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Feeding habits and habitat use of three sympatric piranha species in the Pantanal wetland of Brazil

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We investigated the diet and habitat use of sympatric piranha species *(Serrasalmus maculatus, S. marginatus, Pygocentrus nattereri)* in three rivers and three lagoons of the Miranda River basin in the Southern Pantanal, Brazil. The three species showed differences in size, weight, abundance, and diet between sites; but not in terms of habitat use. *Serrasalmus maculatus* and *P. nattereri* were most abundant in rivers and lagoons. The low abundance of *S. marginatus* could be due to its solitary and territorial behavior. Stomach content analysis of *S. maculatus* and *P. nattereri* revealed that vegetal material was the main food item consumed. As for *S. marginatus*, fish fins and scales were the most frequent food item, a direct consequence of its specialized feeding habit. Differences in diet composition amongst the three sympatric piranha species suggest that competition for food resources does not play an important role in the trophic interactions of these species in the Pantanal.

Introduction

Piranhas represent a large percentage of the total biomass and abundance of Neotropical freshwater fishes (Mago-Leccia, 1970) and are amongst the main predators of these assemblages (Almeida et al., 1998). Piranhas have the bad reputation of being voracious fishes and many studies have focused on ontogenetic and temporal diet variations (Goulding, 1980; Machado-Allison & Garcia, 1986; Nico & Taphorn, 1988; Winemiller, 1989), dietary nutritional value (Nico & Morales, 1994), and feeding strategies (Nico & Taphorn, 1988; Sazima & Machado, 1990).

Piranhas are endemic of South America and three species occur in the Pantanal wetlands of Brazil: *Pygocentrus nattereri, Serrasalmus maculatus* and *S. marginatus*. Studies on piranha's feeding habits were carried out in the Northern Pantanal, Poconé, Mato Grosso by Sazima & Machado (1990) who investigated the behavior of these same species and found different feeding tactics. In the Southern Pantanal, the research included studies on the reproductive behavior of *P. nattereri* in its

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natural habitat (Uetanabaro et al., 1993), trophic structure of the fish communities in the lower Rio Miranda (Resende, 2000), community structure in Pantanal lagoons at Nhecolândia (Súarez et al., 2001), and interactions between piranhas and its ectoparasitic crustaceans in the Miranda and Abobral regions (Carvalho et al., 2003). Comparative studies analyzing simultaneously the diet and the use of lotic (river) and lentic (lagoon) habitats for piranhas are scarce. In fact, there is only one record of a similar study from the Venezuelan Llanos (Nico & Taphorn, 1988). Our objective was to verify the diet and habitat use of three sympatric piranha species of the Southern Pantanal (*S. maculatus*, *S. marginatus*, *P. nattereri*) in rivers and lagoons, in order to get a better understanding of resource partitioning among fishes in the Brazilian Pantanal.

Study site

The Pantanal is located in the central-west region of Brazil and is the largest floodplain in the world, with approximately 130920 km^2 (Mittermeier et al., 2005). The dry and wet seasons are well-defined, with the rainy season occurring between November and March and an average yearly rainfall varying between 1000-1700 mm (Mittermeier et al., 2005). In the Pantanal the period from January to March is characterized as the beginning of the flood and is known as 'dry-flooding', since the water level remains low. The months between April and June are characterized as the flooding period, and the water only starts to recede in June, which is known as the 'flood-drying' season. During the peak of dry season (November-December) many lagoons dry out completely and the water is confined to the river channels.

We conducted our study in the Miranda River basin in the Pantanal sub-regions of Miranda and Abobral, Central Brazil (Silva & Abdon, 1998). We sampled three rivers, and three permanent-flooded lagoons, locally known as 'Baías'. The study sites were located on the lower Miranda, Vermelho and Abobral Rivers. Both Vermelho and Abobral Rivers have headwaters in the Pantanal floodplain. Vermelho River is a right margin tributary of Rio Miranda, and Abobral River have an area of inundation that interconnects with Miranda River during the highest flood periods (Resende et al., 1995). 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 lagoons are known as 'Baía da Medalha' (UTM 498, 7835; 4.3 ha in area), 'Baía Negra' (UTM 489, 7842; 26.7 ha in area) and 'Baía Platina' (UTM 499, 7835; 2.0 ha in area). During the flooding season these lagoons are connected to the Miranda River. The lagoons are characterized by shallow-water and surrounded by dense stands of floating aquatic macrophytes, mainly *Eichhornia azurea* and *E. crassipes* (Pontederiaceae).

