Host-parasite interaction between branchiurans (Crustacea: Argulidae) and piranhas (Osteichthyes: Serrasalminae) in the Pantanal wetland of Brazil

Lucélia Nobre Carvalho^{a,b}, Kleber Del-Claro^b & Ricardo Massato Takemoto^c

^aPrograma de Pós-Graduação em Ecologia e Conservação, CCBS, Universidade Federal de

Mato Grosso do Sul, C.P. 549, Campo Grande, Mato Grosso do Sul, 79070-900, Brazil

^bUniversidade Federal de Uberlândia, Instituto de Biologia, C.P. 593, Uberlândia, Minas Gerais, 38400-902, Brazil (e-mail: delclaro@ufu.br)

^cUniversidade Estadual de Maringá, Núcleo de Pesquisas em Limnologia Ictiologia e Aquicultura (Nupélia), Bloco G-90 – Av. Colombo, 5790, Maringá, Paraná, 87020-900, Brazil

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Synopsis

Ecological studies of host-parasite interactions in the tropics are generally restricted to descriptive taxonomic aspects. The present study had as its objective identification of the metazoan ectoparasites of piranhas Pygocentrus nattereri, Serrasalmus spilopleura and S. marginatus in lentic and lotic environments in the Pantanal region, Brazil. We collected the samples in the Miranda River basin and in three ponds. We caught fishes using hook and line. We found that branchiuran crustaceans infested about 30% of the piranhas. We found four branchiuran species: Dolops carvalhoi, Argulus elongatus, Argulus aff. juparanaensis and Dipterolpetis hirundo, which represent new findings in host-parasite relationships in the Neotropics. When comparing lotic and lentic environments, we observed higher infestation rates in rivers than in ponds for all the hosts. P. nattereri had the highest prevalence and the intensity rates in both the environments. The body parts of hosts with the highest frequencies of parasitism were the ventral area in P. nattereri, the gullet area in S. spilopleura and ventral areas and external gills in S. marginatus. In relation to the prevalence of the parasites we observed significant differences between the hydrological seasons and the piranha species, nevertheless hosts were more parasitized in the dry season. The species with highest rates of infestation, P. nattereri and S. spilopleura, live in schools, which indicates that the high parasite load may be a direct consequence of the proximity between individuals. We believe that the higher rates of infestation in the dry season result from the increase in host density in drying ponds imitating the conditions found in fish farming. Seasonal changes in water level and temperature can also influence the rates of parasitism.

Introduction

Fishes are vertebrates that demonstrate the major levels of parasitic infestation due to the fact that aquatic systems facilitate the reproduction, dispersion, survivorship and life history of parasitic organisms (Malta 1984). Directly and indirectly parasites reduce host growth and survival (Pennycuick 1971, Rawson 1977, Kabata 1981). Direct effects like host weakness can

cause indirect consequences such as low foraging rates (Crowden & Broom 1980, Milinski 1984), increase in vulnerability to predators (Arme & Owen 1967, Pennycuick 1971), higher oxygen requirements (Lester 1971) and decreased resistance to environmental stress (Lewis & Hettler 1968).

According to Szalai & Dick (1991), many studies have been conducted regarding the biology of endoparasites, and many of these studies have dealt with

Osteichthyes and their hosts. However, little information is available on infestation levels and the transmission of crustacean ectoparasites in natural conditions (Szalai & Dick 1991). Malta (1982a) and Tanaka (2000) pointed out that the majority of published studies of parasitic crustaceans of fish (Branchiura) in South America are related to taxonomy.

Branchiurans are a worldwide group of fish ectoparasites occasionally occurring in reptiles and amphibians (Malta 1982a). They range from 2 to 30 mm in length and both sexes are fish parasites. Transmission is direct, since they swim actively to a fish and attach by themselves. In general, the infestation results in ulcerative lesions that allow secondary infections by fungus, virus and bacteria (Thatcher 1991).

