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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

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Abstract

The Pantanal is a large ecosystem located in South America. This preserved area is seasonally flooded due to abundant rainfall during the summer and the subsequent overflow of the Paraguai River. In this paper, we examine the helminth community structure in the wild rodent *Thrichomys pachyurus* during the wet and dry seasons in two locations of the preserved and cattle ranching areas in the Southern Pantanal. We identified 12 species of helminth, and, although we did not find any differences in species richness between locations within the Pantanal, we found that richness was higher during the wet season. Helminth species were largely aggregated in both farm locations and during seasons. The most common helminth species were more abundant during the dry season than during the wet season, which may have been due to the increased habitat availability and rodent population increase. The intensity of the infection also followed the same pattern for most helminths. The trichostrongylids (*Heligmostrongylus crucifer*, *H. almeidai* and *Pudica cercomysi*) were dominant at both farm locations. The land use of each area was not correlated with helminth diversity. However, species composition of the helminth community of *T. pachyurus* differed between locations and may be correlated with environmental differences between the habitats. The seasonality of the Pantanal was highly correlated with helminth parasitism in *T. pachyurus*.

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Introduction

The structure of parasite communities is influenced by several factors, including biogeography and abiotic parameters (environmental factors) as well as host density and life history (Abu-Madi *et al.*, 2000). Helminth communities are also influenced by host–parasite and parasite–parasite interactions within the host (Poulin, 2001). In discrete or isolated host populations, susceptibility to infection by parasitic organisms is strongly influenced by intrinsic host factors, including age and life history (Barnard *et al.*, 2002; Behnke, 2008).

Comparing parasitological parameters of a specific host species in different habitats may be an important approach in evaluating the impact of environmental factors on helminth community structure and host–parasite relationships. Moreover, climatic factors are known to influence the development of free-living stages of parasites and can affect survival, transmission and host infection (Haukisalmi & Henttonen, 1990; Behnke, 2008).

Helminth parasites have been studied extensively in European rodents (Montgomery & Montgomery, 1990; Behnke *et al.*, 1999, 2001; Fuentes *et al.*, 2004; Sainz-Elipe *et al.*, 2007). Most helminth studies focusing on Brazilian mammals are strictly taxonomic reports (Travassos, 1927; Travassos & Freitas, 1941; Gomes *et al.*, 2003; Durette-Desset *et al.*, 2006). The helminth community structure of Brazilian rodents has been reported for *Nectomys squamipes* in the Atlantic Forest (Maldonado Jr *et al.*, 2006). In the Brazilian Pantanal, studies of small mammal helminths have been performed only for the marsupial *Gracilinannus agilis* (Feijó *et al.*, 2008; Lopes Torres *et al.*, 2009).

Species of the genus *Thrichomys* (Rodentia: Caviomorpha) occupy diverse ecosystems in South America. *Thrichomys pachyurus* is a widespread rodent from Paraguay to western Brazil, occurring in the Pantanal biome (Bonvicino *et al.*, 2002; Braggio & Bonvicino, 2004). The species has a long gestation period of approximately 3 months and small litter size, with an average of 2.5 ± 0.9 offspring (Teixeira *et al.*, 2005). Recent parasitological studies of *Thrichomys* in the wild have shown its involvement in the transmission cycles of *Trypanosoma cruzi* (L. Herrera *et al.*, 2005; Xavier *et al.*, 2007). In the areas studied, this rodent species is abundant and is often infected with *T. evansi*, a flagellate that causes severe disease in horses and dogs (H.M. Herrera *et al.*, 2005, 2007).

The effects of land use and seasonal floodplain events on the helminth community structure have remained unclear in the Pantanal region. In this study, we evaluated and compared the helminth community structure and the parasitological parameters of *T. pachyurus* in two Brazilian Pantanal locations with different land-use histories. We considered the effects of these different areas and the effects of Pantanal seasonality on variation in the respective helminth communities.

