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# Fish thieves: An alternative tactic of food capture in a Neotropical frugivorous species (*Brycon falcatus*)

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**Abstract** Frugivorous fishes switch their diets seasonally in response to fluctuating food availability; a strategy that maximizes energy and nutrient intake and reduces competition for food. Kleptoparasitism is a form of competition that involves the stealing of already-procured items, for which the host has invested energy in prey capture. We did not find previous studies on kleptoparasitism among Neotropical fish. Here we contribute the first record of kleptoparasitism among a frugivorous fish species. The matrinxã (*Brycon falcatus*) is a member of an iconic genus of broadly distributed frugivorous fishes. We made focal daylight underwater observations (by snorkeling) of frugivorous fish behavior in an Amazonian stream. Opportunistic feeding interactions between a school of juvenile matrinxã, (*B. falcatus*) and an individual of threespot leporinus (*Leporinus friderici*) were observed. The matrinxã stole the fruit that was captured in the substrate by the leporinus. *Brycon falcatus* usually lives between the middle of the water column to the surface of rivers and streams while *Leporinus friderici* occupies the lower portion of the water column and it actively forages close to the substrate. This suggests that stealing food from a benthic feeder is an opportunistic ecological interaction to take advantage of scarce resources during the period of food scarcity. This alternative technique of capturing fruits may be advantageous (*i.e.*, save energy expenditures related to searching) for young matrinxã who do not eat fruit as frequently as adults. Our results reflect the trophic plasticity and foraging opportunism characteristic of most tropical freshwater fish. We believe that the hydrological period in which the observations were made, when a few trees were bearing fruit, can favor fruit stealing by *Brycon falcatus*.

**Key words:** food-stealing, opportunistic interactions, facultative kleptoparasitism, feeding behaviour, underwater observations.

Frugivorous fishes change their foraging behaviour to maximize energy and nutrient intake in response to temporal variations in the quality and availability of food (Correa & Winemiller 2014). Trophic niche segregation among Amazonian frugivorous fishes is achieved through seasonal partitioning of food, a pattern consistent with competition theory (Correa & Winemiller 2014). Kleptoparasitism is a form of competition that involves the stealing of already-procured items, for which the host has invested energy in prey capture and consumption by the host is imminent (Iyengar 2008). Kleptoparasites do not injure the hosts in any direct way other than through loss of nourishment (Iyengar 2008). Historically, most kleptoparasite studies have focused on birds, and reports of fish involved in kleptoparasitism are rare. One of the most detailed studies of kleptoparasitic fish involves the subtropical reef fish, *Kyphosus cornelii* which defend algal gardens. When algal gardens are frondose and difficult to defend, fish lower the time invested in defending their own gardens and instead kleptoparasitized the gardens of conspecifics (Hamilton & Dill 2003). Among freshwater fishes, the Northern pike (*Esox lucius*) changes feeding behaviour and chooses smaller prey than predicted by energy budgets to lower the risk of intraspecific kleptoparasitism (Nilsson & Bronmark 1999). Some fish steal food from non-piscine species, like cichlids in West Africa that opportunistically steal food from crabs (Dominey & Snyder 1988). Undoubtedly, many more aquatic kleptoparasitic interactions occur, but sightings of them are infrequent, likely due to the difficulty of observing natural interactions underwater (Iyengar 2008). We did not find previous studies on

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kleptoparasitism among Neotropical fish. Here we report on kleptoparasitism involving an Amazonian fruit-eating species. *Brycon falcatus* (Bryconidae), is a member of an iconic genus of broadly distributed frugivorous fishes (from Mexico to the Rio de la Plata Basin, Argentina; Lima 2017), represented by medium- and large-sized species (16–70 cm SL) that in addition to fruits and flowers, also eat insects, other fish, and even small vertebrates (Goulding 1980; Lima 2017). Multiple *Brycon* species disperse seeds of diverse riparian plant species (Banack *et al.* 2002; Correa *et al.* 2015; Gomiero et al. 2008; Horn 1997; Reys *et al.* 2009). *Brycon* species typically undergo a dietary shift during ontogeny; younger fish are mostly carnivorous, while older fish are predominantly frugivorous (Drewe et al. 2004). Recent studies, however, demonstrated that even young individuals can act as seed dispersers when ingesting fruits and swallowing intact seeds (Santos et al. 2020). *Brycon falcatus* is likely the most important seed disperser in the middle stretch of the Teles Pires River, in Southern Amazonia, given that it consumes more fruit than other fish species therein (Matos *et al.* 2016; Santos *et al.* 2020; L.N. Carvalho, unpubl. data 2021).

