

Uncovering mechanisms of seed predation by fish

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Abstract

Our experiment revealed unexpected behavioral strategies involved in seed predation of *Mabea fistulifera* by fish (*Brycon cephalus*), including temporal storage of seeds in the stomach followed by regurgitation and reingestion of individual seeds. Larger fish were faster at removing the seed coat and exposing the endosperm, due to precise oral manipulation of seeds.

Abstract in Portuguese is available with online material

KEYWORDS

Brycon cephalus, dyszoochory, feeding behavior, oral manipulation, plant–animal interaction

1 | INTRODUCTION

Frugivore–fruit interactions are ubiquitous in tropical ecosystems where fruits represent a key food resource to animals and in turn animals disperse seeds. However, frugivorous mammals and generalist birds often play dual roles as seed dispersers and predators (Guerrero & Tye, 2009; Norconk et al., 1998). Such mutualistic and antagonistic interactions enhance recruitment and shape the composition of plant communities (Caughlin et al., 2014). In tropical wetlands, ≈ 150 fish species consume fruits (Horn et al., 2011) and contribute to both seed dispersal and predation (Correa et al., 2015; Gottsberger, 1978; Goulding, 1980; Reys et al., 2009).

Frugivorous fish in the genus *Brycon* (Bryconidae) are important seed dispersers of riparian and wetland plants (Correa, Araújo, et al.,

2015; Horn, 1997; Reys et al., 2009; Santos et al., 2020). *Brycon*, however, have a great ability to crush food due to multicuspid oral dentition (Lima, 2017). Such dentition is shared with other characiform fishes and makes them potential seed predators (Goulding, 1980). Here, we investigated the seed predation behavior of *Brycon cephalus* under a controlled environment.

Our experiment was conducted at the Laboratório de Ictiologia Tropical (LIT) of the Federal University of Mato Grosso, Brazil, for 12 days during July 2019. *Brycon cephalus* individuals (range: $N = 8$, 10.1–28.0 cm standard length measured from the tip of the snout to the base of the caudal fin; the maximum size recorded for the species is 45 cm total length measured from the tip of the snout to the end of the caudal fin; www.FishBase.org Froese et al., 2021) were retrieved from a nearby fish-farm. Individual fish were kept in 61-liter

aquaria, equipped with a water recirculation system, and water quality was monitored daily (mean \pm SD temperature: 28.5 ± 0.6 °C, pH: 7.03 ± 0.04 , and dissolved oxygen 5.78 ± 0.42 mg/L).

Aquaria were shielded by a black screen with a small aperture for the investigator, to reduce the impact of the viewer on the fish's behavior (Sabino & Carvalho, 2008), and equipped with remotely operated Go Pro cameras positioned above and on the sides of the tanks. During the experiment, focal fish were fed daily at 0800 h with individual seeds (one by one) extracted from ripe fruits of *Mabea fistulifera* (mean \pm SD seed width: 6.04 ± 0.77 mm, length: 8.48 ± 0.22 mm, weight: 0.5 ± 0.4 g) and later, at 1700 h, with extruded commercial feed made up of 32% protein to fulfill dietary requirements of the species. *Mabea fistulifera* Mart. (Euphorbiaceae) is a pioneer tree commonly found in riparian forests. The fruit is a dry, subglobose capsule (length: ≈ 15.5 – 19.0 mm), whose epimesocarp cracks in explosive dehiscence and ballistically disperses seeds (three seeds per capsule; Vieira, 1991). Our experiment mimics the natural conditions under which fish encounter seeds on the water following ballistic dispersal by feeding individual seeds to fish. Seed ingestion occurred *ad libitum* (free feeding, Altmann, 1974), and we considered as satiated a fish that did not show interest in a seed after 15 min of it being offered. At that point, we removed nonconsumed seeds. Observations during a pilot trial revealed that *B. cephalus* regurgitate seeds. We sacrificed fish during the pilot trial as soon as they finished seed ingestion and confirmed that they stored seeds in the stomach before regurgitation. Thus, we searched the tanks for regurgitated seeds at 15-min intervals, over 4 hrs following the last feeding event. After 4 hrs, visual surveys were extended to 30-min intervals until the last regurgitated seed was observed (i.e., the fish regurgitated all the ingested seeds). We repeated the experiment four times per individual, with a 24 h period between trials.