Materials and methods

Collecting sites

The Pantanal is a large ecosystem located in central South America, with a seasonal floodplain that varies with local rainfall and flooding of the Paraguai River. Although the Pantanal is a distinct ecosystem, it is dominated by species of the Cerrado biome and contains areas that differ in landscape and hydrological characteristics, forming a mosaic of local hydrological conditions, soil types and vegetation communities. Local climatic conditions are divided into two distinct seasons, which are the wet (summer and autumn) and dry (winter and spring) seasons. During the wet season, the local fauna share restricted areas and resources that are reduced in their availability. Another important feature of this region is the increase of ranching activities and the consequent habitat disturbance, which modify the characteristics of this environment and increase contact between wildlife and domestic animals (H.M. Herrera *et al.*, 2007). This may predispose the area to an increase in the transmission of helminths from low-specificity hosts to more distantly related hosts.

The study was performed at two farms in the Brazilian Pantanal, Mato Grosso do Sul State. The first site was the Rio Negro Farm, located in the sub-region of Aquidauana (19°34′54″S, 056°14′62″W). This area is a private, protected area used for ecological tourism and scientific research by Conservation International. The second research site was the Alegria Farm, situated in the municipal district of Corumbá (19°15′01″S, 057°01′29″W). This site is a private ranch used primarily for cattle breeding. In both sites, the landscape includes the following elements: (a) ‘*cerrado*’, characterized by small, twisted or gnarled trees that are thinly spaced by herbaceous layers formed by grasses and shrubs; (b) ‘*cordilheira*’, which is characterized by higher ground that is covered by dense, semi-deciduous forest and is free of seasonal floods; (c) ‘grassland’, characterized by open fields that are eventually flooded under great inundations; and (d) ‘edge of lakes’, which is characterized by areas that are covered by grass and are seasonally flooded.

The climate is sub-humid tropical with two distinct seasons: the rainy summer from October to April and the dry winter from May to September. The average annual temperature of the region is 26.9°C during the summer and 23.7°C during the winter, with a mean annual rainfall of 1066 mm.

Parasitological procedures

Small mammals were trapped between February and June 2002 at the Rio Negro Farm, and between February and September 2003 at the Alegria Farm. Each trapping session consisted of 5 days. Traps were placed in four transects representing different habitats: *cerrados*, *cordilheiras*, grassland and edge of lakes. Each transect had four trapping stations spaced 20 m apart. At each station, two live-traps, a Tomahawk® trap (model 201; 16 × 5 × 5 inches (40.6 × 12.7 × 12.7 cm)) and a Sherman® trap (model XLK; 3 × 3.75 × 12 inches (7.6 × 9.5 × 30.5 cm)) were placed on the ground. Traps were baited with a mixture of peanut butter, banana, oatmeal, bacon and manioc, and were checked daily in the morning.

Captured *Thrichomys pachyurus* were transported to a base camp for euthanasia and necropsy. All animals were preserved by taxidermy and deposited as voucher specimens in the Mammal Collection of the National Museum in Rio de Janeiro State. All animal procedures followed the guidelines for capture, handling and care of mammals of the American Society of Mammalogy and the bio-security procedures of the Brazilian Health Ministry. Animals were collected under the authority of the Brazilian Government Institute for Wildlife and Natural Resources (IBAMA, CGFAU 009/2002 and CGFAU 137/2002). Bio-security techniques and individual safety equipment were used during all procedures involving animals or biological samples (Lemos & D'Andrea, 2006).

We examined the abdominal and thoracic cavities of the rodents for helminths, searching the oesophagus, stomach, small and large intestines, liver, pancreas, kidneys, lungs, heart and gall bladder. Organs were separated in Petri dishes and dissected under a stereomicroscope to remove small helminths. Collected parasites were washed twice in saline in order to remove tissue debris and were fixed in hot AFA (2% acetic acid, 3% formaldehyde and 95% ethanol). Specimens were cleaned in LAF (40% lactophenol, 20% acid lactic and 20% phenol, in water) for later species identification (Yamaguti, 1961; Durette-Desset & Chabaud, 1981; Durette-Desset, 1985; Vicente *et al.*, 1997).

Data analysis

Helminth species richness was considered to be the number of species present. Helminth diversity was calculated using the Shannon index (H') and compared using H_{max} and H_{min} (Ludwig & Reynolds, 1988; Magurram, 1988). Helminth richness and diversity were calculated at each farm, for each season and for the entire dataset.

