The parasitism of *Schistosoma mansoni* (Digenea–Trematoda) in a naturally infected population of water rats, *Nectomys squamipes* (Rodentia–Sigmodontinae) in Brazil

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SUMMARY

Schistosomiasis is a health problem in Brazil and the role of rodents in maintaining the schistosome life-cycle requires further clarification. The influence of *Schistosoma mansoni* on a population of *Nectomys squamipes* was studied by capture-recapture (1st phase, from June 1991 to November 1995) and removal (2nd phase, from April 1997 to March 1999) studies at Sumidouro, Rio de Janeiro, Brazil. During both phases coproscopic examinations were performed. At the 2nd phase the rodents were perfused and worms were counted. The population dynamics of parasites was studied. During the 1st phase, female reproductive parameters, longevity, recruitment and survivorship rates and migration patterns were studied in relation to schistosome prevalence. Water contamination (source of *miracidia*), abundance intermediate host and rodent migration were related to prevalence. The *N. squamipes* population was not obviously influenced by the infection, as shown by the high number of reproductive infected females, high longevity of infected individuals and the absence of a relationship between recruitment or survivorship rates and the intensity of schistosome infection. The data indicate that *N. squamipes* can increase transmission of *S. mansoni* in endemic areas and carry it to non-infected areas. Furthermore, this rodent can be used as an indicator of a transmission focus.

Key words: *Schistosoma mansoni*, *Nectomys squamipes*, Brazil, schistosomiasis, population dynamics.

INTRODUCTION

Schistosoma mansoni was introduced in Brazil during the colonization in the XVI and XVII centuries (Després *et al*. 1992; Tchuem Tchuenté *et al*. 1995). The snail intermediate host (*Biomphalaria*) was already available with a large geographical distribution, which facilitated the establishment and spread of this helminth. During the 1950's it was discovered that *S. mansoni* infected both human and wild mammals (Rey, 1993). Several species of the Sigmodontinae rodent, genus *Nectomys*, are the primary candidates to become natural reservoirs of *S. mansoni* because of their semi-aquatic habits (Ernest & Mares, 1986) which expose them to infection. They are distributed throughout a large area along watercourses including most endemic areas of schistosomiasis (Ribeiro *et al*. 1998). When mature these rodents weigh 140–400 g and have a

body–tail length of 250 mm. They feed on aquatic insects, snails (that may be infected with *S. mansoni*), tadpoles and fruit (Ernest & Mares, 1986). Their reproduction occurs throughout the year but mostly during rainy periods (Gentile *et al*. 1999). The mean permanence time observed in the field is $75 \cdot 4 \pm 144 \cdot 5$ days (D'Andrea *et al*. 1999) but in captivity *N. squamipes* can live up to 3 years (personal observation). Under semi-natural conditions *N. squamipes* can support the full development and transmission of *S. mansoni* (Antunes *et al*. 1973; Kawazoe & Pinto, 1983). Other experimental studies have also documented their high susceptibility to *S. mansoni* infection (Souza *et al*. 1992; Maldonado *et al*. 1994) and their ability to eliminate viable eggs (Rodrigues *et al*. 1992). High infection rates with *S. mansoni* have also been reported in many natural *Nectomys* populations (Rey, 1993).

Understanding the role of rodents in transmission of *S. mansoni* is important for at least 2 reasons. Schistosome-transmitting rodents may significantly complicate efforts to control schistosomiasis, and the use of rodents as hosts may alter some of the basic properties of the worms, such as shedding patterns,

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length of pre-patent period, or virulence. Studies on a natural population of *N. squamipes* in the municipality of Sumidouro, Rio de Janeiro State, Brazil are reported. These studies characterize the parasitism of *S. mansoni* on this species and its influence on host population size, longevity and female reproductive capacity.

MATERIALS AND METHODS

Study area

The study was conducted in the Pamparrão and Porteira Verde adjacent valleys in Sumidouro, State of Rio de Janeiro, Brazil (22° 02′ 46″ S; 42° 41′ 21″ W). These valleys are part of a common hydric system with many small permanent streams, irrigation channels and some flooded areas (Fig. 1). The landscape is composed of small rural properties with vegetable plantations, pasture lands and a few small Atlantic Forest fragments.

The region has a humid-mesotermic climate (Nimer, 1979). Rainfall is seasonal and heaviest between November and March (normal temperatures between 23·2 and 25·4 °C, normal rainfall between 269·4 mm and 153·5 mm). The driest months generally extend from May to August (normal temperatures between 18·3 and 20·3 °C, normal rainfall between 24·7 mm and 44·2 mm). The mean temperature during the study period was 24·3 ± 2·4 °C and the mean rainfall was 121·7 ± 126·1 (data obtained from National Institute of Meteorology of Rio de Janeiro).