We assessed four metrics of seed predation, including the (1) number of ingested seeds (NIS); (2) time to regurgitation of the first seed (TRFS), defined as the period between the ingestion of the last seed, without the fish having any food in their mouth, until the beginning of the oral manipulation activity; (3) time to regurgitation of the last seed (TRLS), defined as the period between the ingestion of the last seed, without the fish having any food in the mouth, until the time when oral manipulation activity of the last

regurgitated seed was observed; and (4) total handling time (THT), defined as the average time to chew all regurgitated seed that were reingested. We analyzed whether fish size (measured as standard length) influences these metrics of seed predation via separated mixed effects regression models, where fish size was the predictor variable and fish identity was included as a random effect to account for the lack of independence between multiple trials ($N = 4$) per fish. Prior to analysis, we transformed NIS via square root to enhance homogeneity of the variance. Regression models were implemented in R (version 3.6.3), package lme4 (Bates et al., 2015); significance of the fixed factor was assessed with Wald's test, package car (Fox & Weisberg, 2019); and plots were created in package ggplot2 (Wickham, 2016).

Direct observations and video revealed that *B. cephalus* readily swallowed *M. fistulifera* seeds without chewing and ingested intact seeds until satiety. Once the last seed was ingested, fish stopped mandibular movements and did not keep any food in their oral cavity. After a period of inactivity (TRFS: 4–40 min; Table 1), mandibular movements returned with the regurgitation of individual intact seeds. Each regurgitated seed was then reingested, followed by coordinated chewing movements that yielded precise removal of the seed coat, so as not to leave endosperm adhered to the discarded shells, and culminating in swallowing of masticated endosperm. All observed fish, independent of body size, performed these ingestion, regurgitation, reingestion, and oral handling behaviors. Of the 2,201 seeds offered to eight fish individuals, only two whole seeds were recovered, one unharmed and the other with a slight damage ($\approx 5\%$ of the seed surface), those seeds had previously been ingested by some of the smallest fish in our sample (11.8 and 12.3 cm SL, respectively).

Fish ingested a variable number of seeds (NIS: 8.2–146.5 seeds average; Table 1). However, larger fish ingested more seeds (NIS: Wald's test $\chi^2 = 226.51$, $p < 0.0001$, Figure 1a) and took a longer period to regurgitate all seeds (TRLS: Wald's test $\chi^2 = 39.21$, $p < 0.0001$, Figure 1b). The maximum duration of regurgitation was 2 h 03 min (Table 1). In contrast, time to the onset of regurgitation was independent of body size (TRFS: Wald's test $\chi^2 = 0.02$, $p = 0.897$; 0.5–38.5 min average, Table 1). Interestingly, larger fish processed seeds more rapidly (Table 1); the average total handling

TABLE 1 Assessed metrics of seed predation of *Mabea fistulifera* by characid fish *Brycon cephalus* in controlled laboratory experiments. Abbreviations: standard length (SL), total length (TL), number of ingested seeds (NIS), time to regurgitation of the first seed (TRFS), time to regurgitation of the last seed (TRLS), and total handling time (THT) in minutes. Values represent mean (and range in parenthesis)

Fish	Weight (g)	SL and (TL) (cm)	NIS	TRFS (min)	TRLS (min)	THT (min)
1	35.5	12.3 (14.4)	34.5 (7–127)	15.2 (13–16)	81.7 (72–98)	139.4 (93–191)
2	16.9	10.0 (11.6)	29 (7–100)	13.5 (13–15)	57.7 (37–79)	93.2 (70–105)
3	104.7	17.8 (21.0)	37.1 (5–183)	0.5 (4–8)	69.7 (52–94)	83.7 (67–105)
4	34.8	11.8 (14.5)	13.2 (8–16)	18.7 (18–21)	48.5 (44–54)	132.0 (126–150)
5	168.6	20.0 (23.0)	48.5 (36–66)	10.7 (7–12)	118.5 (98–148)	91.5 (66–108)
6	447.8	28.0 (32.0)	146.5 (100–183)	28.7 (26–33)	172.5 (149–203)	59.4 (35–83)
7	26.5	11.3 (13.0)	8.2 (8–9)	38.5 (36–40)	65.5 (54–77)	125.6 (100–150)
8	25.5	11.8 (13.0)	11 (5–13)	16.0 (14–19)	49.2 (43–63)	136.5 (132–144)