The distribution pattern of each helminth species was determined using the index of dispersion, calculated as the ratio between the variance of parasite abundance and the mean of parasite abundance (Ludwig & Reynolds, 1988; Bush *et al.*, 2001; Combes, 2001). If the ratio was close to one, the distribution was considered to be random; if it was less than one, distribution was regular; if it was greater than one, distribution was aggregated. In the latter case, the higher the variance to mean ratio, the more aggregated the distribution.

To analyse helminth community structure, we considered prevalence, intensity of infection and abundance of each species, taking into account all captured rodents and using methods described by Bush *et al.* (1997). Each community parameter was also compared between seasons and farms, using a 2×2 contingency chi-square test whenever possible. When a helminth species occurred in only one farm, we compared abundance between seasons using a chi-square goodness of fit test (Zar, 1999). The presence/absence of each helminth was analysed considering both location and season using a logistic regression with a stepwise backward likelihood ratio model.

We investigated the co-occurrence of helminths by examining the Spearman correlations of the intensities for each pair of helminths. Since data were not normally distributed, only rodents that contained both species of a particular pair were considered in this analysis (Zar, 1999). The Jaccard index of species association (Ludwig & Reynolds, 1988) was calculated for each pair of species with sufficient data, in order to investigate relationships between helminth species.

The helminth community structure was characterized according to Thul *et al.* (1985). We used an importance index to classify each helminth species in the community, based on the number of infected hosts and the number of individuals of each parasite species. The more parasites and number of animals infected with a parasite, the more dominant a parasite was considered in the community. The importance value, I, was calculated for each helminth species as follows:

$$I_j = M_j \times \left[\frac{(A_j \times B_j)}{\sum_i (A_i \times B_i)} \right] \times 100,$$

where A = number of individual parasites of a particular species; B = number of hosts infected with parasites of that species; j is the parasite species considered, i is any parasite species, and M is a maturation factor equal to 1.0 if at least one mature individual of the species considered was found, and otherwise equal to 0. If the importance index $I \geq 1.0$, the species was considered to be a dominant species; $0.01 \leq I \leq 1.0$ identified co-dominant species which contributed significantly to the community, though to a lesser degree than dominant species; $0 < I < 0.01$ characterized subordinate species that occurred infrequently, and, although they may have developed and reproduced, they did not contribute significantly to the community; and $I = 0$ characterized unsuccessful pioneer species that had gained access to a host but were not able to mature or reproduce, they contributed little to the community and were characteristic of another host (Thul *et al.*, 1985). Statistical significance was considered at $P < 0.05$.

Results

Helminth species richness

Seventy specimens of *Thrichomys pachyurus* were collected during this study. Eighteen animals were collected during the wet season and 14 during the dry season at the Rio Negro Farm. At the Alegria Farm, 26 *T. pachyurus* were collected during the wet season and 12 during the dry season (table 1).

The overall helminth richness was 12 species and there was no difference between locations. At both Rio Negro and Alegria, the richness was greater during the rainy season, although this difference was not significant.

Table 1. Number of host animals analysed in each study area and season.

	Rio Negro season			Alegria season		
	Wet	Dry	Total	Wet	Dry	Total
Males	12	13	25	15	6	21
Females	6	1	7	10	6	16
Total	18	14	32	26[a]	12	38

[a] One animal was not sexed.

Table 2. Richness and diversity indices of helminths recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil.

Farm	Season	Richness	H'	H_{max}	H_{min}
Rio Negro	Wet	9	1.46	2.19	0.063
	Dry	6	1.39	1.79	0.039
	Both	9	1.68	2.19	0.063
Alegria	Wet	8	1.34	2.07	0.055
	Dry	7	1.35	1.94	0.047
	Both	9	1.52	2.19	0.063
Total		12	1.81	2.48	0.086

H', Shannon diversity index, H_{max}, maximum diversity index; H_{min}, minimum diversity index.

Further, there was no significant difference in diversity between seasons (table 2).