The study design was dictated by the semi-aquatic habits of the water rat, *N. squamipes*. All the capture lines were established along watercourses and flooded areas with 1 wire live trap set at intervals of 13 metres. The capture sessions were carried out every other month for 5 nights. The capture sites varied in their proximity to human habitations and, therefore, in the level of water pollution from domestic sewage (a source of *S. mansoni* miracidia to the snail population).

Water contamination of each capture site was evaluated considering data on the prevalence of human population living nearby and the kind of domestic sewage (such as cesspool or direct discharge into the watercourses). The abundance of *N. squamipes*, snails (*Biomphalaria glabrata*) and vegetable types were distinct among sites (Table 1). Site 1 and its extension, 1a, were characterized by open vegetation composed of sparse thickets, and by the absence of human habitations. Site 2 had an irrigation channel receiving water from the main stream of Pamparrão valley and from a non-polluted small effluent stream; it had sparse high trees, shrubs and razor grass. Sites 3, 3a and 3b were located along the same irrigation channel but differed in their

proximity to the sewage source of a small village. They had an open vegetation consisting of razor grass, sparse shrubs and trees, with a secondary forest at one of the edges of sites 3a and 3b. Site 4 was along the same irrigation channel in an open flooded area with one major stream that received water and all the sewage from sites 3a and 3b. Site 4a was adjacent to site 4 but the trap line was established inside a forest fragment with a dense midstory and a high closed canopy. Site 5 was characterized by a continuous dense vegetation of *Hedychium choronarium* (Zingiberaceae) in a flooded area, and had no human habitation. Site 6 had only razor grass and was located very close to human habitations but above their sewage discharge (Fig. 1).

Field study

The study was divided in 2 phases. In the first phase, June 1991 to November 1995, a mark-recapture program was conducted to study the population dynamics (Gentile *et al.* 1999) and the infection rates of the *N. squamipes* population at Pamparrão valley. The size of the population was estimated using the Minimum Number Known Alive estimator, MNKA (Krebs, 1966), which considers as the population size, the number of animals captured and released at a given session, plus those not captured at this session but captured before and after that. The survivorship and recruitment rates (Fig. 3) were estimated using the Jolly–Seber estimator (Jolly, 1965; Seber, 1965). Survivorship is the rate of animals that survived from one capture session to the subsequent one, and recruitment is the rate of animals that were added to the population from one capture session to the following one (in our case by birth or immigration). All captured rodents were weighed, sexed and individually marked by toe clipping. The reproductive condition of the females was assessed by groping and visual observation of the dilatation of abdomen, and sexual maturity was assumed as the minimum age and weight of males with scrotal testes and females with open vagina (D'Andrea *et al.* 1996).

Diagnosis of schistosome infection was based on coproscopic examinations (Katz, Chavez & Pellegrino, 1972). Surgical dischargeable hoods were placed at the bottom of each trap acting as a faeces-collecting bag. Faecal samples were collected from every individual at each capture or recapture. The faecal samples from each individual were mixed (during the capture session) and later analysed using 2 slides. The mean number of eggs per gram of faeces was calculated following the modified Kato method (Katz *et al.* 1972).

