

Mutilating predation in the Cheirodontinae *Odontostilbe pequira* (Characiformes: Characidae)

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We observed individuals of *Odontostilbe pequira*, a small characid, approaching and biting individuals of larger-bodied fishes of other species. This observation was made in two clear water headwater streams of the Cuiabá basin, Paraguay River system, located in Nobres, Mato Grosso State, Brazil, which led us to investigate the behavioral interactions of these fish. We characterized behavioral interactions between species by direct underwater observations using snorkelling and video recordings. Additionally, we proceeded diet analyses of *O. pequira*, obtaining intestinal coefficient and the index of alimentary importance. During underwater observations we checked the relative frequency of attacks by *O. pequira* on larger fish species. *Odontostilbe pequira* attacked individually or in large groups, and the anostomid *Leporinus friderici* was the preferred target prey species, while *Prochilodus lineatus* was apparently avoided. Our study sustains that *O. pequira* is omnivorous, with a diet that varies seasonally. It feeds mainly on plants, but also on animal prey, including the scales of small fishes, and, possibly, the mucus and epidermis of larger fish species. We suggest the term “mutilating predation” to describe the latter relationship.

Observamos indivíduos de *Odontostilbe pequira*, um caracádeo pequeno, abordando e mordendo peixes maiores de outras espécies. Essa observação foi feita em dois riachos de cabeceira com águas cristalinas na bacia do rio Cuiabá, sistema do rio Paraguai, localizados em Nobres, Mato Grosso, Brasil, o que nos levou a investigar a interação comportamental desses peixes. Nós o fizemos através de observações subaquáticas diretas usando mergulho livre e vídeo. Adicionalmente, realizamos a análise da dieta de *O. pequira*, obtendo seu coeficiente intestinal e índice de importância alimentar. Nas observações subaquáticas avaliamos a frequência relativa dos ataques de *O. pequira* sobre peixes maiores. *Odontostilbe pequira* ataca individualmente ou em grupos grandes, o anostomídeo *Leporinus friderici* foi a presa preferida, enquanto *Prochilodus lineatus* foi evitado. Este estudo sustenta que *O. pequira* é um peixe onívoro cuja dieta varia sazonalmente. Ele come principalmente plantas, mas também presas animais, como escamas de peixes pequenos e, possivelmente, muco e epiderme de peixes maiores. Sugerimos o termo “predação mutilante” para descrever essa relação.

Key words: Animal behavior, Feeding plasticity, Lepidophagy, Underwater observations.

Introduction

Many fish species have markedly plastic diets (Abelha *et al.*, 2001; Dabrowski & Portella, 2005). The changes in their food may relate to the ontogeny (Santos *et al.*, 2009), the supply of certain food within portions of their geographic distribution (Dias, 2007), or the seasonal availability of those items (Hahn *et al.*, 1992; Ferretti *et al.*, 1996).

Odontostilbe pequira, popularly known as pequira in western Brazil, is a small species (maximum length of 56 mm,

Malabarba, 1998) of the order Characiformes (Characidae: Cheirodontinae) occurring in the La Plata River basin in Brazil, Paraguay and Argentina (Malabarba, 2003). Species of the subfamily Cheirodontinae are distributed through Central and South America (Malabarba, 2003).

Studies on the diet of *O. pequira* in different locations have suggested that it can be classified as an herbivore or omnivore based on the index of alimentary importance (IAi), depending on the study area. In macrophyte beds of the

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Pantanal the species was described as herbivore (Santos *et al.*, 2009); in reservoirs, it had an insectivorous-herbivorous diet (Luz-Agostinho *et al.*, 2006); in floodplain lakes along the Cuiabá River, *O. pequira* was described as an omnivore (Ximenes *et al.*, 2011); finally, Dias (2007) described it as a detritivore-carnivore in the Ibicuí River, Rio Grande do Sul, Brazil. Thus, there is no consensus on the diet of this species, which seems to vary geographically due to plasticity.