Helminth species recovered from the rodents in Rio Negro included the nematodes *Heligmostrongylus crucifer*, *H. almeidai*, *H. interrogans*, *Pudica cercomysi*, *P. maldonadoi*, *Thrichuris* sp., *Avellaria intermedia* and *Stilestrongylus inexpectatus*. The latter three species were observed only during the wet season. Only one species of Cestoda *Raillietina* sp. was recorded. The helminth species recovered from rodents in Alegria included the nematodes *H. crucifer*, *H. almeidai*, *H. interrogans*, *P. cercomysi*, *Thrichuris* sp., *Paraspidodera uncinata* and *Physocephalus lassancei*. *Thrichuris* sp. was observed only during the dry season, and *P. lassancei* was only found during the wet season. Two species of Cestoda were also observed: *Raillietina* sp. and *Rodentolepis* sp. The latter species was only detected once in one host during the dry season. All helminths were recovered from the small intestine except *P. uncinata*, which was found in the large intestine, and *P. lassancei*, which was recovered from the stomach.

Helminth distribution and infection levels

The distribution of most nematode helminths was highly aggregated (table 3). In particular, the trichostrongylids *H. almeidai* and *H. crucifer* showed aggregated distributions at both farms during both seasons. *Heligmostrongylus interrogans* was randomly distributed in Rio Negro during the wet season, and *P. cercomysi* was randomly distributed during the dry season. *Avellaria intermedia* showed an aggregated distribution in Rio Negro during the wet season. The distribution of *Thrichuris* sp. was aggregated in Rio Negro and Alegria during the dry season and was randomly distributed in Rio Negro during the wet season. The distribution of *P. uncinata* was aggregated in Alegria during the dry season. The cestoda *Raillietina* sp. was consistently randomly distributed (table 3). The distributions of other species could not be adequately evaluated.

The nematode *H. interrogans* showed significantly higher abundance in Alegria during the dry season, and *P. cercomysi* showed significantly higher abundance in Rio Negro during the wet season (tables 4 and 5). The other species did not show any significant differences in abundance between farms or seasons (tables 4 and 5). The highest abundances in Rio Negro were observed for *H. almeidai* and in Alegria for *H. crucifer* (table 4).

In Rio Negro, *P. cercomysi* was much more abundant during the wet season and *H. almeidai* and *A. intermedia* were more abundant during the dry season; these species were abundant in this farm location (tables 4 and 5). *Heligmostrongylus crucifer* and *H. interrogans* were more abundant in Alegria during the dry season and were most abundant in this farm (tables 4 and 5).

Most species (*H. crucifer*, *H. interrogans*, *P. cercomysi*, *P. uncinata* and *Raillietina* sp.) were more abundant in Alegria during the dry season (tables 4 and 5). Only *Trichuris* sp. showed significantly higher prevalence in Rio Negro, also during the dry season (tables 4 and 5).

The logistic regression analysis assessing the presence of the helminths with respect to both the location and season showed that, for *H. almeidai*, *Thrichuris* sp. and *Raillietina* sp., the season exerted a stronger influence on species presence than the location (table 6). For *H. crucifer*, *H. interrogans*, *P. maldonadoi*, *A. intermedia* and *P. cercomysi*, no significant differences were found between locations or seasons. Other species could not be tested.

There were no significant correlations between the helminth intensities of infection (table 7). The Jaccard indices of association did not show co-occurrence or segregation between any pair of helminth species (table 8). The nematodes *H. crucifer*, *H. almeidai* and *P. cercomysi* were dominant at both Rio Negro and Alegria (table 9). *Trichuris* sp., *A. intermedia* and *Raillietina* sp. were dominant only in Rio Negro, and *H. interrogans* and *P. uncinata* were dominant only in Alegria (table 9). The other helminths were either co-dominant or unsuccessful pioneer species at both farms (table 9).

Discussion

Thrichomys pachyurus is an abundant rodent in the Pantanal and acts as a wild reservoir for *T. cruzi* and *T. evansi* (H.M. Herrera *et al.*, 2007). Studies have investigated other parasites and their life cycles in this caviomorph rodent species.

Table 3. Dispersion indices for each helminth recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil.

Farm	Season	*H. crucifer*	*H. almeidai*	*Pudica cercomysi*	*Thrichuris* sp.	*Avellaria intermedia*	*H. interrogans*	*P. uncinata*	*Raillietina* sp.
Rio Negro	Wet	12.62	1.38	32.34	0.20	6.43	0.40	–	0.13
	Dry	11.13	27.43	0.18	11.95	–	–	–	0.40
Alegria	Wet	38.48	4.43	8.77	–	–	2.67	–	–
	Dry	32.47	3.56	7.87	1.50	–	60.53	1.33	0.19

Table 4. Abundance, intensity and prevalence (95% confidence limits) of each helminth species recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil.