Schistosome prevalence in the *N. squamipes* population was calculated for each capture session except those where less than 5 animals were examined. The numbers of infected and non-infected animals
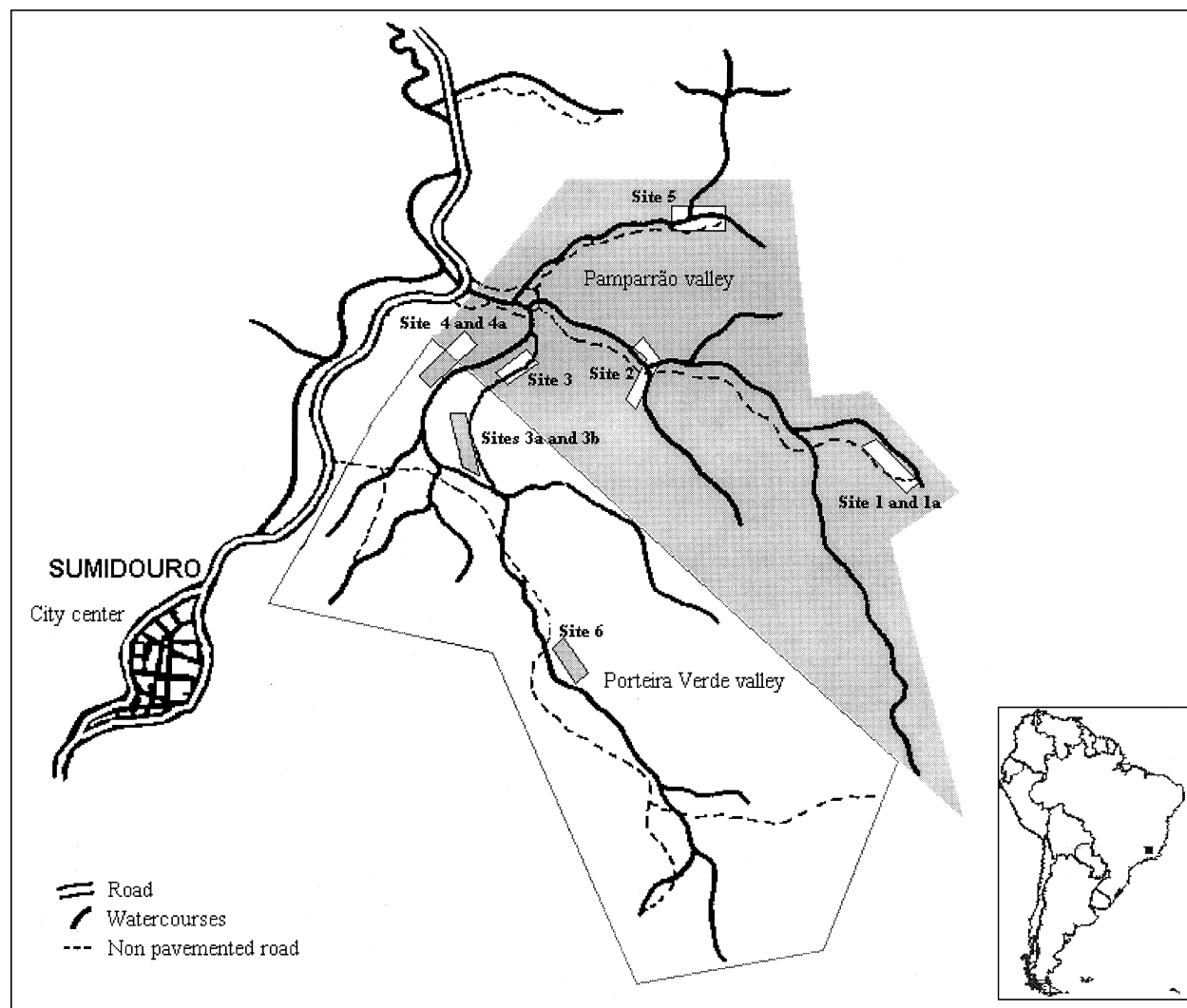
Fig. 1. Map of the study area, Sumidouro city, Rio de Janeiro State, Brazil, showing adjacent valleys (Pamparrão and Porteira Verde) and capture sites (1–6).

Table 1. *Brief description of each studied site considering trapping effort (number of trap nights), water contamination, snail and rodent abundance*

(Mean values and standard deviation for *Nectomys squamipes* abundance.)

Site	Trapping effort 1st phase	Trapping effort 2nd phase	Water contamination by human sewage	*Biomphalaria glabrata* abundance	*Nectomys squamipes* abundance 1st phase	*N. squamipes* abundance 2nd phase
1	2325	900	Absent	Absent	$1·3 \pm 1·8$	$0·8 \pm 1·3$
1a	775	—	Absent	Absent	$0·5 \pm 0·9$	—
2	2325	900	Medium	Rare	$3·5 \pm 2·1$	$2·5 \pm 1·7$
3	2325	—	High	High	$1·6 \pm 2·1$	—
3a	—	900	Very high	High	—	$1·7 \pm 1·3$
3b	—	300	High	High	—	$0·1 \pm 0·3$
4	—	1200	High	Medium	—	$0·6 \pm 1·2$
4a	1550	—	High	Absent	$1·4 \pm 1·5$	—
5	1550	600	Absent	Absent	$1·9 \pm 1·8$	$1·7 \pm 1·0$
6	—	300	Absent	Absent	—	$0·5 \pm 1·0$

