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Original article

Frugivory by the fish *Brycon hilarii* (Characidae) in western Brazil

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ABSTRACT

Frugivory and seed dispersal have been poorly studied in Neotropical freshwater fishes. We studied frugivory and seed dispersal by the piraputanga fish (*Brycon hilarii*, Characidae) in the Formoso River, Bonito, western Brazil. We examined the stomach contents of 87 fish and found the diet of piraputanga consisted of 24% animal prey (arthropods, snails, and vertebrates), 31% seeds/fruits and 45% other plant material (algae/macrophytes/leaves/flowers). The piraputangas fed on 12 fruit species, and were considered as seed dispersers of eight species. Fruits with soft seeds larger than 10 mm were triturated, but all species with small seeds (e.g. *Ficus*, *Psidium*) and one species with large hard seed (*Chrysophyllum gonocarpum*) were dispersed. Piraputangas eat more fruits in the dry season just before the migration, but not during the spawning season. Fish length had a positive relation with the presence of fruits in their guts. The gallery forest of the Formoso River apparently does not have any plant species that depend exclusively on *B. hilarii* for seed dispersal because all fruit species are also dispersed by birds and mammals. Based on seed size and husk hardness of the riparian plant community of Formoso River, however, the piraputangas may potentially disperse at least 50% of the riparian fleshy fruit species and may be particularly important for long-distance dispersal. Therefore, overfishing or other anthropogenic disturbances to the populations of piraputanga may have negative consequences for the riparian forests in this region.

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1. Introduction

One of the most interesting topics in ecology is how aquatic and terrestrial ecosystems interact and influence one another (Polis et al., 1997). For instance, it has been shown that fishes indirectly affect plant pollination by controlling the major predator of bees (Knight et al., 2005). Recent studies are bringing forth increasing evidence with respect to the role of

fishes as seed dispersers and predators (Correa et al., 2007). Birds, primates, and rodents are the most studied frugivores with respect to fruit consumption and seed dispersal (see Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002) and studies on fish frugivory are poorly documented (e.g. Goulding, 1980).

In riparian forests and flood plains in the Neotropics, fishes may play important roles in ecosystem dynamics, acting as

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upstream carriers of seeds (Goulding 1980; Kubitzki and Ziburski, 1994; Horn, 1997). For instance, in flooded forests of the Amazon, fish species such as the tambaqui (*Colossoma macropomum*, Characidae) and the bacu-pedra (*Lithodoras dorsalis*, Doradidae) may represent important seed dispersers of several plant species, whereas birds and monkeys seem to be of secondary importance (Kubitzki, 1985; Kubitzki and Ziburski, 1994). In the Rio Paraná basin, the thorny catfish *Pterodoras granulosus* (Doradidae) acts as a seed disperser for small seeds, such as those of *Ficus*, *Cecropia* and *Polygonum* (Souza-Stevaux et al., 1994).

The destruction of riparian forests and building of dams are having deleterious impacts on aquatic ecosystems worldwide, and threaten the seasonal migratory movements of frugivorous fishes (Correa et al., 2007). Consequently, there are few pristine rivers, such as in the Pantanal and Amazon flooded forests and in a few seasonal rivers in southeast Brazil (Souza-Stevaux et al., 1994; Gomiero and Braga, 2003), where seed dispersal by fishes remains an important ecological process (Goulding, 1980; Galetti et al., 2008).

In the Pantanal of Mato Grosso do Sul, in the Upper Paraguay River, which includes the system of Bonito in the Serra da Bodoquena, several frugivorous fishes can be found, but two are particularly common: the piraputanga (*Brycon hilarii*, Characidae) and the pacu (*Piaractus mesopotamicus*, Characidae). These species are important in sport and commercial fishing and their populations are declining throughout the Pantanal basin (Catella and Albuquerque, 2007). Therefore, it is of paramount importance to study the role of frugivorous fishes on seed dispersal in riparian systems if we want to understand the consequences of anthropogenic disturbance on ecosystem services (Fargione et al., 2005). Thus, the objective of this study was to evaluate the importance of fruits in the diet of *B. hilarii*, and assess the availability of fruit resources for this fish throughout the year. Moreover, we aimed to investigate if fish size was related to frugivory and how fruit size influenced the fishes' role as a seed disperser.