	Heligmostrongylus crucifer	*Heligmostrongylus almeidai*	*Heligmostrongylus interrogans*	*Pudica cercomysi*	*Pudica maldonadoi*	*Thrichuris* sp.	*Avellaria intermedia*	*Stilestrongylus inexpectatus*	*Paraspidodera uncinata*	*Physpcephalus lassancei*	*Raillietina* sp.
Abundance											
Rio Negro, wet season	4.56 (1.61–10.50)	2.22 (0.78–4.50)	1.11 (0.28–2.39)	17 (7.94–34)	0.67 (0–2)	0.28 (0.06–0.56)	1.94 (0–6.11)	0.89 (0–2.67)	–	–	0.44 (0.17–0.72)
Rio Negro, dry season	5.36 (1.71–13.07)	13.79 (4.93–32)	–	1.57 (0–4)	–	2.29 (0.57–8)	3.07 (0–9.21)	–	–	–	0.86 (1.50–2.75)
Rio Negro, total	4.91 (2.41–9.03)	7.28 (3.25–15.09)	0.63 (0.16–1.41)	10.25 (4.97–20.38)	0.38 (0–1.13)	1.16 (0.41–3.75)	2.44 (0.31–7.09)	0.50 (0–1.50)	–	–	0.63 (0.34–0.94)
Alegria, wet season	6.35 (1.58–18.42)	0.81 (0.04–2.35)	0.69 (0.08–2)	1.92 (0.69–5.08)	–	–	–	–	0.04 (0–0.12)	0.23 (0–0.69)	0.23 (0–0.69)
Alegria, dry season	9.25 (2.75–29.42)	1.50 (0.25–3.58)	17.83 (6.17–58.17)	8.33 (4.50–14.08)	–	1.17 (0.33–2.33)	–	–	0.75 (0.08–2.0)	–	0.75 (0.25–1.08)
Alegria, total	7.26 (3.11–16.29)	1.03 (0.32–2.18)	6.11 (2.18–19.66)	3.74 (2.03–6.45)	–	0.37 (0.11–0.95)	–	–	0.26 (0.05–0.76)	0.16 (0–0.47)	0.39 (0.16–0.89)
Intensity											
Rio Negro, wet season	10.25 (4.25–19.50)	8 (5.20–10.60)	5 (4–6.25)	27.8 (14.91–51.64)	12 (0–0)	1.25 (1–1.50)	17.50 (10–17.50)	16 (0–0)	–	–	1.14 (1–1.29)
Rio Negro, dry season	15 (5.20–25.20)	27.57 (11.71–51.86)	–	11 (10–12)	–	4.57 (1.29–13.14)	43 (0–0)	–	–	–	2 (1.17–2.50)
Rio Negro, total	12.08 (6.38–18.85)	19.42 (9.92–39.08)	5 (4–6.25)	25.23 (14.6–45.92)	12 (0–0)	3.36 (1.27–9.09)	26 (10–37)	16 (0–0)	–	–	1.54 (1.15–1.92)
Alegria, wet season	33 (13.20–68.40)	7 (1–10.67)	6 (2–8.67)	6.25 (2.88–13.25)	–	–	–	–	1 (0–0)	6 (0–0)	6 (0–0)
Alegria, dry season	15.86 (5.14–41.14)	3.60 (1–6.20)	26.75 (9.75–70.13)	10 (6.10–16.40)	–	2.80 (1.20–4.20)	–	–	3 (1–4.33)	–	1.29 (1–1.57)
Alegria, total	23 (10.92–44.92)	4.88 (1.88–7.63)	21.09 (8.55–61.82)	8.35 (5.47–13.41)	–	2.80 (1.20–4.20)	–	–	2.50 (1–4.0)	6 (0–0)	1.88 (1.13–3.50)
Prevalence											
Rio Negro, wet season	44.4 (0.21–0.69)	27.8 (0.10–0.53)	22.2 (0.06–0.48)	61.1 (0.36–0.83)	5.6 (0.001–0.27)	22.2 (0.06–0.48)	11.1 (0.01–0.35)	5.6 (0.001–0.27)	–	–	38.9 (0.17–0.64)
Rio Negro, dry season	35.7 (0.13–0.65)	50 (0.23–0.77)	–	14.3 (0.02–0.43)	–	50 (0.23–0.77)	7.1 (0.002–0.34)	–	–	–	42.9 (0.18–0.71)
Rio Negro, total	40.6 (0.24–0.59)	37.5 (0.21–0.56)	12.5 (0.03–0.29)	40.6 (0.24–0.59)	3.1 (0.0007–0.16)	34.4 (0.18–0.53)	9.4 (0.02–0.25)	3.1 (0.0007–0.16)	–	–	40.6 (0.24–0.59)
Alegria, wet season	19.2 (0.066–0.39)	11.5 (0.02–0.30)	11.5 (0.02–0.30)	30.8 (0.14–0.52)	–	–	–	–	3.8 (0.0009–0.20)	3.8 (0.0009–0.20)	3.8 (0.0009–0.20)
Alegria, dry season	58.3 (0.28–0.85)	41.7 (0.15–0.72)	66.7 (0.35–0.90)	83.3 (0.52–0.98)	–	41.7 (0.15–0.72)	–	–	25 (0.5–0.57)	–	58.3 (0.28–0.85)
Alegria, total	31.6 (0.18–0.49)	21.1 (0.09–0.37)	28.9 (0.15–0.46)	44.7 (0.29–0.62)	–	13.2 (0.04–0.28)	–	–	10.5 (0.03–0.25)	2.6 (0.0006–0.14)	21.1 (0.10–0.37)