were estimated using the MNKA estimator. The prevalence rate was based on the estimated number of infected animals divided by the estimated number of non-infected animals in the population. Since there is no known self-cure of schistosome infection, all animals were considered infected at subsequent
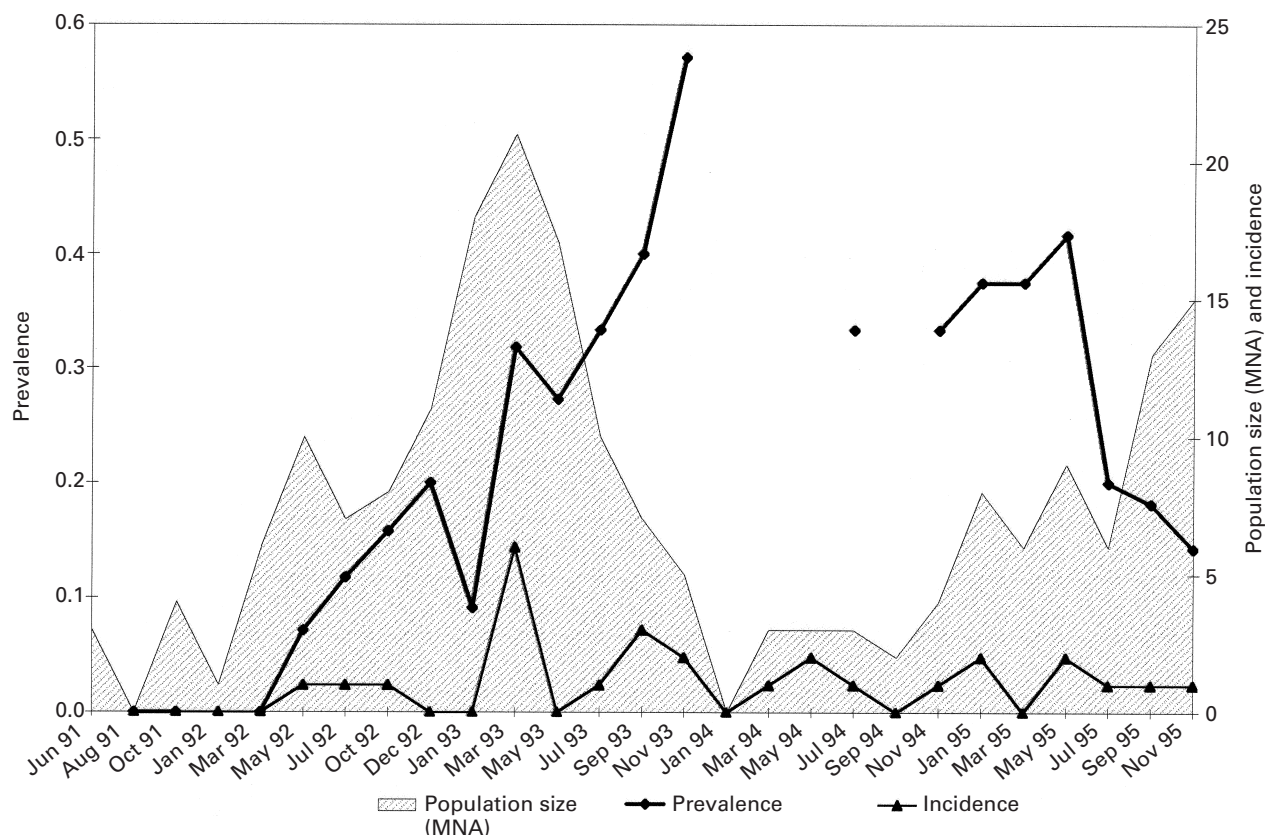
Fig. 2. Population size, schistosome incidence and prevalence rate of the *Nectomys squamipes* population in the Pamparrão Valley, Sumidouro, Rio de Janeiro State, Brazil (1st phase of the study). Empty data when less than 5 individuals were captured.

captures after their first positive examination. Then, incidence was the number of individuals diagnosed as positive for the first time in a given capture session (number of infected animals never captured before plus the number of infected individuals found to be uninfected on previous capture sessions).

The second phase, from April 1997 to March 1999 was conducted at Pamparrão and Porteira Verde valleys. The captured animals were removed and sacrificed in the laboratory. Schistosome prevalence was based on both the coproscopic (Katz *et al.* 1972) and perfusion techniques (Smithers & Terry, 1965), the latter allowed determination of worm burden. The presence of host embryos was also recorded and the number of captured animals was used to calculate rodent abundance.

Both phases (the mark-recapture and the removal phases) had the same capture effort per capture session (400 trap nights), totalling 10 800 trap nights in the first phase (27 capture sessions) and 4800 trap nights in the second phase (12 capture sessions). Classification of *N. squamipes* age was evaluated by weight (Gentile *et al.* 1999). Juveniles are non-reproductive individuals weighing less than 110 g for both sexes. Subadults are individuals in full reproductive condition with the lowest recorded weights or the heaviest individuals not yet mature (between 110 and 190 g for males and 110 and 215 g

for females). Adults are fully mature individuals, weighing more than 190 g for males and more than 215 g for females.

The relationship between the infection rates of rodents and their population parameters was tested using Spearman correlation. Time lags from 2 to 6 months (1–3 capture sessions) were used in correlation tests. These time lag periods were chosen considering the biological cycles of *S. mansoni* and its hosts, since the lower limit corresponds to the time it takes for the infection detection and the upper limit corresponds to the maximum time to rodent population turn-over. The Mann–Whitney test was used to seek for differences between variables (Zar, 1996).

The influence of *S. mansoni* parasitism on the water rat was considered only for the patent phase. Thus, when comparing infected and non-infected individuals, the infected group included only rodents eliminating eggs in their faeces.