Material and methods

Field and laboratory methods. We made monthly excursions to the study area between January-June 2000, of five days fishing activities. During April (highest river water level = 4.2 m) we recorded the lowest dissolved oxygen values of all samples (<2.0 mg$\cdot$l^{-1}). In this same period we found a few dead specimens of *P. nattereri* in Miranda and Vermelho Rivers, and we didn't catch any piranhas in our sampling (see Carvalho et al., 2003). Details of some abiotic factors such as pH, temperature, dissolved oxygen and hydrological period of the rivers and lagoons studied are available in Carvalho et al. (2003).

We sampled five microhabitats: marginal and central regions of rivers; marginal and central regions of lagoons; and isolated pools during the dry season. In the rivers, we characterized the marginal habitat as the littoral zone within 3 m from the shore, and the central habitat as 10 m from the shore. In lagoons, due to the abundance of aquatic macrophytes in the littoral zone, we considered the marginal area to begin where the macrophyte vegetation ended (within 2 m from the shore). Similarly, the central region began at a distance of 10 m from the macrophytes towards the center of the lagoon. During the dry season (January-March) the Vermelho and Abobral Rivers had some sections where water flow had been interrupted, creating isolated pools. As a consequence, it was not possible to distinguish the marginal and central river microhabitats during this period.

We captured piranha specimens using fishing line and three different sizes of hooks (baited with raw cow meat) in order to catch individuals of different sizes and developmental stages. We fished for 30 minutes with each hook size at the

different microhabitats (marginal or central region of the river stretches and lagoons), summing up 1h30min of monthly sampling in each site. We sampled the marginal and central microhabitats of each site with a time interval of 2-3 days in order to avoid a possible interference among the samples (cf. Carvalho et al., 2003).

Immediately upon capture we fixed the piranhas by injecting a solution of 10 % formalin into the musculature and into the abdominal cavity, to halt further digestion of the food ingested. Each specimen was measured (standard length, SL, in cm), weighted (g), and later stored in 70 % ethanol. In function of the characteristics of the stomach contents of piranhas (that usually include pieces of different food items) we chose to apply the frequency of occurrence method (Hyslop, 1980).

Piranha species identification follows Britski et al. (1999). We used the name *S. maculatus* for the fish from the Paraguay River drainage previously referred to as *S. spilopleura*, following Jégu & Santos (2001). Voucher specimens have been deposited in the Coleção Zoológica de Referência of Universidade Federal de Mato Grosso do Sul, UFMS, Brazil (ZUFMS-PIS 000914-000935).

Data analysis. We applied *t*-tests to compare the length and weight of specimens between habitats. We used two-way ANOVA (species and microhabitat) to determine whether there was any difference in the distribution and microhabitat use by piranha species. Since the frequency of empty stomachs did not correspond to a normal distribution, we employed a Mann-Whitney nonparametric test (U-test) to compare monthly number for each piranha species and habitat (Zar, 1999).

To evaluate the variation in diet composition among the three piranha species and habitats, we used Hybrid Multidimensional Scaling (HMDS; Faith et al., 1987) to ordinate the samples. In this ordination, we used frequency of occurrence of food items in fish stomachs to create a Bray-Curtis matrix of dissimilarity (Bray & Curtis, 1957). Since the Bray-Curtis dissimilarity matrix is affected by sample size, we standardized the frequency of occurrence data for each sample (Ferreira, 1997). To decide on the number of dimensions the samples would be summarized, were compared r^2 values obtained from linear regression analyses of the original values from the dissimilarity matrix, and those obtained in ordinations of one, two and three dimensions (e.g. Azevedo-Ramos et al., 1999). The results of this procedure determined that the ordination would be optimal in two-dimensional solution (stress = 0.16 and $r^2 = 0.87$). We then used the resulting ordination scores in a Multivariate Analysis of Variance (MANOVA) to evaluate the differences in food items composition among species and habitats, and we applied Pillai-Trace statistics to test the significance of all differences ($p < 0.05$).