Table 5. Results of the chi-square test for abundance, intensity and prevalence in relation to farm and season for each helminth recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil.

	Abundance		Intensity		Prevalence	
	χ^2	P	χ^2	P	χ^2	P
H. crucifer	0.229	$0.75 > P > 0.50$	4.974*	$0.05 > P > 0.02$	15.380*	<0.001
H. almeidai	0.657	$0.50 > P > 0.25$	7.061*	<0.01	2.998	$0.10 > P > 0.05$
H. interrogans	11.654*	<0.001	14.015*	<0.001	56.412*	<0.001
P. cercomysi	15.527*	<0.001	5.353*	$0.05 > P > 0.02$	53.081*	<0.001
Thrichuris sp.	0.138	$0.75 > P > 0.50$	0.703	$P > 0.10$	15.926*	<0.001
A. intermedia	0.255	$0.75 > P > 0.50$	10.747*	<0.01	0.879	$0.50 > P > 0.25$
P. uncinata	0.638	$0.50 > P > 0.25$	1.00	$0.90 > P > 0.75$	15.60*	<0.001
Raillietina sp.	0.029	$0.95 > P > 0.90$	2.150	>0.10	29.043*	<0.001

*Significant results.

Table 6. Significant results of the stepwise logistic regression of presence/absence of each helminth recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil, considering the location and the season.

Species	Significant parameter	Chosen model	Estimate	SE	*P* value	Odds ratio	95% confidence interval
H. almeidai	Season	Step 1	1.350	0.555	0.015	3.857	11.437–1.301
Thrichuris sp.	Season	Step 0	2.120	0.674	0.002	8.334	31.232–2.224
Raillietina sp.	Season	Step 1	1.658	0.555	0.003	5.250	15.567–1.771

Table 7. Spearman correlation coefficients of the intensities of infection between helminths recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil. Samples sizes (number of host animals) are in parentheses.

	Heligmostrongylus almeidai	*Heligmostrongylus crucifer*	*Heligmostrongylus interrogans*	*Pudica cercomysi*	*Thrichuris* sp.
H. almeidai	–	–	–	–	–
H. crucifer	0.193 (7)	–	–	–	–
H. interrogans	−0.857 (6)	0.354 (10)	–	–	–
P. cercomysi	0.482 (11)	0.103 (18)	−0.316 (15)	–	–
Thrichuris sp.	0.171 (6)	−0.303 (10)	0.783 (5)	−0.205 (9)	–
Raillietina sp.	0.442 (9)	−0.113 (8)	0.131 (6)	−0.361 (10)	0.413 (8)

Table 8. Jaccard indices of association between helminth species recovered from *Thrichomys pachyurus* (Rodentia: Echymyidae) on the Rio Negro and Alegria Farms in the Pantanal, Brazil.

