



No choice is not a choice: food selectivity occurs in different ontogenetic stages of *Phasmahyla jandaia* (Anura: Phyllomedusidae)

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Abstract. Amphibians play important roles in aquatic habitats and also constitute important elements connecting aquatic and terrestrial food webs. The majority of tadpoles consume a large amount of aquatic resources before they metamorphose and move to the terrestrial habitat. However, the diets and specially the foraging behavior of tadpoles are largely unknown. Some studies have been showing that they can respond to factors as varied as tadpole ecomorphotype, seasonality, habitat structure, and tadpole developmental stage. Here we studied the diet of the morphologically specialized neustonic tadpoles of *Phasmahyla jandaia* in three different developmental stages to test for ontogenetic differences in their diet and food preferences. We found tadpoles in all stages to feed on food items available at the water surface as expected based on their morphological features, leading to great niche overlap among them. However, tadpoles in different stages still showed different electivity values related to consumed food items, showing active food choice, even within ecomorphotype restrictions. Our results corroborate the complexity of tadpole foraging behavior and its influencing factors, advocating for more attention to these aquatic consumers.

Key words. Amphibia, *Phasmahyla jandaia*, tadpole diet, tadpole ecomorphotype, optimum foraging.

Introduction

Anurans are important invertebrate predators and are responsible for a relevant amount of energy transfer between aquatic and terrestrial habitats due to the biphasic life cycle of most species (ALFORD 1999, DUTRA & CALLISTO 2005). In this context, the larval phase of most anurans is extremely important, as they consume large amounts of aquatic organisms (ALTIG et al. 2007, SCHIESARI et al. 2009) and experience extensive growth and development in bodies of water until they become terrestrial adults. Besides, tadpoles experience very high predation rates, an additional contribution to aquatic food webs (WELLS 2007). However, the diets of tadpoles are understudied, and even their trophic roles are often difficult to establish (SCHIESARI et al. 2009).

Diet is an important aspect of a species natural history, as consumed items provide information on species interactions within the food web, whose comprehension is fundamental for biodiversity conservation (ALTIG et al. 2007, MONTAÑA et al. 2019), as well as for individual species conservation itself (GELWICK & MATTHEWS 2006, CHIPPS &

GARVEY 2007). Tadpoles have been shown to have diversified diets and choose their food items under the influence of used microhabitats, seasonality, and developmental stage (KLOH et al. 2018, 2019). Contrary to previous pre-conceptions, they can also actively feed on preferential, more nutritive items, even when it requires foraging at microhabitats not normally occupied by them (KLOH et al. 2021).

Tadpole ecomorphotypes have been defined based on morphological features (e.g., oral disc position and direction, body shape) that favor feeding on specific microhabitats (e.g., bottom vs. water column; ALTIG & JOHNSTON 1989). Tadpoles with different morphologies are thus expected to have different diets (CANDIOTI 2007), that they acquire in different microhabitats (KLOH et al. 2019). However, we recently demonstrated that this rule has exceptions, as the benthic tadpoles of *Scinax machadoi* (BOKERMANN & SAZIMA, 1973) actively swim to the water surface to consume large amounts of pollen (KLOH et al. 2021). Pollen has been shown to be an important source of proteins and lipids for pollinators (HUANG 2012, RUEDENAUER et al. 2019) and could therefore be a nutritive food for other ani-

mals as well (ROULSTON & CANE 2000), what would justify the behavior of *S. machadoi* tadpoles according to the optimal foraging theory (MACARTHUR & PIANKA 1966, KLOH et al. 2021). This shows that the behavior of tadpoles can be complex and ultimately influence energy transfer outcomes both within aquatic food webs and between aquatic and terrestrial species. Changes in diet composition could occur depending on the ontogenetic stage (KLOH et al. 2019) and the acquired nutrients are likely to influence growth and metamorphosis (BOWEN et al. 1995, KUPFERBERG 1997).