Results

Total fishing time for the three sizes of hooks at each site (central and marginal regions of lagoons and rivers) summed up 99 hours. From 33 samplings, 264 specimens of *S. maculatus* (170 in lagoons and 94 in rivers), 33 of *S. marginatus* (16 in lagoons and 17 in rivers), and 228 of *P. nattereri* (142 in lagoons and 86 in rivers) were captured.

Serrasalmus maculatus did not present significant differences in standard length ($t = -1.329$, $p = 0.185$) or weight ($t = -1.113$, $p = 0.267$) between habitats. Specimens of *S. marginatus* were significantly larger ($t = -2.572$, $p = 0.015$) and heavier ($t = -2.818$, $p = 0.008$) in rivers than in lagoons, which also occurred for *P. nattereri* (length: $t = -9.732$, $p < 0.001$; weight: $t = -8.316$, $p < 0.001$) (Fig. 1).

There were no significant differences in the distribution of the three piranha species in the five micro-habitats (marginal and central regions of rivers and lagoons and isolated pools) (Fig. 2). Two-way ANOVA showed a significant difference in the number of piranhas captured among species ($F_{2,28} = 5.146$, $p = 0.008$); however, there were no significant differences among microhabitats ($F_{4,28} = 1.824$, $p = 0.132$) or the interaction between these factors ($F_{8,28} = 0.777$, $p = 0.624$).

In lagoons, the average number (± standard error) of empty stomachs recorded for *S. maculatus* was 5.67 ± 3.18 and for *P. nattereri* was 9.33 ± 2.85. *Serrasalmus marginatus* did not show empty stomachs in that habitat. In rivers, average number of empty stomachs was 3.00 ± 1.53 for *S. maculatus*, 1.33 ± 0.67 for *S. marginatus* and 8.67 ± 0.33 for *Pygocentrus nattereri*. The frequency of empty fish stomachs did not present any significant difference between lagoons and rivers (*S. maculatus*, $U = 5.50$, $p = 0.658$; *S. marginatus*, $U = 1.50$, $p = 0.114$; *P. nattereri*, $U = 3.00$, $p = 0.507$).

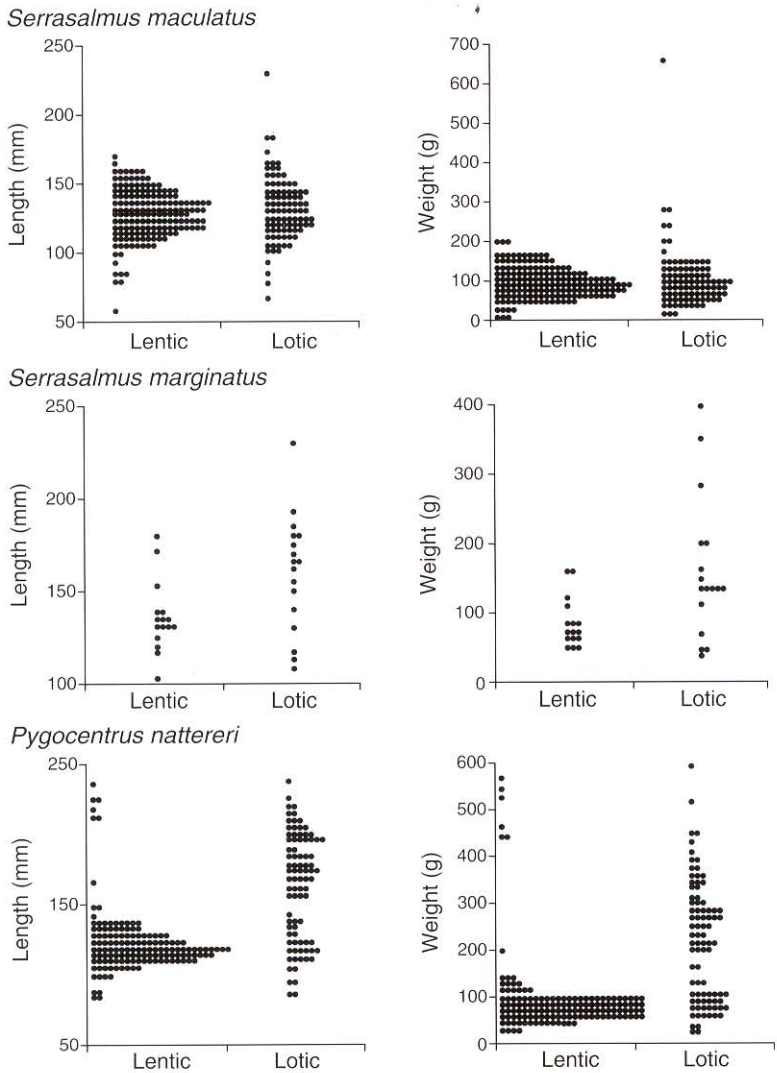

Fig. 1. Standard length and weight of *Serrasalmus maculatus* (n = 264), *S. marginatus* (n = 33) and *P. nattereri* (n = 228) in lotic (lagoons) and lentic (rivers), during January-June 2000.