	Heligmostrongylus almeidai	*Heligmostrongylus crucifer*	*Heligmostrongylus interrogans*	*Pudica cercomysi*	*Thrichuris* sp.
H. almeidai	–	–	–	–	–
H. crucifer	0.179	–	–	–	–
H. interrogans	0.207	0.333	–	–	–
Pudica cercomysi	0.289	0.333	0.500	–	–
Thrichuris sp.	0.200	0.300	0.160	0.235	–
Raillietina sp.	0.281	0.216	0.207	0.225	0.276

This is the first report on the helminth fauna of *T. pachyurus* with new records of the geographic distributions for most of the helminth species. Four of the ten sampled nematode species were previously registered in another biome for the closely related species *T. apereoides* which lives in the Brazilian Cerrado and Caatinga. Although *H. crucifer* had only been observed in the Pantanal, *H. almeidai*, *H. interrogans* and *S. inexpectatus* have been described previously in the Caatinga, and *S. inexpectatus* has also been described in Cerrado.

Table 9. Importance indices for the helminths on the Rio Negro (RN) and Alegria (A) Farms in the Pantanal, Brazil.

	Heligmostrongylus crucifer	*Heligmostrongylus almeidai*	*Pudica cercomysi*	*Thrichuris* sp.	*Avellaria intermedia*	*Heligmostrongylus interrogans*	*Pudica maldonadoi*	*Stilestrongylus inexpectatus*	*Paraspidodera. uncinata*	*Physocephalus. lassancei*	*Railleitina* sp.
RN	21.59 dominant	24.03 dominant	44.09 dominant	3.39 dominant	2.68 dominant	0.92 co-dominant	0.14 co-dominant	0.18 co-dominant	0.00 unsuccessful pioneer	0.00 unsuccessful pioneer	2.98 dominant
A	35.22 dominant	3.32 dominant	27.11 dominant	0.74 co-dominant	0.00 unsuccessful pioneer	31.93 dominant	0.00 unsuccessful pioneer	0.00 unsuccessful pioneer	1.17 dominant	0.19 co-dominant	0.32 co-dominant

The larger helminth diversity in *T. pachyurus* when compared with congeneric species from the Caatinga and Cerrado suggests an environmental adaptation of life cycles of most helminths to the Pantanal habitat, which is more humid than other biomes, in spite of the influence of the surrounding Cerrado on the Pantanal fauna (Alho & Gonçalves, 2005). In addition, the great diversity of helminth species found in this rodent could have resulted from sharing the habitat with other mammals. The infection of *T. pachyurus* likely results from sharing the habitat with other rodents and deer during the flood periods. Indeed, *P. lassancei* has been described from the stomach of the cervid *Mazama simplicicornis* from Lassance, Minas Gerais State (Cuocolo, 1943). This genus preferentially inhabits forested areas in Pantanal (Rivero *et al.*, 2005), and *T. pachyurus* are found preferentially in this habitat in the '*cordilheiras*' (H.M. Herrera *et al.*, 2007). Thus, these two species may overlap during the flood season.

Paraspidodera uncinata is a parasite of the large intestine of *Cavia porcellus*, *C. aperea* and *C. fulgida* and has been found infecting caviomorph rodents of the families Cavidae and Agoutidae (Travassos & Freitas, 1948; Pinto *et al.*, 2002). Moreover, it has also been reported infecting lagomorphs (Vicente *et al.*, 1997), demonstrating that it has little vertebrate host specificity. Although this is the first report of *P. uncinata* infecting *T. pachyurus*, previous studies have reported this nematode infecting *Cavia* sp. in Mato Grosso do Sul State (Travassos & Freitas, 1941). Further, a *Cavia* sp. was trapped in the same habitat where the rodents were collected, reinforcing the importance of co-habitation as a determinant of co-occurring parasites. Likewise, *A. intermedia* has also been observed infecting caviomorph rodents such as *Dasyprocta fuliginosa* in Jauari, Amazonas (Durette-Desset *et al.*, 2006).