The piranhas (Characidae: Serrasalminae) are some of the main predators in freshwater neotropical ecosystems. Although, occasionally occupying a major part of the total fish biomass in many ecosystems (Mago-Lecia 1970), there are few studies about their interactions with ectoparasites. Piranhas are endemic to South America (Goulding 1980) and in the Pantanal wetlands of Brazil three species occur: *Pygocentrus nattereri* Kner, 1860, *Serrasalmus spilopleura* Kner, 1860 and *S. marginatus* Valenciennes, 1847.

Although scarce, there are interesting papers dealing with piranhas and their ectoparasites (Malta 1982a,b, 1984, Malta & Varella 1983, Sazima & Machado 1990, Hamman 1995/1996, Hamman 1997/1998, Tanaka 2000). However, only the study by Sazima & Machado (1990) was conducted in the Pantanal region of Poconé, Mato Grosso. Those authors studied a small pond and a stream, where they were able to observe the piranha, *S. marginatus*, picking the branchiuran, *Dolops* sp., from the bodies of other piranha, *P. nattereri*, in what was described as a cleaning interaction.

In our study we identified the metazoan ectoparasites of three sympatric piranha species: *P. nattereri*, *S. spilopleura* and *S. marginatus* in lotic and lentic environments of the Pantanal wetlands of the state of Mato Grosso do Sul, Brazil. We also investigated the variation in the levels of host infestation by branchiuran crustaceans in relation to hydrological cycles.

Materials and methods

Study site

The Pantanal, located in western Brazil, is the largest continuous freshwater floodplain on earth. (Silva & Abdon 1998). We conducted our study in the Miranda

River Basin in the Pantanal sub-regions of Miranda and Abobral (Silva & Abdon 1998). We sampled three rivers and three ponds, locally known as 'baías'. The study sites were located on the: lower Miranda, Vermelho and Abobral Rivers (both the Vermelho and Abobral Rivers have headwaters in the Pantanal floodplain). On the Miranda River we sampled a stretch of 26.3 km upriver from coordinate UTM 498, 7834 on the Vermelho River, 6.1 km upriver from UTM 502, 7835 and on the Abobral River 18.4 km downriver from UTM 494, 7851.

The sampled ponds are known as 'Baía da Medalha' (498, 7835; 4.3 ha in area), 'Baía Negra' (489, 7842; 26.7 ha in area) and 'Baía Platina' (499, 7835; 2.0 ha in area). During the flooding season these ponds are connected to the Miranda River. The ponds are bordered by dense stands of aquatic macrophytes, mainly by *Eichhornia azurea* and *E. crassipes* (Pontederiaceae).

Procedure

We made five 1-day trips each month between January and June 2000. On each trip, we conducted fishing only during the day, and piranhas were caught in four microhabitats: the border and middle regions of both rivers and ponds. In the rivers, we used 'middle' to refer to the central region (up to 10 m away from the border), and considered the 'border' to be the region up to 3 m from the bank. In ponds, due the presence of large amount of aquatic macrophytes, the edges of the macrophytes stands determined the border region. In general this was at a distance of 2 m from the bank.

On each field trip we collected data on a set of abiotic factors of the water at each sampling site. The pH was taken with pH-indicator strips (Merck Co.); water temperature (°C) and dissolved oxygen (mg l⁻¹) were recorded using a WTW microprocessor oxygen meter (OXI 196), 50 cm below the surface. The variation in water levels was measured by the Hydraulic Department of the Universidade Federal de Mato Grosso do Sul.

We divided the monthly samples into two hydrologic seasons. The period from January to March is characterized in the Pantanal by the beginning of the flooding, but the water level is still low, and considered 'dry-flooding'. The months between April and June are characterized by the flooding period in the Pantanal, and the water starts receding only in June. This season is called 'flood-drying'.

To catch the piranha we used rod, line and hook, with beef bait. Three different sizes of hooks

(numbers 1, 6/0 and 6, Mustad Co.) were employed to catch the three piranha species in different developmental stages. We fished with each size hook for 30 min at each sampling site, border and middle region of the rivers or ponds. We did not fish on the border and middle region of the same sampling stations to avoid interference between the sample sites.