The three piranha species presented a diet composed of several food types (Table 1). Plant material was the most frequent food item found in the stomachs of *S. maculatus* and *P. nattereri* in both, rivers and lagoons, while fish fins predominated in the diet of *S. marginatus* (Table 1). HMDS ordination of the samples revealed significant differences in the composition of the diet of the three species (MANOVA, Pillai-Trace = 1.081, $F_{4,22} = 6.474$, $p = 0.001$, Fig. 3a), but not between lagoons and rivers (MANOVA, Pillai-Trace = 0.100, $F_{2,10} = 0.554$, $p = 0.591$, Fig. 3b).

Discussion

Distinct species of the same guild can present morphological and behavioral differences that restrict interspecific competition in natural habitats (Towsend et al., 2000). The three sympatric piranha species studied showed differences in size and weight, abundance and diet, but not in terms of habitat use, which suggests there is some other kind of resource sharing among them. In our study, *S. maculatus* and *P. nattereri* were most abundant in rivers and lagoons. Sazima & Mach-

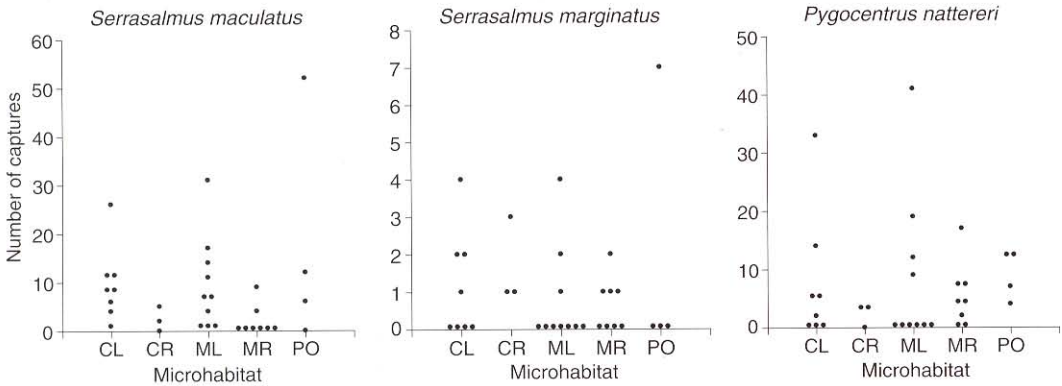

Fig. 2. Numbers of *Serrasalmus maculatus*, *S. marginatus* and *Pygocentrus nattereri* captured in five microhabitats (CL, center of lagoon; CR, center of river; ML, margin of lagoon; MR, margin of river; PO, pool), during January-June 2000.

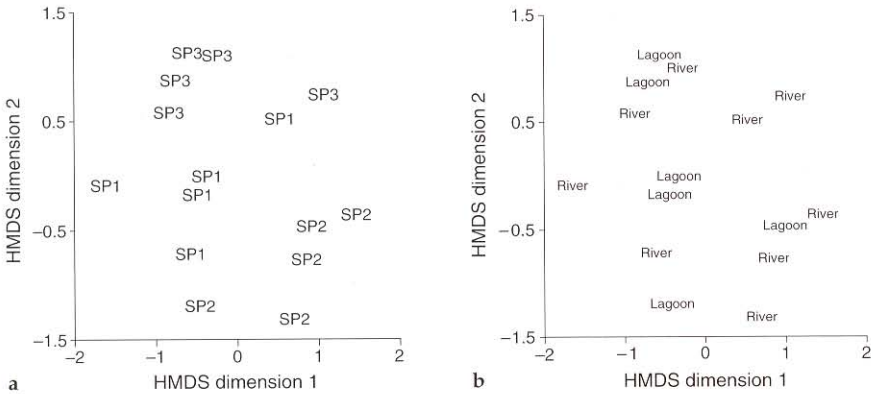

Fig. 3. Ordination (HMDS) in two dimensions (stress = 0.16 and $r^2 = 0.87$) of the diet of: **a,** *Serrasalmus maculatus* (SP1), *S. marginatus* (SP2) and *Pygocentrus nattereri* (SP3), and **b,** in lentic (lagoons) and lotic (river) environments, during January-June 2000.