RESULTS

Characterization of S. mansoni *infection in* N. squamipes

In the first phase, the mean prevalence rate of *S. mansoni* in *N. squamipes* was $26 \pm 14 \cdot 2 \%$, varying
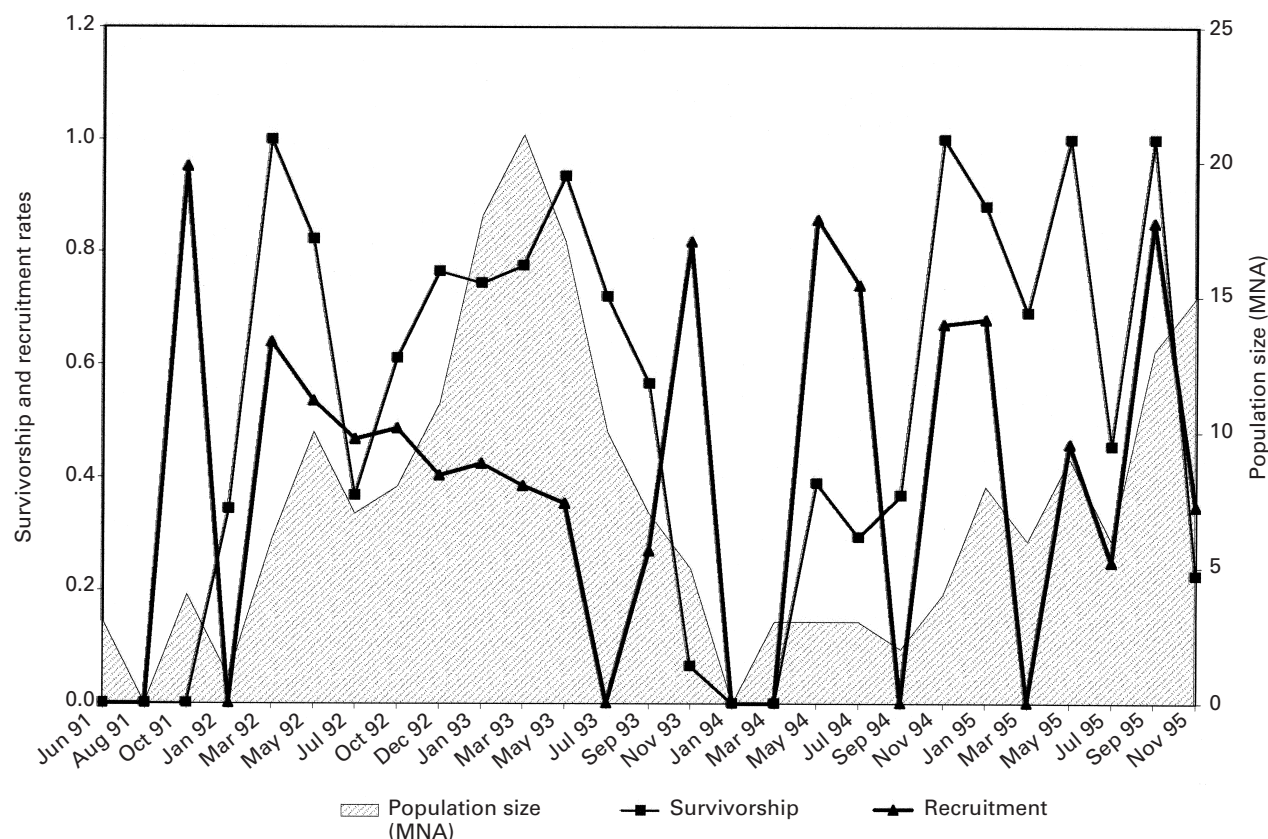
Fig. 3. Population parameters of the *Nectomys squamipes* in the Pamparrão Valley, Sumidouro, Rio de Janeiro State, Brazil (1st phase of the study). Empty data when less than 5 individuals were captured.

from zero to 57 % among capture sessions. Prevalence rates higher than 20 % were observed in 63 % of the cases. Incidence varied from zero to 30 % (Fig. 2). The number of eggs per gram of faeces ranged from 12 to 300 eggs for infected individuals. In this study, 145 *N. squamipes* individuals were captured (87 males, 58 females), 119 of which were examined (72 males, 47 females), 29 of which were infected (16 males, 13 females). There were no differences in prevalence between males and females ($\chi^2 = 0.817$, D.F. 1, N.S.).

In the second phase the mean prevalence rate was 21.0 ± 14.5, varying from zero to 42.9 % among capture sessions in which 5 or more individuals were captured (Fig. 4). In this phase, 96 *N. squamipes* were captured (66 males, 30 females), 38 of them were infected (30 males, 8 females). The mean number of eggs per gram of faeces in infected individuals was 132.2 ± 119.5 (ranging from 12 to 480). Despite the larger number of infected males there was no significant difference in the prevalence rate between sexes ($\chi^2 = 2.18$ N.S.) nor in the worm burden ($z = 0.7$ N.S.). The worm burden increased with the weight of the animals, although the correlation was significant only for the most contaminated area, site 3b (rs $= 0.559$, $P = 0.05$, $\alpha = 1$). Only 1 of 8 recently weaned animals from the juvenile age class was already infected, and all worms were immature. A total of 1309 worms were collected

in 35 perfused *N. squamipes*. The sex ratio of worms was 1.89 biased towards males (880 males, 464 females – the parasites of 1 host were not sexed). Fifty percent of the worm population was concentrated in only 4.2 % of the entire host population and 90.0 % was in 14.6 % of the hosts. Considering only the infected individuals, 11.4 % of the hosts harbour half of the parasite population. The mean worm load was 37.4 ± 59.6 worms/infected host (1–309 worms) and the mean abundance was 17.61 ± 41.6 worms/captured host. The distribution of the *Schistosoma* population, across the entire host population, had a high coefficient of variation, 281.4 % (mean $= 14.7$ and s.d. $= 41.4$) indicating a clumped worm distribution which could be described by a negative binomial distribution ($k = 0.315$). Due to the dispersed nature of the data, no statistical test to detect significance could be performed.