2. Material and methods

2.1. Study site

Data were collected in the riparian forests of the Reserva Ecológica Baía Bonita (21°09' S, 56°25' W) located 7 km from Bonito, Mato Grosso do Sul, western Brazil (Fig. 1). The region is characterized by calcareous soils, and extremely clear rivers that drain in the direction of the Pantanal plain (Sabino and Sazima, 1999). The ranch covers 80 ha and attracts tourists to an area known as the Natural Aquarium, which receives visitors throughout the year (Sabino and Andrade, 2003). Three rivers cross and/or border the ranch: the Formoso River, the Formosinho, and the Baía Bonita. This study was restricted to Formoso River (Fig. 1). The region of Bonito receives annual precipitation of 1300–1700 mm and has an average temperature of 22 °C.

2.2. Data collection

The presence of fruits in the natural diet of *B. hilarii* was assessed over 14 months (March 2000 to May 2001, but in July

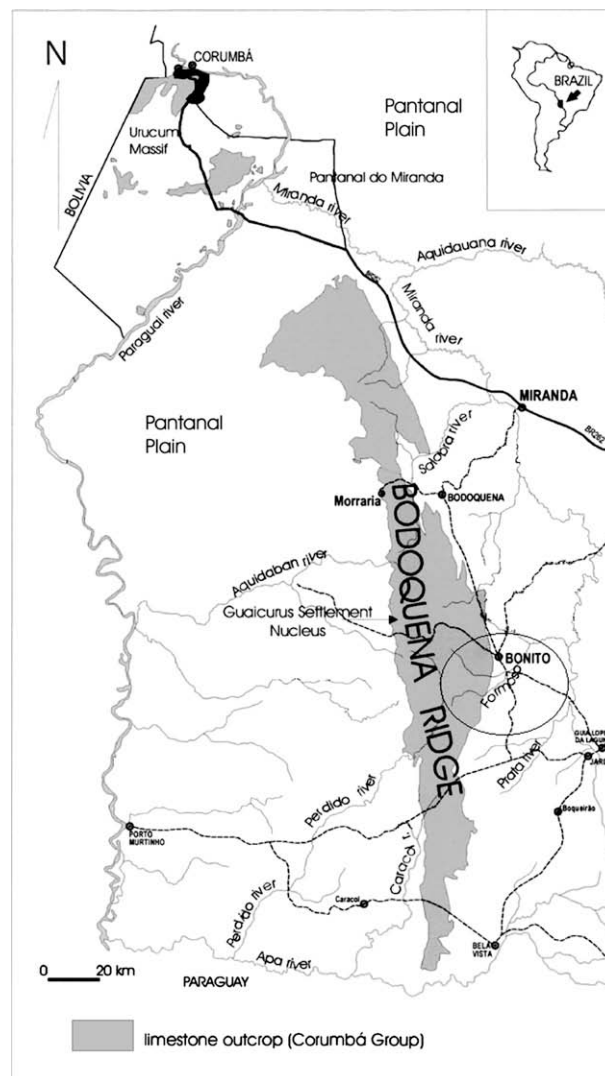


Fig. 1 – Location of the Bodoquena Massif and the Formoso River, Mato Grosso do Sul, western Brazil (based on Galati et al. 2006). Circle shows the study site.

2000 we did not collect any fish due to tourist disturbance in the area), by collecting up to ten individuals/month using a 0.5 mm fish line and hook baited with corn (*Zea mays*). Fish were immediately weighed, measured and dissected to remove the stomach for analysis later. The contents of 87 stomachs were examined and fruits and seeds separated from other items and identified. The contents were weighed and the frequency of occurrence calculated of each of the three food categories: (1) animal prey items, which include snails, arthropods and vertebrates, (2) fruits/seeds, and (3) other vegetation, which include algae, macrophytes, leaves and flowers (Gomiero et al., 2008). The seeds were classified according to size (small seeds <10 mm length; large seeds >10 mm length) and seed husk hardness, which we divided into two categories: (1) soft seeds (for seeds that we could crush between two fingers) and (2) hard seeds (for seeds that we could not crush).