Considering the complexity of factors influencing tadpole diets, much of which remains to be studied, we chose to investigate the composition of the diet of a species with very specialized morphology and its variation among different developmental stages throughout the tadpole phase. We expected that tadpole morphology would influence diet composition and that diet composition would change with developmental stage, reflecting possible varying nutrient needs along tadpole growth/development. We have previously shown that tadpoles with more generalized ecomorphotypes can diversify their diets through behavioral plasticity (KLOH et al. 2021). Here we also intended to test whether this rule would apply to species with more specialized ecomorphotypes such as the neustonic *Phasmahyla jandaia* tadpole.

Materials and methods

Study system and sampling

We collected tadpoles of *Phasmahyla jandaia* in a permanent stream (19°15'24.25" S, 43°32'49.64" W – 1374 m a.s.l.) bordered by riparian forest and close to a two-lane paved road (MG-010) with constant flow of trucks, buses, and cars. The region has a marked rainy season from October to March and a dry season from April to September. Mean monthly rainfall varies between 1460 and 2490 mm, mean temperatures range from 13 to 29°C (VIVEROS 2010).

The genus *Phasmahyla* contains only eight species, *P. cochranae* (BOKERMANN, 1966), *P. cruzi* CARVALHO-E-SILVA, SILVA & CARVALHO-E-SILVA, 2009, *P. exilis* (CRUZ, 1980), *P. guttata* (A. LUTZ, 1924), *P. jandaia* (BOKERMANN & SAZIMA, 1978), *P. lisbella* PEREIRA, ROCHA, FOLLY, SILVA & SANTANA, 2018, *P. spectabilis* CRUZ, FEIO & NASCIMENTO, 2008, and *P. timbo* CRUZ, NAPOLI & FONSECA, 2008, all of them typical from Atlantic Forest formations or remnants (LEITE et al. 2008, ETEROVICK et al. 2020). The tadpoles of all species have a neustonic ecomorphotype (sensu ALTIG & JOHNSTON 1989). Their umbelliform oral disc is projected towards the water surface, from where they seem to filter food particles (LEITE et al. 2008, COSTA & CARVALHO-E-SILVA 2008).

At the Serra do Cipó, adult males of *P. jandaia* call at the onset of the rainy season (October–December) from the vegetation (ETEROVICK et al. 2020). The eggs are laid on leaves hanging over the water, so that tadpoles fall directly into the stream when they hatch (ETEROVICK et al. 2020, COSTA & CARVALHO-E-SILVA 2008). The tadpoles show

tones of yellow and grey and usually aggregate in groups of 10 to 15 individuals (LEITE et al. 2008, COSTA & CARVALHO-E-SILVA 2008) (Fig. 1). These groups are mixed, including individuals from different clutches, what is evidenced by their diversified developmental stages (J. S. Kloh, pers. obs.).

We collected a total of 60 tadpoles of *P. jandaia* from mixed groups, 20 at each of three developmental stages (stages 25, 30 and 40 sensu GOSNER 1960). Tadpoles were identified based on the original description (BOKERMANN & SAZIMA 1978) and this is the only species of *Phasmahyla* at the study site, preventing misidentifications. All samplings were conducted by two persons in three occasions: 14 October and 11 December 2018, 24 March 2019. We captured tadpoles with dipnets throughout an extension of 150 m along the stream, with tadpoles at different stages being collected from the same groups in order to randomize the effect of specific groups and locations throughout these 150 m stream section. We also collected tadpoles from the three different stages at each sampling occasion, to standardize any possible temporal effect in diet composition (Table 1). Tadpoles were immediately euthanized with 10% xylocaine and preserved in 10% formalin to retain all gut contents (see KLOH et al. 2019). All tadpoles were meas-