We measured the piranhas (SL, cm) and identified them according to Britski et al. (1999). We fixed each piranha in 10% formalin for 15 days and later transferred them to ethanol (70%). We examined the gills and external body surfaces of all fish we caught with a magnifying glass for parasites prior to fixation. We also registered the area in the fish body where each parasite was found, collecting it manually with soft forceps. We preserved all collected parasites, individually, in ethanol (70%), and later identified them according to Thachter (1991) and Castro (1985). We divided the external surfaces of the fish into dorsal area, ventral area, head (also divided into gullet and upper-head), fins and lateral line. We examined the gills through the mouth and gill openings.

We calculated the prevalence (number of infested hosts as a proportion of the total number of hosts examined) and the mean intensity (total number of parasites as a proportion of the number of infested hosts) according to Bush et al. (1997). We considered a value of p < 0.05 as significant in all statistical tests. We deposited voucher specimens of piranhas and parasites at Coleção Zoológica de Referência at the Universidade Federal de Mato Grosso do Sul (ZUFMS-PIS 000914-000935 and ZUFMS-CRU 000193-000194, 000199-000200).

Results

During our field data collection, a natural limnological phenomenon occurred between April 13 and 17, 2000.

This phenomenon called 'dequada' (Hamilton et al. 1997, Calheiros & Hamilton 1998 and references therein) is characterized by a depletion of the dissolved oxygen (0–2.0 mg l⁻¹) followed by a higher water level during the year. The dequada resulted in the death of a large number of fishes in the Miranda and Vermelho Rivers including specimens of *P. nattereri*. We were unable to collect piranhas in April as a result of this factor. The hydrological seasons had a direct influence on all investigated abiotic factors (Table 1).

We had a total of 99 hours of bait exposure to predators during 30 sampling trips. We captured 237 individuals of *P. nattereri* (92 in rivers and 145 in ponds), 273 *S. spilopleura* (94 in rivers and 179 in ponds) and 35 *S. marginatus* (17 in rivers and 18 in ponds). Our data showed that 31.56% of all collected fish had metazoan ectoparasites, with a mean intensity of 2.27 and up to 13 parasites per host.

We found leeches (Hirudinea, unknown species) feeding on the external gills (*P. nattereri*, N = 1) and anal fin (*S. spilopleura*, N = 1) of some piranhas. All the other ectoparasites we observed on piranhas were branchiurans crustaceans. We found four different branchiuran species, *Dolops carvalhoi* Lemos de Castro, 1949; *Argulus elongatus* Heller, 1857; *Argulus* aff. *juparanaensis* Lemos de Castro, 1950 and *Dipteropeltis hirundo* Calman, 1912.

Table 2. Composition (%) of branchiuran species (Crustacea: Argulidae) found attached to piranhas (Osteichthyes: Characidae) sampled from the Abobral, Miranda and Vermelho Rivers and Baía da Medalha, Baía Negra and Baía Platina ponds in the South Pantanal Mato-Grossense, between January and June 2000.

Hosts	D. carvalhoi	A. elongatus	A. aff. juparanaensis
P. nattereri	91.3	4.1	4.6
S. spilopleura	76.2	19.04	4.8
S. marginatus	25	25	50

Table 1. Characterization of abiotic factors from the Miranda, Abobral and Vermelho Rivers and Baía da Medalha, Baía Negra and Baía Platina ponds in the South Pantanal Mato-Grossense during the two studied hydrological seasons between January and June of 2000.