Previous studies also revealed that scales were found in the digestive tract of *O. pequira*, although in small amounts (Dias, 2007; Santos *et al.*, 2009). The presence of scales was attributed to accidental capture while feeding on benthic items (Dias, 2007). As part of this study, we sought to further investigate the possibility of lepidophagy, or non-facultative scale-eating, in *O. pequira*.

In the streams of Bom Jardim, Mato Grosso, Brazil, a large number of *O. pequira* was frequently seen biting larger fish. Co-occurring in these streams are many 'piraputangas' (*Brycon hilarii*), 'piaú-três-pintas' (*Leporinus friderici*), 'curimbas' (*Prochilodus lineatus*) and 'dourados' (*Salminus brasiliensis*), among various other species. Fish approached by *O. pequira* often show signs of stress, such as changes in color (Rodrigues *et al.*, 2009) and swimming pattern (Kanea *et al.*, 2004). These observations raised the question as to what constitutes the diet and characterizes the feeding behavior of *O. pequira*, and its effects on other fish.

Our objective was to elucidate the feeding behavior and interactions between *O. pequira* and other local abundant fish species, including the anostomid *Leporinus friderici*, the characids *Brycon hilarii*, *Salminus brasiliensis*, and the prochilodontid *Prochilodus lineatus*. We used two approaches: (1) we made direct underwater observations of the feeding behavior of *O. pequira* and evaluated interspecific interactions relative to abundance of each of the targeted prey species; and (2) we studied the morphology and diet of *O. pequira*, to determine the intestinal coefficient and characterize the items by frequency, volume and alimentary importance of the ingested food. We conclude with a discussion of terminology employed to describe this type of behavioural interaction among fishes and the possible nutritional benefits associated with lepidophagy and muciphagy.

Material and Methods

Study area

The streams that flow through Bom Jardim, Mato Grosso State, Brazil, belong to the Paraguay basin, which forms the La Plata-Uruguay-Paraná-Paraguay system, which extends over an area of 3.2 million km² (Lowe-McConnel, 1999). The Estivado and Salobra rivers are headwater tributaries of the rivers that form the Pantanal flood plains, flowing into the Cuiabá River. These streams have clear waters due to the deposition of the sediments caused by the calcium ions from the soil. Visibility often exceeds 40 m.

Most observations were made in the Estivado River, in Bom Jardim, district of Nobres Municipality (14°43'13"S 56°19'9"W) (Fig. 1). Additional observations were made in Salobra River (14°35'25.5"S 55°57'41.8"W). Nobres is a popular area sought by tourists for fish-watching, due to its crystalline water streams.

Underwater observations

Daytime observations on the behaviour of *Odontostilbe pequira* were made in August and December 2009 in 15 sessions of up to 60 min each, within various sections of a 120-m reach of the Estivado River (Fig. 1). We used the sequence-sampling method, in which the focus is a behavioural sequence (Martin & Bateson, 2007), in our case, the act of approaching other fish apparently aiming to feed on mucus and/or scales. We completed a total of 12.5 h of snorkelling, taking notes on an underwater writing slate. We also photographed and recorded the behavior on video, using a camera enclosed in a waterproof housing.

Additionally we observed the frequency with which *O. pequira* attacked each of the main target species (*B. hilarii*, *L. friderici*, *S. brasiliensis*, and *P. lineatus*) in ten sessions