While conducting daylight underwater observations (by snorkelling) of frugivorous fish behaviour in a stream of the Teles Pires River basin, Mato Grosso state, Brazil (−11.63405, −55.68031), focal observations of feeding were carried out in the month of August 2018, during the dry season at a water depth of 1 m. Individuals were observed along a 100 m stream reach. Each focal observation lasted 10 min and was carried out between 0800 and 1500 h (N = 32 focal observations total). We observed unusual interactions between a school of matrinxã (*Brycon falcatus*) and an individual of threespot leporinus (*Leporinus friderici*) (Bloch, 1794). Eight juvenile individuals of matrinxã (≈14 cm; maximum total length is ≈44 cm SL; Lima 2017) were observed at half water following an adult threespot leporinus (≈23 cm; maximum total length is 40 cm, www.FishBase.org) foraging on the substrate at a 45° angle. The threespot leporinus found a small fruit hidden between the leaf litter and snapped it up, changing its posture horizontally and rising slightly in the water column. Suddenly, a matrinxã individual from the school swam fast towards the threespot leporinus and steeled the fruit from its mouth (Fig. 1), *Brycon falcatus* usually lives between the middle of the water column to the surface and does not occupy the bottom of rivers and streams while *Leporinus friderici* occupies the lower portion of the water column and it actively forages close to the substrate (see Video S1). This suggests that stealing food from a benthic feeder is an opportunistic ecological interaction that allows *B. falcatus* to take advantage of scarce resources in the period of food scarcity (i.e. low fruit availability). This alternative technique of capturing fruits may be advantageous (*i.e.* save energy expenditures related to searching) for young matrinxã who do not eat fruit as frequently as adults.

There are limited underwater observations of fish frugivory. For instance, while snorkelling in the Pantanal wetland (Brazil), Costa-Pereira *et al.* (2011) observed multiple fish species consuming fruits. The congeneric *B. hilarii* formed small shoals of three to nine individuals, actively swimming around *Banara arguta* (Salicaceae) trees. They captured the fruit at the surface or in the water column, mostly whole. Adult *Leporinus friderici* manipulated the fruit in the mouth before swallowing it, while young individuals nibbled on fruit tearing small pieces out, but both adult and juvenile *Leporinus* captured fruits from the floodplain substrate. The behaviours observed by Costa-Pereira *et al.* (2011) corroborate our observation that the species involved in our study use a shared resource at different depths. Because *L. friderici* manipulates the fruit in its mouth before swallowing, it makes fruits visible to *B. falcatus*, giving it time to react and invest in the 'theft' of the fruit from other fish's mouth. *Leporinus friderici* servers as a nuclear–facilitator species capturing food items that were made available to follower species in streams of the central-west region of Brazil (Teresa *et al.* 2011; Sabino *et al.* 2016). And it also plays an ecosystem engineering role by continuously disturbing the benthos while feeding on sunken fruits and seeds (Boujard *et al.* 1991). A study about positive co-occurrence between savannah fishes supported the hypothesis that the feeding activity of *L. friderici* facilitates the co-occurrence of its congeneric *L. octomaculatus* by feeding association (Arnhold *et al.* 2019). The reaction of *L. friderici* to *B. falcatus* seems like one of the strategies used for dealing with kleptoparasites, which do not pose any threat to kleptoparasites and appear to have no defence against kleptoparasitic activities, tolerating theft (Barnard 1984).

*Brycon* is a versatile frugivore and findings from previous research show remarkable behaviours related to fruit consumption and a degree of specialization in fruit consumption. Large adults of *B. guatemalensis* increase their fruit-catching success by positioning themselves downstream from trees releasing ripe figs to compensate for drift (Krupczynski & Schuster 2008). A feeding experiment with *B. cephalus*, to assess seed predation by fish on dehiscent seeds, observed that *B. cephalus* rapidly swallowed whole seeds, then later regurgitated them, and reingested and processed one by one. The study highlighted remarkable precision in the oral manipulation of seeds where fish were able to remove the seed coat of individual seeds and masticate the endocarp (Carvalho *et al.* 2021).