The total prevalence rates including all the individuals captured at any particular site, varied among study sites (Table 2). Some sites could be compared between phases due to the continuity of the study at the same place (site 1, 2, 3 and 3a and 5). Although the prevalence rates varied among phases at the same study site, no statistically significant difference was detected. Prevalence rates at site 3 and 3a were very different between study phases (25 % and 61.9 %) but, again, this was not statistically significant ($\chi^2 = 3.13$; $P < 0.1$). Only 1 infected
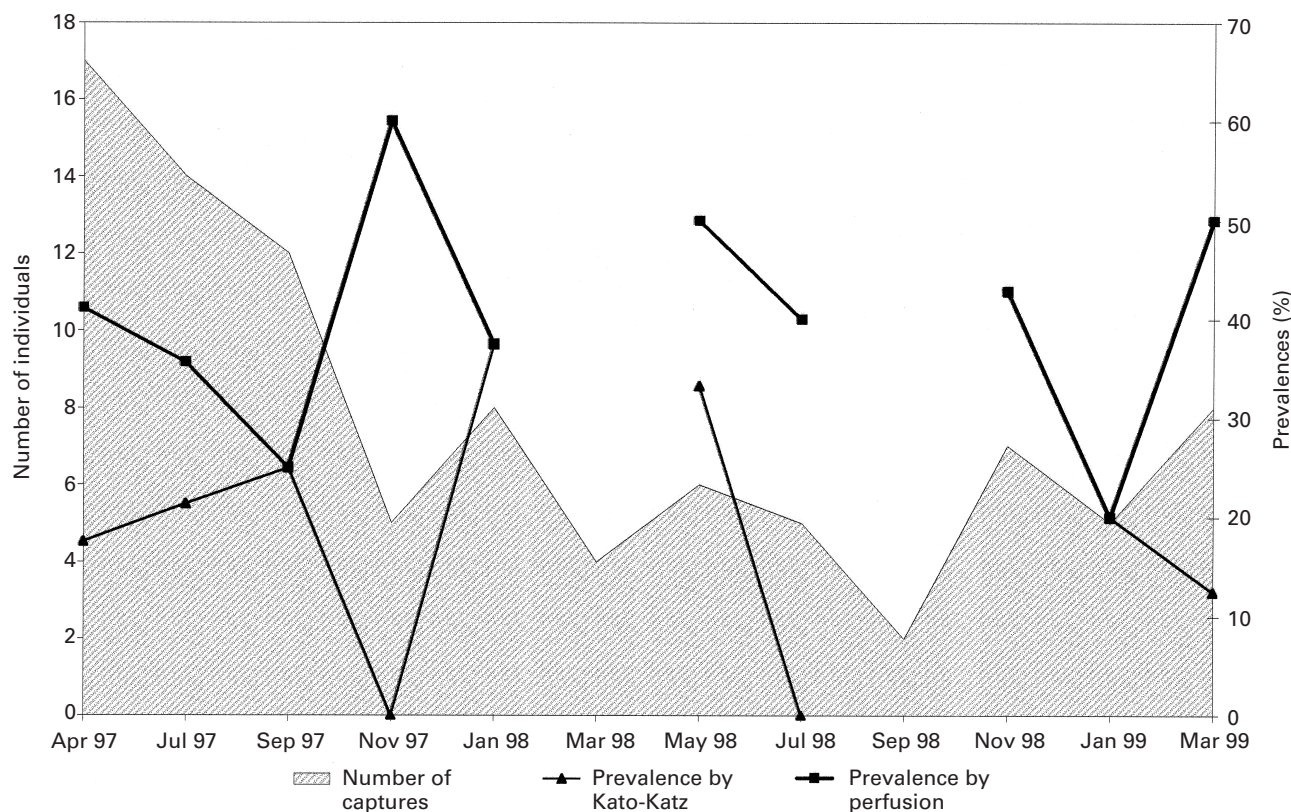
Fig. 4. Population size and prevalence rates of the *Nectomys squamipes* in the Pamparrão and Porteira Verde Valley, Sumidouro, Rio de Janeiro State, Brazil (2nd phase of the study). Empty data when less than 5 individuals were captured.

Table 2. Prevalence, eggs per gram of faeces and infection rates (abundance and intensity) of *Schistosoma mansoni* in *Nectomys squamipes* in each capture site, for both phases of the study

(Mean values and standard deviation for eggs per gram of faeces considering the infected individuals, in parenthesis number of examined individuals.)