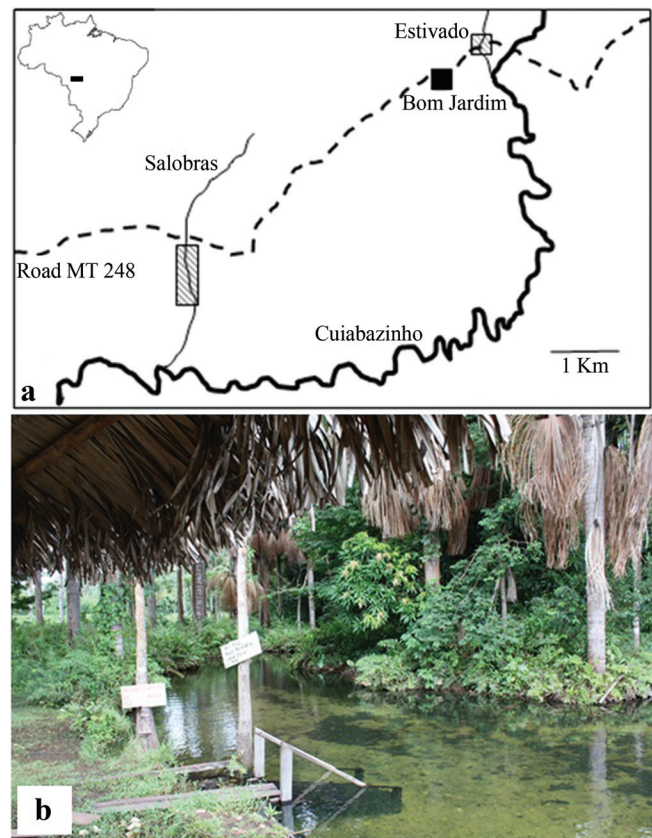


Fig. 1. Study area. **a)** Detailed map of the study area, black rectangle on the map of Brazil indicates the location of Bom Jardim. Dashed areas indicate the main study area (Estivado River) and a comparison area (Salobra River). **b)** Photo of the study site in Estivado River by Eduardo Bessa (December 2009).

of 15 min each, for each species. This data were used to infer the preference for a target fish species, combining the previous data with visual census of the target's abundance. The significance of the results was verified by a Chi-square test in which the frequency of attacks was the observed value and the target's abundance was the expected value, with $\alpha = 0.05$. Ten censuses were made in different 10-m reaches of the Estivado River with visibility of at least 6 m. The reaches were measured with a meter tape and snorkelled at constant speed for 10 min, thus evaluating an area of 10 m x 12 m (length of the transect times twice the visibility). Low standard deviation between counts allowed us to be more confident in this method for estimating populations; nevertheless, every visual method is limited, especially with larger schools and fast-moving fish (Labrosse *et al.*, 2002). In order to avoid between-observer bias, all counts were made by the same observer.

Diet Analysis

For the diet analysis we used 30 specimens of *O. pequirá* captured in August plus other 30 caught in December 2009. We captured fish with 70-cm wide seines with 2.5 mm mesh, and 2 L fish traps made of PET plastic bottles. The traps were left amid the vegetation for 3 h baited with a mixture of cassava flour and sardine oil in a container that allowed the attractive odor to disperse, but prevented the fishes from eating the bait. Collected specimens were fixed in 10% formaline and preserved in 70% ethanol within three days. All the fishes, including *O. pequirá* and the scale-bank fishes (see below), were identified with taxonomic keys (Britski *et al.*, 2007) and the support of specialists. Voucher specimens of *O. pequirá* are deposited in the Coleção de Peixes do Departamento de Zoologia e Botânica da Universidade Estadual Paulista, São José do Rio Preto (DZSJRP 14800).

Standard length (SL) and intestine length (IL) were measured to the nearest mm. The intestinal coefficient (IC) was calculated for each individual as $IC = SL/IL$. We present here a mean value \pm standard deviation and the data range. The intestinal coefficient is indicative of a relationship between anatomy (intestine length and standard length) and the types of food consumed (Fugi & Hahn, 1991). Stomach contents were examined under a stereomicroscope; food items were identified as algae, autochthonous insects, allochthonous insects, scales from other fishes, and plant debris. The scales were identified by comparison with a scale bank assembled from a reference collection of fishes from Bom Jardim. All scales were taken from the middle-body upper right flank of the fish, where most attacks occurred. Scale measures were taken from its shortest axis. This collection is housed at the Museu de Zoologia de Tangará da Serra, UNEMAT.