Extrinsic factors play a major role in determining the structure of helminth communities, with strong evidence in support of temporal variations in helminth communities arising from seasonal and annual changes in the environment (Langley & Fairley, 1982; Haukisalmi *et al.*, 1988; Montgomery & Montgomery, 1989). Helminth species composition differs in space and time, suggesting that each site and season sampled has specific habitat characteristics that allow for the occurrence of helminth species that are better adapted to these particular conditions. In this study, differences in spatial scale are demonstrated by the occurrence of *A. intermedia*, *S. inexpectatus* and *P. maldonadoi* only at Rio Negro, and *P. uncinata* and *P. lassancei* only at Alegria. With regard to temporal variations, seasonal differences in helminth community structure could potentially be a consequence of changes in mammal aggregation patterns as a result of the seasonal shrinkage and expansion of their natural habitats in response to the weather conditions.

The aggregated distribution observed for most nematodes analysed is a frequent pattern of parasite distribution in the wild (Bush *et al.*, 2001; Poulin, 2007). The random distribution in both localities for the cestoda *Raillietina* sp. may result from strong intra-specific competition between the species, which has been observed with other cestoda infections (Keymer, 1982). Further, the existence of several intermediary and definitive hosts suggests the occurrence of the transmission cycle in different habitats (Ackert, 1922; Horsfall, 1938).

The most common helminth species showed higher abundances, intensities and prevalences during the dry season, which may be a consequence of the regular expansion of habitat availability that is due to the shrinking bays, favouring helminth life cycles and dispersion (Lacher *et al.*, 1986). The higher abundance and intensity of *P. cercomysi* during the wet season at Rio Negro may be due to the low host specificity of this helminth in combination with the spatial restrictions of this season, which may favour the transmission of parasites among different host species, such as *Gracilinanus agilis* and *Clyomys laticeps*. The highest prevalence observed in this study was for *P. cercomysi* at the Alegria farm during the dry season, where more than 80% of the animals were infected. This extremely high infection rate indicates that parasites were frequently transmitted between *T. pachyurus* individuals. These data suggest that the potential host species for *P. cercomysi* at Alegria are reduced due to anthropogenic activities.

The less common species (*P. maldonadoi*, *S. inexpectatus*, *P. uncinata* and *P. lassancei*), which were characterized as either co-dominant or unsuccessful pioneer species, were favoured by flooding and appeared only during the wet season. Given that the abundance and intensity of infection of the dominant species were generally reduced during the wet seasons, other helminth species could have became established in the host population during these periods. Considering the higher prevalence of the dominant nematode species in the study areas during the dry season (except for *A. intermedia*, which showed higher prevalence in the wet season) and the higher prevalence of co-dominant species during the wet season (except for *P. uncinata*, which was dominant at this time), we propose the hypothesis of niche constriction for the helminth community during the wet season in this study. Considering the overall host population, the lack of correlation in the helminth intensities may indicate that habitat niche reduction for helminth species allows coexistence of these parasite species.

In conclusion, land use and seasonal effects of weather conditions in the Brazilian Pantanal region may lead to modifications in the patterns of rodent parasitism due to habitat alterations and habitat reduction imposed by flooding or cattle ranching. Although land use did not seen to affect helminth diversity and did not result in a loss of helminth biodiversity, the species composition of each helminth community in *T. pachyurus* differed between locations, and we suggest that this difference may result from habitat differences between regions (preserved versus disturbed). Seasonality in the Pantanal was an important factor in modulating helminth parasitism. The availability of habitat, one of the most important niche dimensions in mammal communities, was equally important in helminth communities. Habitat restriction may favour parasite transmission or the occurrence of co-dominant parasites and, consequently, dissemination of helminths between low-specificity hosts, increasing the supra-population or the prevalence of parasites in *T. pachyurus*. The Pantanal region is located in central South America with the Amazonian Forest to the north, the Cerrado to the east, the dry Chaco to the southwest and rain forest to the southeast. Since *T. pachyurus* is an abundant rodent in this large plain, the Pantanal region may be acting as a corridor of dispersion between these large ecosystems for some of the helminth species that are not specific parasites of *T. pachyurus*.

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