Abiotic factors	Rivers		Ponds			
	Dry-flooding $\overline{X} \pm SD$ (range)	Flood-drying $\overline{X} \pm SD$ (range)	Dry-flooding $\overline{X} \pm SD$ (range)	Flood-drying $\overline{X} \pm SD$ (range)		
pH	$6.87 \pm 0.94 (5.0 - 7.8)$	$5.72 \pm 0.57 (5.0-7.0)$	$6.43 \pm 0.76 (5.5 - 7.4)$	$6.46 \pm 0.40 (3.7 - 7.0)$		
Temperature (°C)	$31.97 \pm 1.63 \ (28.8 - 33.5)$	26.63 ± 0.91 (24.6–33.3)	31.45 ± 0.75 (28.8–36.0)	$27.32 \pm 0.77 \ (25.2 - 35.0)$		
Dissolved oxygen (mg l ⁻¹)	$4.25 \pm 1.12 (0.5 - 5.9)$	$4.68 \pm 1.40 (0.0 - 6.3)$	$3.92 \pm 1.27 (0.1 - 5.6)$	$3.87 \pm 1.21 \ (0.0-6.5)$		
Hydrological level (m)	$2.05 \pm 0.59 (1.4 – 3.5)$	3.18 ± 1.13 (2.0–4.2)	$2.05 \pm 0.59 (1.4 – 3.5)$	$3.18 \pm 1.13 \ (2.0 - 4.2)$		

Table 3. Prevalence (prev., %) and mean intensity of infestation (m.i.) by branchiurans (Crustacea: Argulidae) in piranhas (Osteichthyes:
Characidae), and prevalence in hydrological seasons collected in lotic (Abobral, Miranda and Vermelho Rivers) and lentic environments
(Baía da Medalha, Baía Negra and Baía Platina ponds) from the South Pantanal Mato-Grossense, during January to June 2000.

Hosts	Environments						Seasons				
	Lotic			Lentic		Total		Dry-flooding	Flood-drying		
	prev.	m.i.	range	prev.	m.i.	range	prev.	m.i.	range	prev.	prev.
P. nattereri	55.43	3.63	0-13	44.14	1.81	0–5	48.52	2.62	0-13	74.63	38.24
S. spilopleura	23.4	1.36	0–5	16.76	1.73	0–4	19.05	1.58	0–5	21.67	11.43
S. marginatus	23.53	1.5	0–3	5.56	1.0	0–1	14.29	1.4	0-3	16.67	11.76

D. hirundo was found only once on an individual of P. nattereri caught in the Abobral River in March 2000.

The parasite species frequency was similar on *P. nattereri* and *S. spilopleura*, and different between both of these and *S. marginatus* (Table 2). The three piranha species showed different infestation rates by branchiurans, and our data showed that *P. nattereri* presented more parasitism than *S. spilopleura* and *S. marginatus*, respectively (Table 3). When comparing lotic and lentic environments we observed that higher infestation rates by branchiurans occurred in rivers for the three host species studied (Table 3). *P. nattereri* was the piranha with major infestation by branchiurans in both the types of environments investigated at Pantanal (Table 3).

Although Branchiurans are motile animals our immediate inspection of captured fishes, allowed us to record parasite preferences on the hosts' body areas. We did not note parasites dropping in the water during capture, probably due their ability to stick tightly to the host. Comparing *P. nattereri* and *S. spilopleura*, we noted significant statistical differences in the parasite frequency between different body sections (χ^2 test, p < 0.05, Figure 1) and we observed ulcerative lesions in the gullet section of *P. nattereri*.

Pygocentrus nattereri had a mean body length of 14.08 ± 4.14 ($\overline{X} \pm 1\text{SD}$; $7.8\text{-}31.0\,\text{cm}$, min.-max.), S. spilopleura of 12.94 ± 1.87 (6.0–22.0) and S. marginatus of 15.15 ± 3.11 (10.8-24.0). We observed a positive correlation between length and parasite intensity among the three species studied, P. nattereri (rs = 0.5696, p = 0.0001), S. spilopleura (rs = 0.2938, p = 0.0001), S. marginatus (rs = 0.4980, p = 0.002) (Figure 2). Correlations between fish length and prevalence between P. nattereri and S. spilopleura did not yield a significant result (rs = -0.2319, p = 0.658 and rs = -0.400, p = 0.600).

When comparing the intensity of parasitism between hydrological seasons, we observed a significant relation only for *P. nattereri* (Mann–Whitney U-test, p < 0.0001). This piranha species was more intensely attacked during the dry flooding (2.7 \pm 2.7, \overline{X} \pm 1SD) than in the flood-drying season (0.67 \pm 1.1, \overline{X} \pm 1SD). In relation to prevalence we observed statistical differences when comparing hydrological seasons and piranhas ($\chi^2 = 54.58$, p < 0.005). Piranhas were most infested during dry flooding than during flood-drying season (Table 3).