To measure the ingested volume of each item we used four 1 mm-thick histological glass slides. Each food item was placed on the top of the slide that had a graph paper attached to the opposite side to serve as a counting grid; then the food item was compressed between two slides, and another slide was placed on the top to limit the height of the mass to

1 mm. Thus, counting the number of 1-mm squares covered by the mass resulted in determination of each item's volume in mm^3 . When necessary an optical microscope was used to better visualize the material.

The diet was quantified using the index of alimentary importance (IA_i), represented as the values for frequency of occurrence (F_i, number of stomachs that contained each item, in relation to the number of stomachs with food) and volume (V_i, volume occupied by each item), where $IA_i = F_i * V_i / 100$ (Kawakami & Vazzoler, 1980). Items with values of IA_i higher than the mean of all items combined were considered important for the species.

Results

Feeding behaviour

Odontostibe pequirá occurred in great abundance in Estivado River, and we visually estimated about 10,000 individuals in a 10 m stretch in December 2009, at the beginning of the rainy season. This species is a midwater dwelling fish that occurs in schools with other small-bodied species of Characiformes. It is more active at daylight, when individuals occupy slowly to moderately flowing stretches over sand, rock, or detritus-covered bottoms. At dusk individuals were found resting near the shoreline.

We observed that *O. pequirá* approached larger fish in two ways: (1) individual attacks or (2) group attacks. When a larger fish (*e.g. Leporinus friderici*) was resting or swimming slowly, one *O. pequirá* approached it swimming perpendicularly towards the target fish's flank, and contacted it with the mouth (Fig. 2). When doing so individually (1), the targeted fish quickly swam away. In the case of (2), a group of *O. pequirá* advanced rapidly towards a target fish that was swimming away, and individuals then appeared to alternately take bites of exposed portions of the target fish. This behavior resulted in a trail of *O. pequirá* following the target, analogous in appearance to a comet (Fig. 2c).

Many of the larger target fish remained motionless at the river bottom, a behavior that apparently reduced the chance of being approached by *O. pequirá*. In these circumstances, only individual attacks occurred. Conversely, when a target fish wandered to forage, group attacks were more common. Targets of a group attack responded to the approach by swimming away rapidly or by performing erratic movements. Accelerated swimming occurred in straight-line bursts for about three seconds, occasionally being repeated if individuals of *O. pequirá* still followed. Erratic swimming involved abrupt changes in swimming direction or tail snaps on the river bottom.

The species attacked more often was the anostomid *Leporinus friderici*; *Brycon hilarii* was second, with about half as many attacks as *L. friderici*, *Salminus brasiliensis*, and *Prochilodus lineatus* were the least attacked large fishes in the area (Fig. 3). Among the targeted fishes *Leporinus friderici* and *B. hilarii* were the most abundant species, followed by *P. lineatus* and then by *S. brasiliensis* (Fig. 4). *Brycon hilarii* and *L. friderici* spent more time near the

stream bottom, and presented darker skin color pattern than their conspecifics from other rivers where fewer *O. pequira* were found, such as the Salobra River (Fig. 1). Chi-square test indicates that the 'pequiras' preferred attacking *L. friderici* and avoided *P. lineatus* ($\chi^2: 5.305 \times 10^{-5}$, $df = 3$, $P = 1,028 \times 10^{-7}$). *Leporinus friderici* and *B. hilarii* were frequently seen with wounds on the flanks, the same region attacked by *O. pequira*.

Diet analysis

In our study *O. pequira* appears to be an opportunistic feeder with a plastic diet, *i.e.* characterised by having no specialisation for a specific food item. On many occasions ledidophagy was observed.