Site	Eggs per gram of faeces 1st phase	Eggs per gram of faeces 2nd phase	Prevalence 1st phase* (%)	Prevalence 2nd phase* (%)	Prevalence 2nd phase†	Abundance 2nd phase	Intensity 2nd phase
1	Zero	Zero	Zero	Zero	10·0	0·2	2·0
1a	Zero	—	Zero	—	—	—	—
2	91·5 ± 116·6(13)	108 ± 152·1(4)	26·0	14·3	35·7	3·1	8·9
3	37·2 ± 13·7(5)	—	25·0	—	—	—	—
3a	—	143·4 ± 122·5(13)	—	61·9	85·7	50·7	59·6
3b	—	—	—	‡	‡	140	140
4	—	—	—	0 %	60·0	1·9	4·3
4a	108·6 ± 116·6(5)	—	27·5	—	—	—	—
5	114 ± 79·3(4)	168 ± 33·9(2)	6·9	10·0	21·1	2·8	17·3
6	—	—	—	Zero	Zero	—	—

* By Kato-Katz method.
† By perfusion methodology.
‡ Only 1 (positive) individual captured.

individual was captured at site 1, in the last capture session. This animal was an adult and probably came from another area since there is low or no possibility of local transmission due to the apparent absence of snails and a human infection source.

In comparison to the perfusion technique, we observed that the coproscopic method gave 17 false negatives when worm burdens of less than 6 couples were present, excluding 2 cases in which a single couple was detected. In general though there was strong correlation between number of eggs per gram of faeces and worm load (rs = 0·636; $P < 0.001$; D.F.

33) and also between *S. mansoni* females and eggs per gram of faeces (rs = 0·659; *P* > 0·001; D.F. 31).

The influence of parasitism over the rodent population

There was no correlation between host population size and its infection rate, nor between infection rate and survivorship or recruitment rates. This was true without time lags or with time lags of 2, 4 or 6 months. Infected rodents weighed more than non-infected ones (mean 209·4 ± 57·0 g, *n* = 34 and mean 175·8 ± 68·3 g, *n* = 36 respectively; *z* = 2·03; *P* < 0·05). The permanence time of infected individuals (estimated longevity) was 125·6 ± 136·6 days (ranging from 1 to 490, *n* = 64) and for non-infected was 40·4 ± 74·2 days (ranging from 1 to 355, *n* = 109), presenting a statistically significant difference (*z* = 4·9; *P* < 0·001). There was no significant difference in infection rates between sexes.

Nectomys squamipes females can maintain pregnancy even though infected. In the first phase of the study all the infected females were pregnant (14 individuals) as were half of the non-infected (21 pregnant in 40 captured) females. This difference is probably due to the higher permanence time of infected females. In the second phase, excluding site 1 that had no infections, 24 females were at adult or subadult reproductive age and 7 were actually reproducing, 3 of which were infected with a low worm burden (3 and 8 worms). Across both phases the percentage of reproducing individuals was 37·5 for the infected group and 25 % for the non-infected group and the mean number of foetuses was 3·67 ± 0·57 and 3·25 ± 0·5, respectively.

The immigration patterns were ubiquitous as measured in the first phase excluding only the site 1 where movements were restricted to a local scale among sites 1 and 1a. There were no significant differences in mobility between infected and non-infected individuals (χ^2 = 0·582 D.F. 1, N.S.).

DISCUSSION

In this study it was observed that the water rat *N. squamipes* has very high susceptibility to infection with *S. mansoni* as shown by the high prevalence rates, high number of *Schistosoma* eggs per gram of faeces and the high worm burdens observed in this population. In other endemic areas of Brazil, water rat infection rates varied but were often over 30 % and sometimes more than 90 % (Veiga-Borgeaud *et al.* 1986, 1987; Picot, 1992; Rey, 1993). In the Caribbean islands, overall prevalence of 40 % was observed in *Rattus rattus*, with annual variations ranging from 28 to 61 % (Théron *et al.* 1992). In African wild rodents, infection rates were much lower, generally less than 10 % (Duplantier, 1991) except in 1 study where the rodent *Pelomys* sp. population had 46 % of the individuals infected (Kawashima, 1978).

Novel host–parasite associations were often considered more harmful to the host but some experimental evidence suggests the contrary (Ebert & Herre, 1996). Considering that *S. mansoni* was introduced in South America about 400 years ago (and much later in Sumidouro) the former hypothesis should be investigated since the high infection rates found in Brazil could reflect the recent host–parasite association between South American rodents and *S. mansoni*. In both South America and Africa, the animal species with greatest transmission potential are semi-aquatic as would be expected. It is believed that schistosomiasis infection started in African rodents and that humans acquired it latter, as a lateral transference (Combes, 1990). Théron & Pointier (1995) discussed the differences found between human and rodent strains of *S. mansoni* in egg morphology, allozymes and behaviour of cercariae, showing a new lateral transference that took place from humans to Caribbean rodents.