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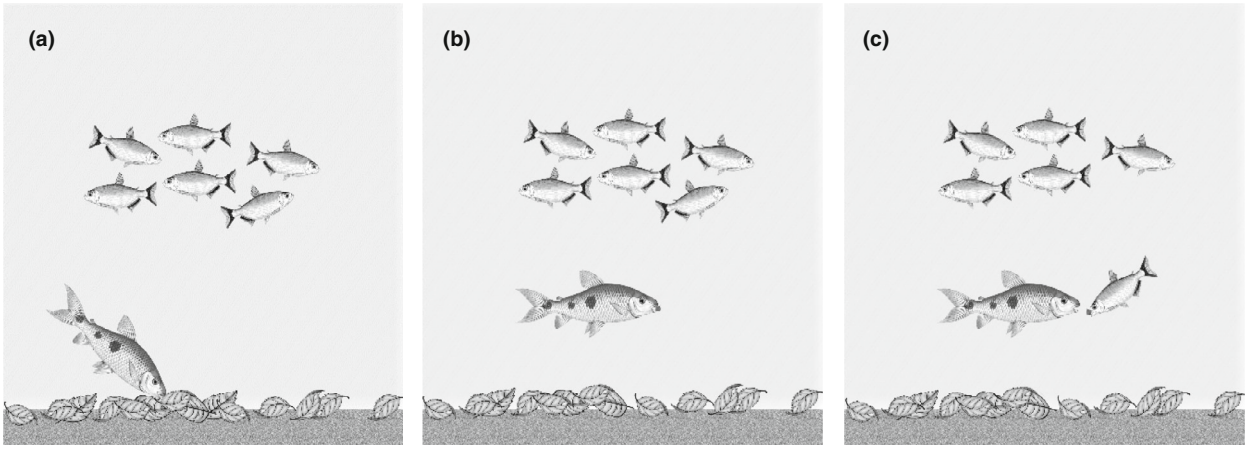


**Fig. 1.** Opportunistic feeding interaction between a school of juvenile matrinxã, (*Brycon falcatus*) and an individual of threespot leporinus (*Leporinus friderici*) observed in a stream in southern Amazonia. (a). A threespot leporinus individual inspects the substrate. (b). Threespot leporinus found and snapped up an unripe fruit of *Bocageopsis mattogrossensis* (Annonaceae) (c). The young matrinxã quickly goes to the threespot leporinus and steals the fruit from its mouth and ingests the fruit.

The observed kleptophagy interaction is not rare as it was witnessed at other times in the same environment and in other streams within the basin. Our observations reflect the trophic plasticity and foraging opportunism characteristic of most tropical freshwater fish. We believe that the hydrological period in which the observations were made, when a few trees were bearing fruit, can favour the robbery of fruits by *B. falcatus*. The importance of fruits and seeds in the diet of young individuals of *B. falcatus* needs to be further investigated. Preliminary observations show fruit consumption by some juvenile fishes (SL 7.9–15.6 cm, $N = 13$) during the dry season (41.6% average volume proportion of stomach contents, SD = 29.3 and range = 1%–99% of fruits and seeds; L. N. Carvalho, unpublished data, 2021).

We encourage future studies to investigate the feeding behaviour of young frugivorous fish both in underwater and in manipulation experiments. There are very few studies on the behaviour of frugivorous fish in nature. This is partly because the fruiting period occurs mainly in the rainy season when the water becomes more turbid. An alternative is to do remote filming which will help to reduce the negative effect of the observer on water turbidity. The use of remote aquatic filming can advance studies of fish frugivory by placing cameras underneath fruiting trees to record feeding behaviour in nature, and interactions with other aquatic species. Additionally, quantitative studies of the costs and benefits of foraging interactions in fishes are currently absent.

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## AUTHOR CONTRIBUTIONS

**Lucelia Nobre Carvalho:** Conceptualization (equal); data curation (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); writing – original draft (lead); writing – review and editing (lead). **Sandra Bibiana Correa:** Conceptualization (supporting); data curation (supporting); validation (equal); writing – review and editing (supporting). **João Batista dos Santos Júnior:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); validation (equal); visualization (equal).

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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## SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

**Figure S1.** The sequence images from stream bank showed an individual of threespot leporinus (*Leporinus friderici*) moving from the bottom of the stream to the upper stratum of the water column occupied by the matrinxã (*Brycon falcatus*).

**Video S1.** Video recording a school of *B. falcatus* and an individual of *L. friderici* at the bottom of the stream in Southern Amazon, Brazil.

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