Individuals collected measured 31.6 ± 1.6 mm in SL (mean \pm standard deviation; $N = 60$). *Odontostilbe pequira*'s intestinal coefficient was $IC = 0.62 \pm 0.12$, ranging from 0.55

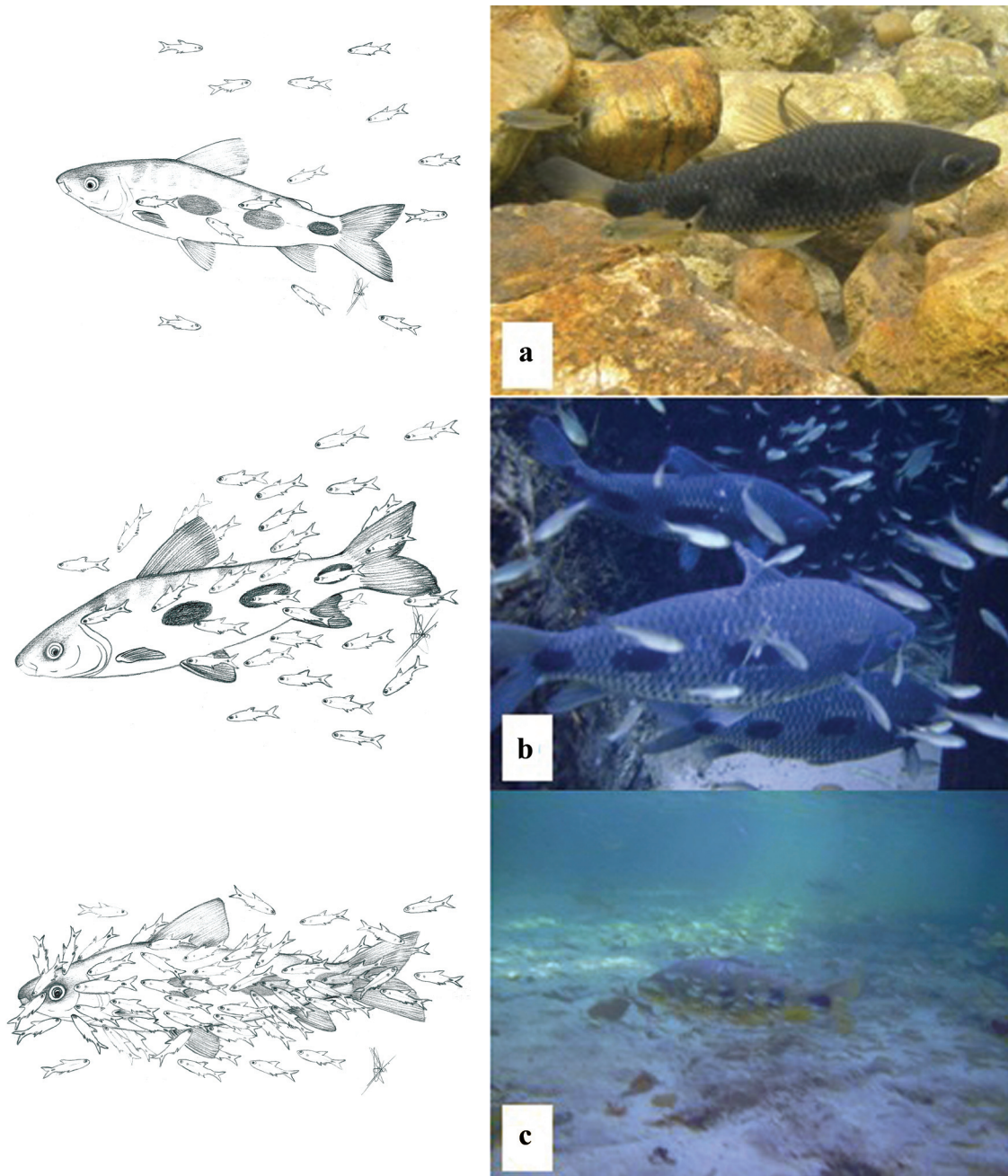


Fig. 2. *Odontostilbe pequira* attacks upon *Leporinus friderici*. **a)** individual attack; **b)** beginning of a group attack; and **c)** group of *O. pequira* in a group attack. Drawings by Cristiane Freitas; photo (a) by Lucélia Carvalho; (b) and (c) by Eduardo Bessa (August 2009).