We conducted a phenological study of the plant community along the banks of the Formoso River to measure the

availability of fruits for *B. hilarii* throughout the year (Reys et al., 2005). The botanical samples of the fruiting trees were deposited in the Herbarium Rioclarense (HRCB) at Rio Claro, state of São Paulo, Brazil.

In order to quantify the availability of fruits for the fishes we also estimated fruitfall along a 2 m wide and 1900 m long transect adjacent to the Formoso River. The total area sampled per month was 0.38 ha. This transect was checked monthly and all whole fruits or fruit fragments from animal dispersed fruits found on the forest floor were collected and weighed.

2.3. Data analysis

To verify if the occurrence of fruits in the diet was related to fish size, we calculated a logistic regression, with fish length and mass as the independent variable and the occurrence of fruits (0 or 1) as the dependent variable. Logistic regressions were also carried out to test if some fruit traits affected their likelihood of consumption by fishes. We analyzed 15 plant species that produced fruits in the study region, using measures of fruit length, diameter and weight. These measures were used as independent variables for analysis. The dependent variable was the presence (0 or 1) of a given species in the diet of fishes. To verify the correlations between consumption of fruits and rainfall, fruitfall and proportion eaten by piraputangas, we used the Pearson's correlation coefficient. We divided our samples into three seasons based on rainfall and fish behavior: (1) rainy season from February to May 2000, (2) dry season from March to September 2000 and (3) pre-spawning and spawning season from October to December 2000 and January 2001 when the piraputangas were migrating to spawning sites.

3. Results

The diet of piraputangas, based on the weight of all items, consisted of 24% animal prey items (arthropods, snails and one rodent species), 31% seeds/fruits and 45% other plant material. Among the snails, *Pomacea canaliculata* (Ampullariidae) were particularly important for piraputangas.

We observed the piraputangas feeding on fruit of 12 species, but found only nine in their guts (Table 1). Besides

feeding on fruits that fall in the water, piraputangas are able to leap and feed on fruits up to 1 m above water level (Fig. 2). In fact, it is a common attraction for tourists to bait fruits above the water to see the piraputangas leaping and catching fruits (<http://www.youtube.com/watch?v=I7oO4zesMsw&feature=related>). The most important species of seeds/fruits found in the stomachs of *B. hilarii*, according to their frequency of occurrence, were *Guibourtia hymenifolia* (14.2%), *Rhamnidium elaeocarpus* (12.5%), *Ficus* spp. (10.7%), *Psidium sartorianum* (5.3%), *Holocalyx balansae* (5.3%), *Chrysophyllum gonocarpum* (2.3%), *Trichilia silvatica* (2%) and *Margaritaria nobilis* (2%), but the importance of fruit species varied monthly (Fig. 3).

The consumption of fruits and seeds by *B. hilarii* was not related to the rainfall, but was positively related to fruitfall (Pearson correlation, $r^2 = 0.32$, $P = 0.04$, Fig. 4). The body mass of piraputanga differed between seasons, and the heavier individuals were found during the dry and spawning season (mean body mass = 860 ± 206 g, $n = 59$ and 960 ± 216 g, $n = 12$, respectively) and differed statistically from fish collected in the rainy season after migration (691 ± 283 g, $n = 15$) (ANOVA, $r^2 = 0.09$, $P = 0.019$). In fact, the piraputangas eat more fruits in the dry and pre-spawning season than in the rainy season when the individuals return from the breeding sites. We found the highest frequency of fruits in piraputanga guts just before the spawning season (October) when heavy storms started and caused the flooding of Formoso River. The increase in the river level allows the piraputangas to overcome natural barriers such as small waterfalls, triggering their migration for spawning upriver. No fish had seeds/fruits during the spawning season (Fig. 3).