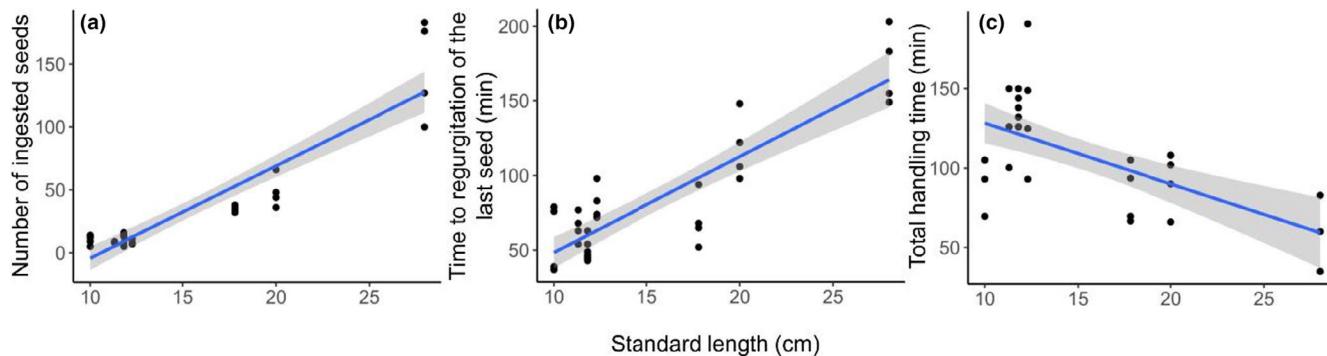


FIGURE 1 Relationship between body size measured as standard length (cm) of individuals of *Brycon cephalus* and a) the number of ingested seeds (NIS); b) time to regurgitation of the last seed (TRLS); and c) total handling time (THT). TRLS and THT are given in minutes. Larger individuals of *B. cephalus* ingested more seeds of *Mabea fistulifera* and took longer times to all regurgitate seeds, whereas the mean of total handling time decreased with fish size

time decreased with fish size (THT: Wald's test $X^2 = 10.75$, $p = 0.001$, Figure 1c), which may suggest that as fish grow, they gain experience processing seeds in their mouths.

For decades, characiform fishes in tropical wetlands have been regarded as seed predators given their strong dentition (Gottsberger, 1978). Recent quantitative analyses of frugivorous fish diets, however, demonstrated that, in general, fish serve both as seed dispersers and seed predators (Anderson et al., 2009; Correa, Costa-Pereira, et al., 2015; Lucas, 2008; Reys et al., 2009). However, the mechanisms by which fish achieve efficient seed predation remain largely unknown (Boedeltje et al., 2015). Our study reveals unexpected behavioral strategies involved in seed predation by fish, including 1) temporal storage of seeds in the stomach followed by regurgitation of individual seeds, 2) the ability to remove the seed coat and expose the endosperm due to a remarkable precision in their oral manipulation of seeds, and 3) the influence of fish size on seed predation rate and handling time.

During our experiments, fish always swallowed entire seeds intact reaching satiation, stored seeds in their stomach, and then later regurgitated one seed at a time within a few hours. By engaging in temporal storage of seeds in the stomach, fish likely optimize food intake and minimize competition with conspecifics within schools and with other species within frugivorous–fish networks (Correa et al., 2016). Moreover, temporal storage of seeds in the stomach could be a strategy of fish to reduce seed loss, due to water current, and ensure a later meal while optimizing energy gain (Krebs & Davies, 1993). Other frugivorous *Brycon* species display remarkable behaviors to optimize fruit consumption in fast moving waters. Large adults of *B. guatemalensis* optimize fruit-catching success by positioning themselves downstream from trees releasing ripe figs to compensate for drift (Krupczynski & Schuster, 2008). To our knowledge, this is the first record of regurgitation behavior in freshwater fish associated with a feeding activity. In marine fish, regurgitation varies among species and increases with sampling depth among species with closed gas bladders (Bowman, 1986; Daan, 1973). In freshwater fish, regurgitation is used as an escape strategy when

fish encounter a threat (Zhao et al., 2020) or induced by capture methods (i.e., gill nets) among predatory fishes (Marçal-Simabuku & Carvalho Peret, 2002; Treasurer, 1988).

Seed predation of *Mabea* sp. seeds by Amazonian fish was previously reported in the wild (Goulding, 1980). However, it remains to be evaluated whether temporal storage of seeds in the stomach and regurgitation behaviors are widespread and whether these behaviors occur when fish consume other fruit types. In the Pantanal wetland, *Piaractus mesopotamicus* (23 to 57 cm SL), consume large amounts of *Sapium obovatum* (Euphorbeaceae) seeds and often masticate them (seed predation frequency: 93%, seed dispersal frequency: 45%, $N = 110$ fish; S.B. Correa, unpublished results). This tree produces dehiscent fruits with a single small seed (width: 5.24 ± 0.13 mm; length: 8.51 ± 0.29 mm; wet weight: 0.07 ± 0.01 g) that have a tiny fleshy aril and are dispersed mechanically by explosion. *P. mesopotamicus* is the largest frugivorous fish (75 cm, maximum total length) in the Pantanal and it is unlikely that such large fish will masticate small seeds, one by one, while keeping-up with the river's current. Based on our results and field observations, we argue that temporal storage of seeds in the stomach followed by regurgitation and reingestion of masticated seeds can optimize the energy gained from the consumption of small grains by fish. Further experiments need to assess these behaviors in other fish species and with fruits of different types and nutrient composition.