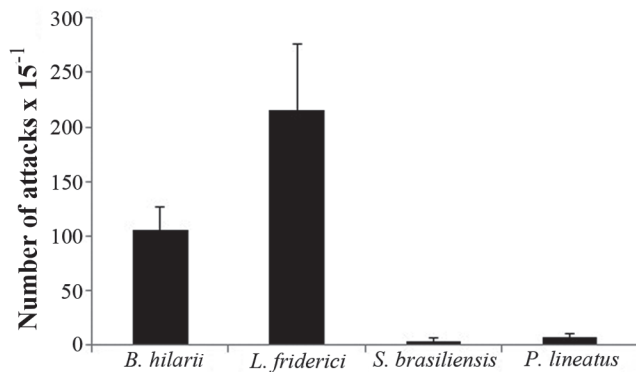


Fig. 3. Mean number (\pm SD) of attacks by *Odontostilbe pequira* towards larger fish during 15-min observation sessions of focal target species. N = 10.

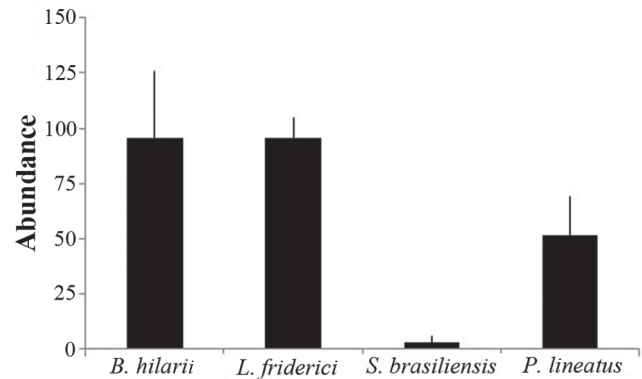


Fig. 4. Abundance of the main targets of *Odontostilbe pequira*. Mean number of individuals recorded in 10 x 12 m area censuses \pm standard deviation. N = 10.

to 1.29 (N = 60), which places the species within the range of omnivorous fishes.

Among food items ingested by *O. pequira* (Table 1), the most frequent were algae and plant debris. Fish scales, allochthonous and autochthonous insects were less frequent in the diet. Forty percent of the 60 individuals analysed were exclusively herbivores (algae and plant debris). The index of alimentary importance verified that algae was the most important food item of *O. pequira* in the Estivado River, followed by plant debris, autochthonous insects, scales, and allochthonous insects.

All stomachs examined from specimens collected in both the dry and rainy seasons contained food items. However, the importance of items varied between seasons (Table 1); plant debris was four times as important, and autochthonous insects were twice as important in the dry season than in the wet season. In contrast, scales and allochthonous insects were half as important in the dry season than in the wet season.

Fish scales were ingested by 23% of the individuals (Fi for dry and rainy seasons summed) and totalled 8% of all the food ingested (Vi for both the seasons summed). Of the scales found in the stomach of *O. pequira*, none belonged to *Brycon hilarii*, *Leporinus friderici*, or *Prochilodus lineatus*, which measured 7.24 ± 0.73 ; 8.37 ± 0.57 ; and 8.51 ± 0.31 mm, respectively (N = 6 for each species). This scale size is wider than the gape of *O. pequira*, which averaged 2.12 ± 0.34 mm (N = 15). Comparing with the local reference scales bank, the ingested scales probably belonged to *Hyphessobrycon*

elachys, *Astyanacinus moorii* and *Serrapinus microdon*; which scales measured 1.23 ± 0.27 mm (for the three above mentioned species combined; N = 27).