The riparian tree community of Formoso River fruits all year round, with an increase in the number of species fruiting from September to November (Fig. 3). In terms of fruit biomass, we found a peak in August, due to the masting of *Guibourtia hymenifolia* (15.7 kg/ha) (Fig. 3). The annual fruit fall in the gallery forest was 27.83 kg/ha, varying from 0.15 kg/ha/month (January) to 15.7 kg/ha/month (August).

The piraputangas dispersed eight of the 12 species eaten, preyed on three species and acted neutrally (i.e. fed on pulp) on *Attalea phalerata* fruits (Table 1). In all ingested fruits with soft seeds larger than 10 mm, seeds were triturated by *B. hilarii*

Table 1 – Characteristics of fruits/seeds ingested by *Brycon hilarii* at Formoso River and their role as seed dispersers, Mato Grosso do Sul, western Brazil

Family	Species/Features	Fruit	Seed length (mm)	Seed hardness	Seed treatment
Amaranthaceae	<i>Gomphrena elegans</i>	Fleshy	≤1	Soft	Disperser ^a
Arecaceae	<i>Attalea phalerata</i>	Fleshy	48.7	Hard	Neutral ^a
Euphorbiaceae	<i>Margaritaria nobilis</i>	Dry	7	Hard	Disperser
Fabaceae	<i>Guibourtia hymenifolia</i>	Dry	12	Soft	Predator
Fabaceae	<i>Holocalyx balansae</i>	Fleshy	13	Soft	Predator
Meliaceae	<i>Trichilia</i> sp.	Fleshy	10	Soft	Predator
Moraceae	<i>Ficus</i> spp. ^b	Fleshy	≤1	Hard	Disperser
Myrtaceae	<i>Psidium sartorianum</i>	Fleshy	4	Soft	Disperser
Rhamnaceae	<i>Rhamnidium elaeocarpus</i>	Fleshy	8	Soft	Disperser
Rutaceae	<i>Zanthoxylum</i> spp.	Dry	5	Hard	Disperser ^a
Sapotaceae	<i>Chrysophyllum gonocarpum</i>	Fleshy	13	Hard	Disperser

a Observed but not collected in the fish stomachs.

b Including *Ficus pertusa* and *F. calyproceras*.



Fig. 2 – School of piraputangas *Brycon hilarii* (Characidae) foraging at Formoso River, Bonito, western Brazil. Note one fish jumping out of the water to feed on *Gomphrena elegans* fruits (Amaranthaceae) (Photo: J. Sabino).

and became unviable for germination (Table 1). The logistic regression results for fruit traits indicate that fruit length has a significant and negative effect on its occurrence in the diet ($\chi^2 = 4.218; P = 0.04$), which implies that fish could be selecting shorter fruits (Table 2). On the other hand, fruit diameter and weight did not have a significant effect ($\chi^2 = 0.113, P = 0.736$ and $\chi^2 = 0.479, P = 0.489$, respectively).

Fruit consumption was related to fish size ($\chi^2 = 4.78; P = 0.028, n = 87$), but not to fish weight, which implies that fish length was a good predictor of frugivory in *B. hilarii*.

4. Discussion

The percentage of fruits found in the guts of *B. hilarii* is lower (31%) than values reported for other riparian forest fish species, such as the catfish *Pterodoras granulosus* in the Rio Paraná Basin (from 49% to 76%; Souza-Steaux et al., 1994) and *Brycon opalinus* in the Atlantic forest (>60%, Gomiero et al., 2008), but similar to the diet of *Brycon hilarii* at Miranda River (33% of fruits; Zuntini et al., 2004). The piraputangas are opportunist feeders at Formoso River, as shown already for other *Brycon* species (see Gomiero et al., 2008), and the lower overall fruit diet of *Brycon hilarii* may reflect the high variation in fruit availability throughout the year (Reys et al., 2005).