Discussion

Although crustaceans are potentially important ectoparasites of fishes, frequently observed in freshwater and marine hosts worldwide, including abyssal species (Eiras 1994), in the Neotropical literature there are very few lists of branchiurans and their hosts (Thatcher 1991, Castro 1985). As far as we know, the four branchiuran species we found on piranhas, *D. carvalhoi*, *A. elongatus*, *A.* aff. *juparanaensis* and *D. hirundo* can be considered new discoveries in host–parasite relationships in the Neotropics.

The higher occurrence observed of *D. carvalhoi* on *P. nattereri* and *S. spilopleura* may be a result of the low frequency of capture of *S. marginatus* during the study. Despite the fact that the three hosts have a great phylogenetic affinity, Malta & Varella (1983) showed that, in the Brazilian Amazon basin *D. carvalhoi* is more of a general species.

Social life can be very advantageous to individuals in a community (Wilson 2000) reducing predation risk and increasing foraging capacity (see Alcock 1993 and references therein for examples). But there are also increases in the risk of transmission of parasites as a consequence of proximity between individuals (Alcock

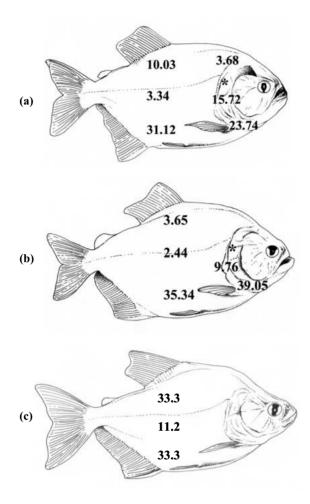


Figure 1. Relative frequencies of attachment sites of branchiurans on piranhas collected in rivers and ponds of the South Pantanal Mato-Grossense in Brazil, a = P, nattereri. b = S. spilopleura and c = S. marginatus. The internal gill area (*) had the following frequencies: A = 1.67 and B = 2.44. The fins (grouped) had the frequencies: A = 10.70, B = 7.32 and C = 22.2.

1993). This is especially true for fishes (Poulin 1991). Tanaka (2000), studying the structure of parasite infracommunities (the community of a parasite population in a single host) on S. spilopleura and S. marginatus pointed out that fish behavior, whether gregarious or solitary, is the main factor to be considered when studying fish ectoparasites. S. spilopleura, a gregarious species, may allow more transfer of branchiuran larvae among individuals due to their close proximity in a population. Sazima & Machado (1990) commented that *P. nattereri* lives in schools (20–30 individuals) that are larger than those of S. spilopleura (less than

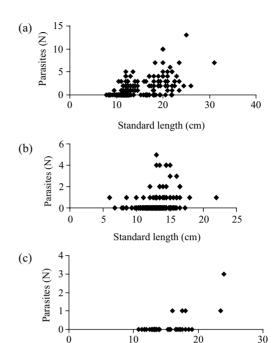


Figure 2. Results of Spearman's correlation between standard length in (a) P. nattereri (rs = 0.5696, p = 0.0001), (b) S. spilopleura (rs = 0.2938, p = 0.0001), (c) S. marginatus (rs = 0.4980, p = 0.002) and the branchiuran number (intensity of infestation) from the South Pantanal Mato-Grossense, between January and June 2000.

20

Standard length (cm)

20 fish) and S. marginatus (solitary species). Our results showed more branchiurans on P. nattereri in both rivers and ponds. We suggest that this is a result of the gregarious behavior of *P. nattereri*. Poulin (1991) studying the freshwater fish fauna of Canada discovered that group-living species do not have more parasite species than solitary species, suggesting that a more intense ectoparasite fauna is not a disadvantage for group-living species. However, Poulin (1991) also explained that there is not enough information to determine whether group-living fishes have a greater prevalence and intensity of contagious ectoparasites than solitary species, or, if so, how parasites can influence the social behavior of fishes.

