	0	100	50.0	0
November	7	42.8	42.8	14.3	0	42.8	0	0
1999								
January	7	57.1	71.4	14.3	0	28.7	0	0
March	8	50.0	62.5	37.5	0	50.0	0	0
May	12	25.0	8.3	16.6	0	25.0	0	0
August	8	37.5	25.0	25.0	50	0	12.5	0

infected mites bite the rodent, transmitting the third stage larvae (Renz & Wenk, 1981). *Nectomys squamipes* hosts at least four species of mites, all potential vectors of *L. chagasfilhoi* (Guitton *et al.*, 1986). *Syphacia venteli*, the most aggregated species, has a direct life cycle without an intermediate host, and its distribution is related to the host.

Nectomys squamipes has also been shown to be aggregated in its distribution (Almeida et al., 2000). Females of S. venteli usually deposit their eggs in the perianal region of the rat which facilitates direct transmission and constant reinfection. Echinostoma paraensei can be potentially transmitted by at least three species of snails found in abundance and clumped in their distribution in the water rat habitat in Sumidouro (Maldonado Jr. et al., 2001c). In addition, this helminth can reproduce by selffertilization (Nollen, 1996). Physaloptera bispiculata may have followed the distribution of its intermediate host, probably an insect (Hobmaier, 1941), whereas Raillietina sp. is transmitted to birds and reptiles by ingestion of insect intermediate hosts, which are probably aggregated. Hassalstrongylus epsilon is a geohelminth and does not have an intermediate host. Eggs of H. epsilon are deposited in specific areas in the soil and the host becomes infected when it has contact with infective larvae. Some of these characteristics of the transmission cycles of those helminths are related to the food web of the host N. squamipes, thus contributing to the helminth community structure.

The structure of the helminth community may in part be determined by host–parasite and parasite–parasite interactions within the host (Poulin, 2001) or environmental factors (Abu-Madi *et al.*, 2000). The dominant status of *S. mansoni* in the community, and a similar status for *H. epsilon*, *P. bispiculata* and *S. venteli*, could be determined by the peculiarities of its interaction with the highly suceptible *N. squamipes* or interspecific interactions between the parasite species. The single cestode species *Rallietina* sp. from *N. squamipes* was found on only two occasions, probably as a result of accidental infections but, as fully mature worms were recoverd, this species was classified as subordinate.

No direct interaction could be observed in the intensities and prevalences of these helminth species. This might suggest that helminth communities of the water rat are well established, even in the presence of the exotic species S. mansoni conferring the dominant status of four of the seven helminth species found. In the UK, Behnke et al. (2005) also found no interactions between the helminth community of the wood mouse, Apodemus sylvaticus. On the other hand, Maldonado et al. (2001a) showed a synergistic interaction between S. mansoni and E. paraensei under laboratory conditions. Infection of N. squamipes by S. mansoni facilitated the establishment of E. paraensei and prolonged the life span in the infected vertebrate host. Maldonado et al. (2001a) showed experimentally that a primary infection with E. paraensei in N. squamipes declined following a S. mansoni challenge infection.

Maldonado et al. (1994) also showed that N. squamipes can be reinfected by S. mansoni without causing any significant pathology to the rat other than peri-ovular modulation and low tissue damage (Silva et al., 2002). The population dynamics of the rat are also unaffected (D'Andrea et al., 2000). Previous studies by D'Andrea et al. (2000, 2002) have demonstrated a high susceptibility of N. squamipes to S. mansoni infections, without influencing longevity nor fecundity in the rat. Nectomys squamipes deposits viable eggs of *S. mansoni* in the faeces with a high infectivity potential during its entire life, confirming its role as a reservoir for schistosomiasis. Thus, this exotic species is completely established in the natural helminth community of the water rat and has adapted to the host, influencing neither host abundance nor the occurrence of other helminth species.

The fact that *S. mansoni* is a parasite of the blood system of the host, a habitat not occupied by other helminth species other than the microfilariae of *L. chagasfilhoi*, may have determined low levels of interspecific interactions. Further studies on helminth communites of the water rat without *S. mansoni* may clarify the importance of interspecific relationships between helminths in natural populations of this rodent host.

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