The gallery forest in the Formoso River apparently does not have plant species that rely exclusively on *Brycon hilarii* for dispersal, such as some plant species in the Amazon basin (Kubitzki and Ziburski, 1994) or Pantanal (Galetti et al., 2008). All species eaten by the piraputangas in our study area are also eaten, and occasionally dispersed, by birds and mammals (P. Reys, personal observation; Sabino and Sazima, 1999; Cazetta et al., 2008). However, the generalist diet of *B. hilarii* does not mean they are not important seed dispersal agents for the plant community, especially for small-seeded plants. Based on the seed size and hardness of the riparian plant community in the region (Reys et al., 2005; Bueno et al., 2007), the piraputangas potentially disperse about 50% of the tree and shrub species ($n = 30$ species). In the Pantanal, the pacu

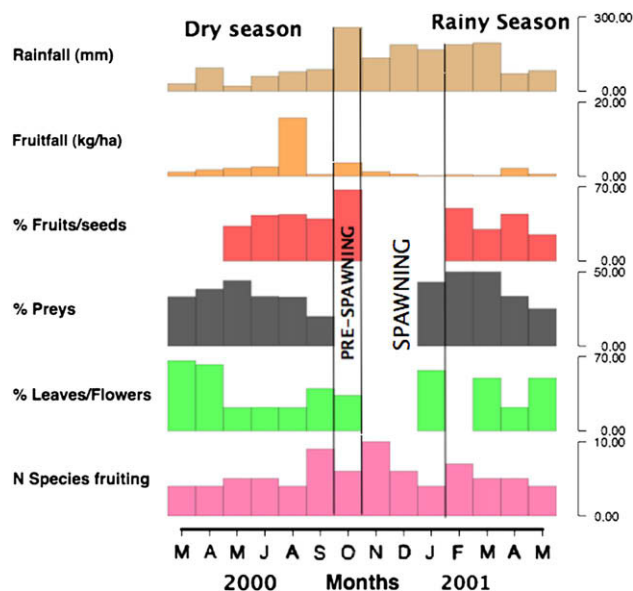


Fig. 3 – Monthly variation of rainfall (mm), fruitfall (kg/ha), number of species with ripe fruits, and the percentage of food items in the diet of *Brycon hilarii* at Formoso River, western Brazil.

(*Piaractus mesopotamicus*) is able to disperse 27% of the tree species in riparian forests of Rio Negro (Galetti et al., 2008). Gomiero (pers. commun.) found that *Brycon opalinus* eat 51 fruit species in riparian Atlantic forests in Brazil. In addition, the piraputangas may be an important vector for carrying small seeds long distances and distributing them in sites suitable for plant recruitment. In fact, the peak of fruit consumption was exactly just before the migration (October), which increases

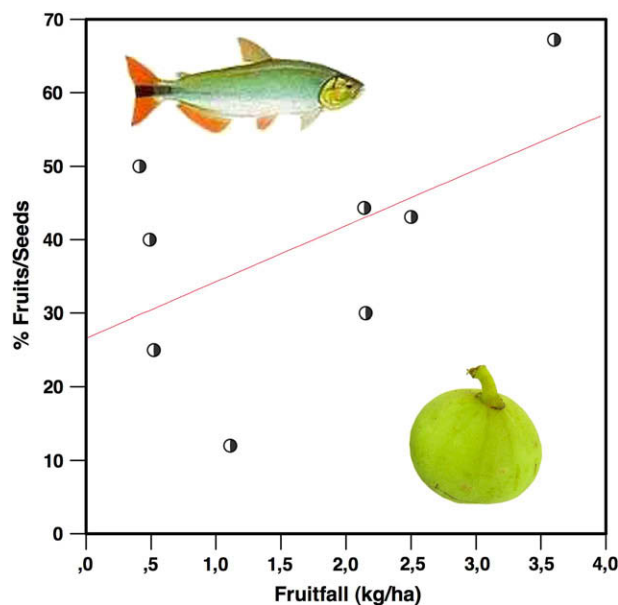


Fig. 4 – Scatterplot and adjusted curve from the linear regression between the percentage of fruits and seeds in the stomachs of *Brycon hilarii* and fruitfall at Formoso River, Baía Bonita, MS, Brazil.