ado (1990) also observed a larger abundance of these species by means of underwater observations in the Pantanal at Poconé. The low number of *S. marginatus* specimens collected could be due to the bait used (cow meat), which might not have been very attractive for this lepidophage species. On the other hand, Sazima & Machado (1990) and one of us (LNC) have noted that *S. marginatus* seems to be in fact less abundant than other piranha species in the Pantanal. Piranhas are generally associated with lentic environments such as lagoons or reservoirs (Gouding, 1980; Sazima & Zamprogno, 1985), but such preferences may vary among species. In the present study, *S. maculatus* was more abundant in lagoons, indicating that it is possibly more adapted to lentic environments. This assumption seems to be corroborated by Agostinho (2003), that found an intense reproductive activity of *S. maculatus* in lentic environments in the upper Paraná River, and no reproductive activity at all in lotic ones. *Pygocentrus nattereri* was more abundant in lagoons than in rivers in our study, although this may reflect the high number of young specimens collected in lagoons in June (72 specimens of less than 142 mm SL).

The analysis of size and weight distribution of *P. nattereri* and *S. marginatus* showed that the larger individuals occupy the rivers whereas smaller ones stay in the lagoons. A higher abundance of young individuals in the lagoons is possibly associated with the great availability of aquatic macrophytes. Aquatic macrophytes constitute the main habitat for juvenile fish and are utilized as refuge against predation and as a rich

and abundant food source (Junk et al., 1997). The use of floating beds of macrophytes as refuge has been noted for young Characiformes and other species of fish in South America (Junk, 1973; Lowe-McConnell, 1975). In the Amazon, juvenile piranhas appear to utilize aquatic macrophytes for feeding and protection also (Araújo-Lima et al., 1986; Sánchez-Botero & Araújo-Lima, 2001). In southeastern Brazil, young *S. maculatus* were recorded foraging for insect larvae among floating macrophytes (Sazima & Zamprogno, 1985). A similar pattern of habitat use could therefore explain the high concentration of young piranhas found in lagoons in our study.

The three sympatric piranha species did not present significant differences in occurrence between the marginal and central regions of the lagoons and rivers. This result was expected for the lagoons due to the high homogeneity of physical factors (current velocity, depth) that prevail in those habitats. The corresponding lack of difference in rivers could be explained by the fact that Abobral, Vermelho and Miranda Rivers have narrow channels (up to 30 m wide), which may reduce the occurrence of habitat segregation among the piranha species. Another source of bias may be the sampling method employed in the present study. Line and hook fishing may result in the catch of piranhas nearby being attracted by the smell of the bait, especially in narrow rivers. A similar result probably would arise from the use of passive capture techniques such as gill nets, since piranhas can be attracted from a considerable distance by the noise and smell of struggling fishes in the net. Underwater investigation, one of the few methods that could allow a more refined analysis of microhabitat preferences by piranha species, couldn't be employed due to the high turbidity in the lagoons and rivers of the sampling area.

Sazima & Machado (1990) suggest that *S. maculatus* may be the most successfully adapted piranha in the Poconé region of the Pantanal, based on its varied diet and opportunistic feeding strategy. Furthermore, *S. maculatus* seems to be more tolerant for extremely low dissolved oxygen levels and high water temperatures when compared to the other piranha species (LNC, pers. obs.), which may help to explain its apparent success in the Pantanal. However, the abundance of *S. maculatus* in the Paraná River basin diminished when *S. marginatus* invaded that river system after the construction of the Itaipu hydroelectric dam (Agostinho, 2003; Agostinho et al., 2003). Diet overlap, as well as aggressive defense of feeding territory and protection of offspring, are argued as the main factors determining the successful colonization of *S. marginatus* in the Paraná River and its competitive advantage over *S. maculatus* (Agostinho, 2003; Agostinho et al., 2003).