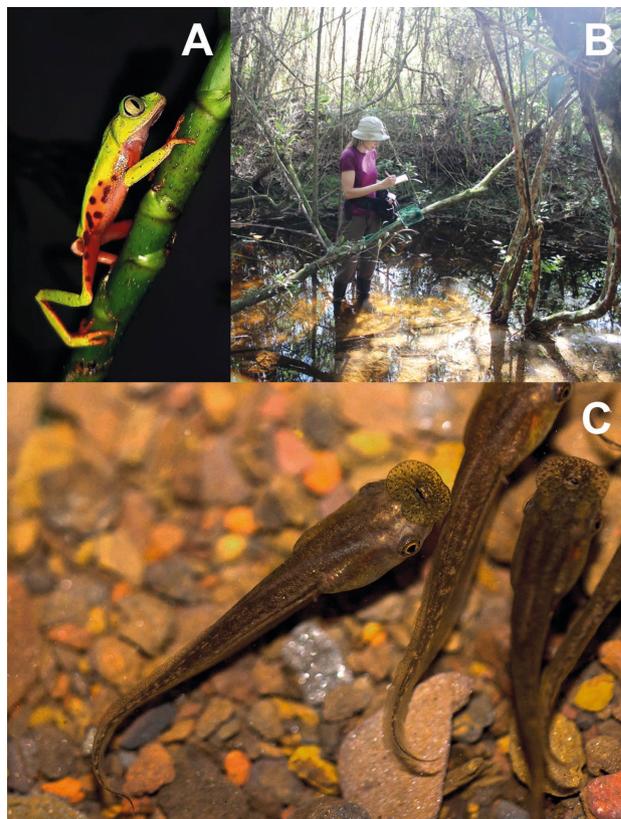


Figure 1. Adult male (A), natural habitat (B) and tadpoles (C) of *Phasmahyla jandaia* at the Serra do Cipó, Southeastern Brazil. Habitat and tadpole pictures (B and C) by ÍTALO M. MARTINS and BÁRBARA ZAIDAN, respectively.

Table 1. Mean (and standard deviation) of *Phasmahyla jandaia* tadpole measurements according to studied developmental stages. TL = total length; BL = body length; BH = body height; TL = tail length; TH = tail height; ODW = oral disc width; ODH = oral disc height; GL = gut length. Measurements follow DUELLMAN (1970). Sampling dates (1, 2, 3) correspond to 14 October and 11 December 2018, 24 March 2019, respectively.

Stage	TL	BL	BH	TL	TH	ODW	ODH	GL	Sample size		
									1	2	3
25	25.25 (0.82)	9.55 (0.34)	3.23 (0.32)	17.05 (0.39)	4.78 (0.53)	3.38 (0.28)	1.53 (0.22)	114.55 (4.22)	7	9	4
30	31.86 (1.94)	12.87 (0.36)	5.7 (0.37)	22.15 (0.46)	8.49 (0.28)	4.98 (0.33)	3.11 (0.17)	126.8 (5.08)	6	6	8
40	47.28 (1.21)	15.92 (0.23)	6.72 (0.27)	24.94 (0.47)	9.92 (0.27)	6.93 (0.21)	4.13 (0.13)	148.5 (6.21)	6	7	7

ured and had their developmental stages confirmed under a stereomicroscope in laboratory (Table 1). After that we removed tadpole guts and separated the first $\frac{1}{3}$ of their length that corresponds to the manicoto and initial gut section (sensu PRYOR & BJORNDALE 2005), as food items in this portion of the gut are still little digested and can be better identified (KLOH et al. 2018). We diluted the contents of this gut portion in 1 ml distilled water and quantified included food items in a Sedgewick rafter counting chamber under an optic microscope (Olympus CX40) under 400 × magnification (as in KLOH et al. 2019).

In order to estimate food availability for tadpoles, we collected three water samples equally distributed (every 50 m) along the 150 m sampled stream section at each of the three sampling occasions. We moved a 300 ml flask with a 4.8 cm opening perpendicularly from the stream surface to the bottom and back, touching the sediment (see Fig. 2), in order to include food items available throughout the water column, as well as on the stream bottom. We moved the water to another container and added 50 ml of 10% formalin to preserve food items for posterior identification under a microscope. In the laboratory, we stirred the

container to homogenize the solution and used 1 ml of it in a Sedgewick rafter counting chamber for quantification of available potential food items as we did for gut contents.