Discussion

Odontostilbe pequira attacked several kinds of fish, individually or in large groups. Despite being fundamentally herbivorous, *O. pequira* complemented its diet with scales. Although our method did not allow us to unequivocally determine if epidermis or mucus constitute a food item of *O. pequira*, these items are presumed to have some importance to this species' diet, as inferred by its behavior towards target species.

Many piscivorous species attack their targeted preys in groups (Keenleyside, 1974; Sazima & Machado, 1990), as observed in our study. Some mathematical models of predation have shown that attacks on prey species with a larger body size than the predator's are generally made in groups, except when the prey is caught unaware or resting (Mchicha *et al.*, 2006). This was consistent with our observations of attacks by *O. pequira* on larger fish.

Fish that were targeted by attacks from *O. pequira* exhibited different strategies for avoiding attacks. Their response included attempts to outswim attackers (straight line burst), foil them (erratic swimming), or avoid being perceived by potential attackers (staying still by the bottom or in crevices), somewhat analogous to strategies known in artiodactyle mammals (Caro *et al.*, 2004).

Table 1. Seasonal variation in the diet of *Odontostilbe pequira*. Fi%: frequency of occurrence; Vi%: volume; IAI: index of alimentary importance.

Food items	Fi%		Vi%		IAI	
	Rainy	Dry	Rainy	Dry	Rainy	Dry
Algae	0.967	0.733	51.320	91.980	0.496	0.674
Plant debris	0.567	0.767	16.950	63.110	0.0961	0.484
Fish scales	0.430	0.100	2.160	0.440	0.009	0.000
Allochthonous insects	0.233	0.100	2.680	0.210	0.006	0.000
Autochthonous insects	0.333	0.200	6.150	22.10	0.020	0.044

Lepidophagy and muciphagy result in negative consequences for the fish attacked, like the wounds we observed in Estivado River. Lepidophagy exposes internal tissues and increases the chances of infection (Fontenot & Neiffer, 2004). Fish mucus is known to function in immune defense, osmotic balance, and hydrodynamics (Ebran *et al.*, 1999). The loss of both, scales and mucus, may reduce the health of the target species and may, therefore, lower their population abundance (Piana *et al.*, 2006).

The number of attacks did not appear to correlate with the abundance of the targeted species; *i. e.* *O. pequirá* showed a preference for *L. friderici* and avoided *P. lineatus*. This may be due to the slower swimming speed of the species (Britski *et al.*, 2007), or to the mucus volume or its different nutritional value (Grutter & Bshary, 2004).

The intestinal coefficient of a fish indicates how the intestinal length relates to the nutritional value of the food items that it consumes (Seixas-Filho *et al.*, 2000). Fish that feeds on items resistant to digestion, such as plant matter or algae, must have longer intestines. *Odontostilbe pequirá* possess an intestine of intermediate length (IC = 0.62), which combined to its diet composition allows to characterise it as an omnivore with a tendency to herbivory (*sensu* Bértin, 1958).

Odontostilbe pequirá was also described as an omnivore with a tendency to herbivory by Fugi & Hahn (1991). This species is plastic in its diet, taking advantage of different food sources along the year, which is common in many tropical fishes (Dias, 2007). According to Shibatta *et al.* (2002), feeding plasticity is characteristic of some species that are subjected to environmental variations that result in shifts in the availability of food items. The Estivado River is under seasonal variations due to the cyclical nature of weather in the Brazilian savannah (Ab'Sáber, 2003).

The diet documented herein for *Odontostilbe pequirá* from the Estivado River did not differ markedly from that found in other studies, although the relative importance of the different food items varies. Oliveira (2003) found that an unidentified species of the genus *Odontostilbe* fed on algae, plant matter, insects, and small fish. Dias (2007) studied eight species of the subfamily Cheirodontinae, including *O. pequirá*, and found a similar diet for this species as we observed, including algae, plant matter, insects, and fish scales.