The observed seed predation behavior by *B. cephalus* may be linked to *M. fistulifera* seed traits (e.g., lack of a fleshy pulp, small seed size, a relatively soft seed coat, and high nutrient content) (Boedeltje et al., 2015). In Amazonian wetlands, seed predation rates by three *Brycon* species were higher for seeds without pulp relative to those of fleshy fruits (Correa, Costa-Pereira, et al., 2015). This suggest that seeds of fleshy fruits are more likely to be dispersed by fish than those of nonfleshy fruits. Fleshy tissues have high carbohydrate and/or lipid contents and as such provide energy for fish (Correa & Winemiller, 2018), without the need to masticate seeds. In addition, the fleshy fruit helps fruits staying longer afloat and available to fish (Correa et al., 2018). In a lowland's river in Central Brazil, *B. hilarii* triturated all ingested soft seeds >10 mm long (Reys et al., 2009). Seed

coat removal may not only facilitate mastication of the endosperm but likely increases the efficiency of digestive enzymes. Nutritional composition can influence food selection by animals (Ruohonen et al., 2007), although there is limited knowledge of nutrient-based fruit selection among frugivorous fish. *M. fistulifera* seeds are oil rich ($\approx 35\text{--}40\%$ dry weight; Silveira-Neta et al., 2012). Seeds of the congener *M. caudata* are oil rich (23.8%) and protein rich (9.6% crude protein) (Silva et al., 2003). Thus, seed mastication gives fish access to energy and protein stored in the seed endocarp (Waldhoff et al., 1996). In Neotropical floodplains, carbohydrates and lipids from fruits constitute building blocks for adipose reserves to be later converted into reproductive tissues of the fish (Junk, 1985).

Our findings complement recent evidence demonstrating the influence of fish body size on seed dispersal effectiveness (Anderson et al., 2009; Correa, Araújo, et al., 2015; Galetti et al., 2008). As with seed dispersal, the greater number of seeds ingested by larger fish can be explained by the greater storage capacity of the gastrointestinal tract of larger animals (Galetti et al., 2008). Among characiform fishes, the proportion of destroyed seeds decreases with body size (Correa, Costa-Pereira, et al., 2015; Kubitzki & Ziburski, 1994). Most fruits reported in those studies have fleshy fruits in which case it makes sense, from an energetic point of view, that large fish swallow large chunks of fruits and thereby many intact seeds. *Mabea*, however, have dry fruits and their seeds are released by explosion. Regardless of size, all fish in our experiment regurgitated and masticated reingested seeds. Larger fish, however, processed seeds faster, including removing the seed coat and masticating and swallowing the endosperm. These findings suggest that seed predation efficiency increases with fish size. In fish, mouth gape increases with body length (Correa, Araújo, et al., 2015). Thus, a bigger mouth likely is correlated with broader or denser dentition and greater biting force that may speed-up food processing.

Finally, even though most seeds in our experiment were predated upon by *B. cephalus* (99.9%), two seeds escaped intact, which suggests the likelihood of long-distance dispersal as fish transport seeds in their stomachs. Given the low proportion of dispersed seeds, our study demonstrates that *B. cephalus* engages in dyszoochory, the dispersal of seeds by granivores that accidentally lose them during transport (Vittoz & Engler, 2007). The dual seed dispersal and seed predation roles played by some frugivorous animals is not uncommon among fish (Anderson et al., 2009; Correa, Costa-Pereira, et al., 2015; Lucas, 2008; Reys et al., 2009). Despite the limited sample size (8 individuals, 12 days), the observed consistent regurgitation of all ingested seeds (2,201) and oral seed handling of reingested seeds (2,199) provides strong support for a previously undocumented mechanism explaining the behavioral adaptations of fish to achieve seed predation. Although antagonistic, seed predation is a key ecological service contributed by vertebrates which directly influences plant regeneration and diversity (Pereira et al., 2014). The conservation of frugivorous fishes, and their various ecological roles, is paramount to maintaining ecological functions in dynamic and diverse wetland ecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.np5hqbztt> (Carvalho et al., 2021).

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