In this study, 3 factors were related to the infection level of *N. squamipes*: (1) contamination from human sewage in the rodent home ranges; (2) abundance of the snail vector populations in the site, and (3) migration of the rodents across capture sites. The infection level of the rodents increased with the proximity of human residences, particularly in site 3a that had the highest human prevalence rates (M. S. Soares, personal communication), the strongest human influence with large sewage discharge, and the most abundant and stable snail population. Intermediate levels of infection were observed in sites, such as 5 and 2, that had no snails and that received intense immigration of *N. squamipes* from transmission areas. Little or no infection was found in the most isolated site, site 1, where there was no observed immigration of rodents from other sites and which had no snail population or input of human sewage.

The data corroborate the expected clumped distribution for host–parasite association in helminths (Mitchell *et al.* 1990; Théron *et al.* 1992). The spatial heterogeneity and low infection rate of the snail population, *B. glabrata* (A. Giovanelli, personal communication) can explain this clumped distribution. These factors restrict the transmission foci to a few very small areas. Rodents living at highly contaminated sites (like site 3), probably have several contacts with infected snails during their life-time. Another factor that can contribute to this aggregated distribution may be heterogeneity in host resistance to the infection acquisition.

The positive correlation between rodent weight and worm burden in the most infected area, together with the rarity and low worm burden of unisexual in-

fections, shows that multiple infections are probably common at least in the very contaminated areas. In areas with little or no contamination, the animals may get infected only occasionally, perhaps once in a life-time. If an infected animal is in a non-transmission area, it is probably an immigrant that carried the worms from another site and may not acquire more worms during its life-time, unless the infection establishes itself in this area.

It was found that 50 % of the parasite population was concentrated in only 4·1 % of the host population (very similar to the 4 % of Théron *et al.* 1992) and 11·4 % of the infected rodents harbour half of the parasite population (9 % of Théron *et al.* 1992). This highly infected host group possibly plays an important role in increasing the transmission rates at a local area, because their life-span does not seem to be reduced and, furthermore, we observed that worm burden was correlated with egg production. But, the importance of the less infected group, which accounts for 88·6 % of the infected hosts, cannot be disregarded since they are numerous and can have a crucial role in occasionally carrying the infection to new areas.

The population parameters (size, recruitment and survivorship) in the *N. squamipes* population did not seem to be affected by schistosome infection. The population dynamics of this rodent was not influenced by the infection during the entire study despite the steadfastness of high prevalence rates. In theory, the parasites might regulate their host abundance (Anderson & May, 1979), but this has been proved to occur only in captive *Mus musculus* populations (Barker, Singleton & Spratt, 1991). It is difficult to state a final conclusion in the absence of controlled experiments to detect the effects of the parasite over wild host populations. The use of intervention experiments would be useful in detecting population regulation by macroparasites.

Amano *et al.* (1990) demonstrated a decreased ability of infected mice (CBA-J strain) to produce viable offspring due to death of the mother, abortions and to a large extent, infanticide with less than 35 % success for infected females versus 70 % for the non-infected one. Our results from field data, did not show such effects, perhaps because of the low tissue aggression and efficient periovular modulation observed in *N. squamipes* infected with *S. mansoni* (Silva & Andrade, 1989). Additional experimental laboratory studies using *N. squamipes* as a model could help explain this further.

Marked changes in locomotor activity and exploratory behaviour of infected mice, together with a body weight reduction, were shown to result from *S. mansoni* infection (Fiore *et al.* 1996). If these deleterious effects occur in natural populations they would decrease the fitness of infected rodents reducing their life-span. In this study we detected no differences in long distance migratory activity in

infected *N. squamipes*. Furthermore, their life-span was not affected since we observed that infected individuals were older, considering body weights, and had longer permanence time in the study area (at the mark-recapture period of study). Despite the fact that older animals are more likely to be correctly diagnosed as positive, because as the coproscopic method is less sensitive to recent and low burden infections the observed pattern still showed no decreased fitness of infected individuals. Laboratory data on experimental infection and pathological studies corroborated this mild host–parasite interaction, since *S. mansoni* infection in *N. squamipes* caused low pathogenicity in spite of the long persistence of the infection (Silva *et al.* 1992).

Understanding the infection dynamics of *S. mansoni* in *N. squamipes* hosts can help clarify the role of *N. squamipes* in schistosomiasis transmission. The presence of infected individuals in places far from areas contaminated with human faeces shows that these rodents can carry *S. mansoni* to places previously lacking transmission, complicating the control of this disease. Our data on epidemiology of *N. squamipes* indicate that this rodent can increase transmission in endemic areas. Furthermore, it can be used as a natural indicator of a transmission focus, because, when the possibility of acquiring parasites exists, the rodent population will test positive to the infection. *N. squamipes* can also be used to access parasitological parameters not available for the human population (Théron *et al.* 1992).

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