Table 2 – Characteristics of fleshy fruit species in the riparian forest of Formoso River, MS, western Brazil

Family/Specie	Life form	Fruit kind	Mean seed number	Fruit length (cm)	Seed length (cm)	Fruit diameter (cm)	Hardness	Fruit weight (g)	Color	Disperser
ANNONACEAE										
<i>Unonopsis lindimani</i>	Tree	Fleshy	1.5	1.18	0.86	1	Soft	0.84	Black	B/M
ARECACEAE										
<i>Attalea phalerata</i>	Tree	Fleshy	1	5.7	4.7	3.15	Hard	35.7	Yellow	M
CAESALPINACEAE										
<i>Holocalyx balansae</i>	Tree	Fleshy	1.2	2.16	1.38	1.78	Soft	6.4	Green	B/M/F
<i>Guibourtia hymenifolia</i>	Tree	Dry	1	1.7	1.305	0.94	Soft	0.1	Red	B/M
CECROPIACEAE										
<i>Cecropia pachystachya</i>	Tree	Fleshy	100	18	0.2	0.2	Soft	0.8	Brown	B/M
MELIACEAE										
<i>Trichilia</i> sp.	Tree	Fleshy	1.45	0.88	0.46	0.46	Soft	0.625	Red	B/M/F
<i>Trichilia silvatica</i>	Tree	Fleshy	1.1	1	0.8	0.5	Soft	0.31	Orange/Black	B/F
MIMOSACEAE										
<i>Inga</i> sp.	Tree	Fleshy	3	10	1	0.8	Soft	2	Yellow	M
MORACEAE										
<i>Ficus</i> spp.	Tree	Fleshy	100	1	0.1	1.3	Soft	0.8	Green	B/F
MYRTACEAE										
<i>Myrcianthes pungens</i>	Tree	Fleshy	6.3	1.5	0.3	1.3	Soft	0.5	Violet	B/M
<i>Psidium sartorianum</i>	Tree	Fleshy	8.1	0.9	0.317	1.04	Soft	1.5	Yellow	B/M/F
RUBIACEAE										
<i>Psychotria cartaginensis</i>	Shrub	Fleshy	1.9	0.79	0.59	0.69	Soft	0.1	Red	B
SAPOTACEAE										
<i>Chrysophyllum gonocarpum</i>	Tree	Fleshy	3.6	1.81	1.05	1.89	Hard	5.4	Yellow	B/M/F
TEOPHRASTACEAE										
<i>Clavija nutans</i>	Shrub	Fleshy	4	3	1.2	2.5	Hard	0.8	Orange	B/M
VERBENACEAE										
<i>Citharexylum mirianthum</i>	Tree	Fleshy	2	0.9	0.74	0.5	Hard	0.4	Red	B/M

Disperser: M = mammals, B = birds, F = fishes.

the chance of long-distance seed dispersal. Horn (1997) found that *B. guatemalensis* disperse *Ficus* seeds after more than 48 h of ingestion and thus move the seeds long distances.

Seed size and hardness determined whether the species of *Brycon* are seed predators or dispersers (Goulding, 1980). Therefore, *Brycon* fishes may be exerting a selective pressure that favors plant species with small and hard-shelled seeds, which could in turn be directly influencing the composition of the riparian forests (Banack et al., 2002).

Seed dispersal by fish may be the oldest of such mechanisms involving plants and vertebrates (Tiffney, 2004) and may be important for the ecological dynamics of gallery forests or flooded regions. However, these antagonistic (seed predation) and mutualistic (seed dispersal) interactions between plants and fishes are being seriously threatened in all freshwater ecosystems (Correa et al., 2007). Nowadays, the populations of many fishes have been declining over their distributional range due to overfishing, deforestation, habitat loss, dam construction and pollution. The local extinction of fish-plant interaction may have negative consequences for the riparian forests and may have far-reaching consequences on ecosystem services.

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