To our knowledge, the present study is the first to compare the contagious ectoparasitic fauna on fishes living in both rivers and lakes. The fact that branchiuran infestations were significantly greater in rivers than in ponds, and knowing that the piranha density in ponds is higher than in rivers, we conclude that the main biotic factor, host availability, was not the

limiting factor. These parasites are able to swim, and can remain free in the water for long periods of time (Pavanelli et al. 1999). It is possible that branchiurans have difficulties swimming in lotic environments, as in rivers. We suggest that fish hosts may be used by these parasites for transportation. Maybe in ponds these crustaceans remain away from hosts for greater periods of time, engaged in other activities such as reproduction (copulation and oviposition). This may occur since the parasites are able to swim in lentic systems and have the facility to find another host. Sazima & Machado (1990) found that piranhas are able to remove ectoparasites from the body of other piranhas. Perhaps the abundance of piranha schools in ponds favors this behavior, resulting in a lower infestation rate in ponds than in rivers. In fact, Sazima & Machado (1990) found branchiuran crustaceans in the stomachs of S. marginatus. However, Carvalho & Del-Claro (unpublished observations) examined the stomach of piranhas collected during the present study (S. marginatus, N = 32; S. spilopleura, N = 262 and P. nattereri, N = 231) but found no branchiuran crustaceans. In the Poconé region of the Pantanal, where Sazima & Machado (1990) conducted their study, the water is cleaner than in our study sites. We suggest that in more turbid environments, such as Miranda and Abobral, cleaning behavior of S. marginatus may be suppressed or minimized, resulting in higher parasite infestation levels.

Szalai & Dick (1991) discussed the difficulties of precisely estimating ectoparasitic crustacean infestation rates in fishes. This is mainly due to the fact that in previous studies the fishes collected were nearly dead, giving time for the parasites to leave the hosts. Szalai & Dick (1991) also pointed out those sampling procedures that minimize host stress, such as live trapping, have been largely ignored as a means for obtaining more accurate estimates of ectoparasite infestation rates (e.g. Malta & Varella 1983, Malta 1982a,b). The procedures that we used did not reduce host stress, but examining the fish prior to fixation proved to be an effective procedure for estimating ectoparasite numbers. Additionally, we were able to observe the preferred areas of attachment to the fish body. Sazima & Machado (1990) reported that branchiurans were more concentrated in the ventral areas of P. nattereri and this is in agreement with our results for P. nattereri and S. spilopleura. The gullet area is a place where fish have thinner skin, which may facilitate parasite attachment and feeding. S. marginatus has a compressed body and narrower snout, which reduces its relative gullet area. We believe that this was the main reason that we did not find parasites in the gullet area of *S. marginatus*.

Some species of fish ectoparasites have been reported more abundantly on larger hosts (Cloutman & Becker 1977, Rawson 1977, Bortone et al. 1978, Hanek & Fernando 1978, Poulin 1991, Poulin et al. 1991). Our results support that generalization, but it is possible that branchiurans do not actively select larger hosts. This higher infestation of larger fish may be a result of the age and size of the individuals. We must remember that the correlation between body length and prevalence was not statistically significant, which reinforces the hypothesis that parasites do not select hosts by size.

The piranhas were most infested during the dryflooding season. During the dry season Pantanal rivers and ponds suffer a severe reduction in water levels, some of them drying completely. This season is characterized by a progressive increase in fish density, scarcity of food resources and water deterioration, with high temperatures and low oxygenation (Lowe-McConnell 1987). These factors may result in serious stress to fishes, which benefits parasites. We believe that during the dry season the rivers and ponds of the Pantanal wetlands are similar to intensive or high-density aquaculture systems, where high parasite infestation rates are positively correlated with an increase in density and fish stress (see Ozer & Erdem 1999, but see also Malta & Varella 1983). From our study it is clear that greater infestation levels by branchiuran ectoparasites on piranhas in the Pantanal occurred during periods of high temperatures, reduced water levels and poor water quality. However, body size, fish anatomy and procedures for collecting fishes are also important aspects to be observed when comparing published accounts on infestation rates on freshwater fish.

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