Lowe-McConnell (1999) concluded that in tropical ecosystems fishes depend primarily on allochthonous material, mainly in the rainy months when this kind of material is washed into the rivers in large quantities. This was the case in our study, in which allochthonous items, such as adult insects, were more common in the rainy season, and autochthonous items, such as algae and insect nymphs, were ingested more often during the dry season. The increase in scale eating in the rainy season may have been related to an increase in the density of the targeted prey species in the Estivado River. Francisco (2004) noted that if availability of certain food items changed throughout the year, fish tend to be opportunistic and changed the diets relative to their availability.

Underwater observations of the behaviour of *O. pequirá* in the Estivado River indicates that this species consumed scales and, possibly, also the epidermis and mucus of targeted fish, as already noted in other studies (Dias, 2007; Santos *et al.*, 2009). Although our methods could not confirm the ingestion of mucus or epidermic tissue, we speculate that these items were part of the diet in the population of *O. pequirá* that we studied. Histological preparations of the gastrointestinal tract stained with Luna's Alcian Blue can indicate the consumption of mucus (Winemiller & Yan, 1989), but only when mucus occur in large amounts, which was not the case in our study.

Scale and/or mucus eating may provide valuable nutrients to *O. pequirá*. Lepidophagy offers proteins and minerals (Géry & Vieira, 1979), mainly from the epidermis that covers the scales. Muciphagy provides an abundant and renewable source of amino acids and sugars (Ebran *et al.*, 1999). It is also possible that ingesting mucus brings immune protection (Buckley *et al.*, 2010). The South American catfish *Ochmacanthus alternus* was described as specialised in muciphagy (Winemiller & Yan, 1989), but other cases of occasional ingestion of this resource are known to benefit fry by species that exhibit parental care (Buckley *et al.*, 2010), as well as species that exhibit cleaning behavior (Grutter & Bshary, 2004). The Estivado River is an oligotrophic environment, and in times of seasonal food limitation and possible competition for food, it is possible that such alternative feeding habit benefits to *O. pequirá*.

There is no consensus of how to define lepidophagy, since differentiating between predation and parasitism itself may be considered merely a matter of recognizing categories within a continuum of feeding strategies (Allaby, 2009). Some authors have categorized lepidophagy as a parasitic habit (Keenleyside, 1979; Wootton, 1998), whereas others have considered it to be a type of predation (Sazima, 1977; Grubh & Winemiller, 2004). Parasitism is typically defined as the relationship in which one species, the parasite, takes nutrients and residency from another, the host, in a close and lasting association that seldom leads to direct death of the host (Zelmer, 1998). Predation, on the other hand, may be defined broadly, and may include the definition of parasitism, in which one species is benefited and the other is harmed (Abrams, 1987), or, narrowly, as the interaction between two species in which one of them, the predator, gains energy by killing and consuming the other, the prey (Pollard, 1992). None of the above definitions adequately describes the relationship between *O. pequirá* and the large fish that it attacks. Herein we consider lepidophagy as a mutilating predation of the targeted species upon which it preys. The term was not introduced by us, Sazima & Pombal-Jr. (1988) described fin-clipping as a mutilating predation. We define mutilating predation as an association in which the predator consumes parts of its prey in a brief encounter, the consequences of which appears to have little chance of killing the victim.

Odontostilbe pequirá is an omnivore, feeding mainly on plants, but also on animal items. Its diet varies seasonally

and it consumes small fish scales and, possibly, the mucus and epidermis of larger fish; of the later in this study, most frequently *Leporinus friderici*. Future studies of captive specimens are needed to fully evaluate how larger species are affected, if at all, by predation on them by *O. pequirá*.

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