We have shown that *S. marginatus* possesses a more specialized diet than the other two sympatric piranha species, which feed more opportunistically on a wide range of items. Floodplains such as the Pantanal are systems where food resources can vary temporally and spatially, and omnivorous and opportunistic species may be more successful in these environments in the long-term. In this sense, the apparent stenophagy demonstrated by *S. marginatus* could be responsible for its low abundance in the Pantanal; nevertheless, it should be noted that fish fins (the main food item of *S. marginatus*) constitute a renewable and abundant resource (Northcote et al., 1987). Therefore, we believe that the lower abundance of *S. marginatus*, if really occurs, may be due to its territorial behavior, as suggested by some authors (Clarke, 1970; Begon et al., 2000).

Stomach content analyses of *S. maculatus* and *P. nattereri* revealed that vegetal material was the main food item consumed in both microhabitats. Plant remains has been cited by many authors as a frequent item in the stomachs of piranha species

Table 1. Frequency of occurrence (%) of food items in the stomachs of sympatric *Serrasalmus maculatus*, *S. marginatus* and *Pygocentrus nattereri* captured in the lagoons and rivers during January-June 2000. l, lagoons; r, rivers.

food items	*S. maculatus*		*S. marginatus*		*P. nattereri*	
	l	r	l	r	l	r
fish (whole)	1.2	0.0	6.2	0.0	4.9	3.5
fish (chunks)	20.6	10.6	25.0	11.8	28.9	26.7
fish (fragments)	16.5	9.6	12.5	0.0	15.5	9.3
fish (eggs)	2.9	3.2	0.0	0.0	0.7	0.0
fins	40.6	54.2	62.5	47.0	5.6	7.0
scales	13.5	13.8	37.5	11.8	5.6	9.3
reptile (scales)	1.2	3.2	0.0	0.0	1.4	1.2
vertebrate meat	2.4	1.1	0.0	0.0	6.3	4.6
mollusks	1.2	0.0	0.0	0.0	0.0	0.0
crustaceans	2.9	4.2	0.0	0.0	2.1	1.2
spiders	0.6	0.0	0.0	0.0	2.8	0.0
insecta	2.9	16.0	6.2	5.9	4.2	4.6
vegetal matter	55.9	62.8	37.5	29.4	54.2	43.0

(Goulding, 1980; Machado-Allison & Garcia, 1986; Nico & Taphorn, 1988; Sazima & Machado, 1990; Oliveira et al., 2004). It should be argued that the frequency of occurrence method may have overestimated the contribution of vegetal material, since the most frequent food item is not always the item with a high volume. Nevertheless, a dietary study of *P. nattereri* in Amazonian lagoons, utilizing both volume and frequency of occurrence data, demonstrated that vegetal material was the most frequent food item in gut contents, and the second-most important in volume (LNC, unpublished data). Another factor that should be taken into consideration is the possible lack of efficiency in cellulose digestion by carnivorous fish, increasing the amount of time that vegetal matter stays in the gut of such fish (Hildebrand, 1995). We believe that the predatory tactics employed by *P. nattereri* and *S. maculatus*, that is biting small pieces of fishes or potential food items in the surface among the aquatic macrophytes, resulted in the high frequency of vegetal matter found in the stomachs (e.g. Sazima & Machado, 1990, for details of feeding behavior).

The absence of plant material in the stomachs of *S. marginatus* seems to reflect its specialized diet, composed almost exclusively by fragments of fish fins and scales, obtained with the use of correspondingly specialized feeding tactics (Sazima & Machado, 1990). In the Paraná River basin, stomach content analyses of *S. marginatus* recorded fragments of fish muscle and fins as the main diet components for this species (Almeida et al., 1998; Agostinho et al., 2003).

The significant differences in diet composition among the three sympatric piranha species revealed by MANOVA suggest that competition for food resources does not play an important role in the trophic interactions of these species. Sazima & Machado (1990) found a similar lack of competition among the same piranha species in the Poconé region. The availability and abundance of food resources in the Pantanal floodplain may also help to explain the lack of differences in the diet and in the frequency of empty stomachs of the three piranha species between river and lagoon habitats. The invasion by *S. marginatus* of the upper Paraná River habitats after the construction of the Itaipu hydroelectric dam and the decline of the populations of the native *S. maculatus* (Agostinho & Júlio, 2002), constitute an example of how a strong dietary overlapping can affect the coexistence of fish species.

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