Statistical analyses

We tested whether developmental stages 25, 30, and 40 had different diets using a discriminant analyses with the packages MASS (VENABLES & RIPLEY 2002), tidyverse (WICKHAM et al. 2019), and caret (KUHN 2020) for R (R Core Team 2016). We also calculated niche overlap between pairs of developmental stages and compared mean niche overlap to randomly expected values based on availability of the food items in the environment using EcoSim 7.0 (GOTELLI & ENTSMINGER 2001). We conducted 1000 simulations of random niche overlap values with the algorithm RA3 (zero values reshuffled and niche breadth retained, PIANKA 1973). We calculated, for each developmental stage, electivity indexes for each consumed food item based on Jacobs (1974).

Results

Tadpoles of *Phasmahyla jandaia* grew along the developmental stages considered, what was followed by a concomitant increase in gut length (Table 1). They hatch in stage 25, in stage 30 their posterior members are being formed and in stage 40 they are completely formed and the anterior members are about to come out.

The diets of tadpoles in all developmental stages considered were in accordance with the neustonic ecomorphotype, as tadpoles did not include periphytic algae in their diets, although these autotrophs were largely available in the environment (Fig. 3). In water samples we identified cyanobacteria, three classes of algae (belonging to three Phyla), a heterotrophic protist (testate amoeba), pteridophyte spores and pollen. We classified these items as filamentous and unicellular *Bacillariophyceae*, filamentous and unicellular *Zygnematophyceae*, *Euglenophyceae*, *Cyanophyceae*, testate amoeba, spores from Pteridophyta, and pollen. Items ingested by tadpoles included only *Euglenophyceae*, testate amoeba, spores from Pteridophyta, and pollen.

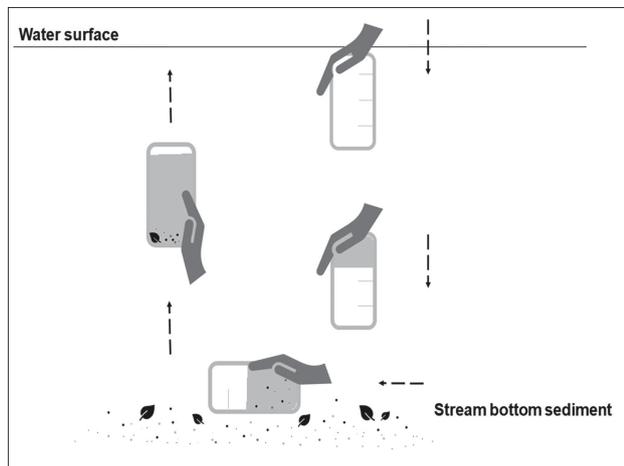


Figure 2. Water sampling procedure for estimation of food availability for tadpoles. The flask had 300 ml capacity and an opening width of 4.8 cm.

Table 2. Discriminant analyses results for the composition of the diet of *Phasmahyla jandaia* tadpoles in stages 25, 30, and 40 (sensu GOSNER, 1960). Pt = Proportion of trace; Pp = Prior probabilities.

Consumed food items	Pollen	Spores	Testate amoeba	<i>Euglena</i>
Group means				
Stage 25 (Pp = 33.3%)	48	4	15	7
Stage 30 (Pp = 33.3%)	32	4	26	12
Stage 40 (Pp = 33.3%)	123	4	47	20
Coefficients of linear discriminants				
LD1 (Pt = 0.9524)	-0.0157	-0.0213	-0.0038	-0.0200
LD2 (Pt = 0.0476)	0.0075	-0.0125	-0.0084	-0.0467

The different developmental stages of *Phasmahyla jandaia* tadpoles showed subtle variations in their diets, which were not enough to classify tadpoles correctly to developmental stage based on what they ate (chances of correct classification were only 33% for any stage; Table 2, Fig. 4). Indeed, niche overlaps between developmental stages were higher than expected by chance ($p = 0.008$; Table 3). However, tadpoles still varied in their preferences for different food items (Fig. 5), with stage 30 showing higher preference for Euglenophyceae and testate amoeba compared to the other stages, as well as a less pronounced preference for pollen. Pteridophyte spores were rejected by tadpoles in all stages (mainly stage 40). Pollen was always the preferred item, although for stage 30 its preference was comparable to Euglenophyceae and testate amoeba.

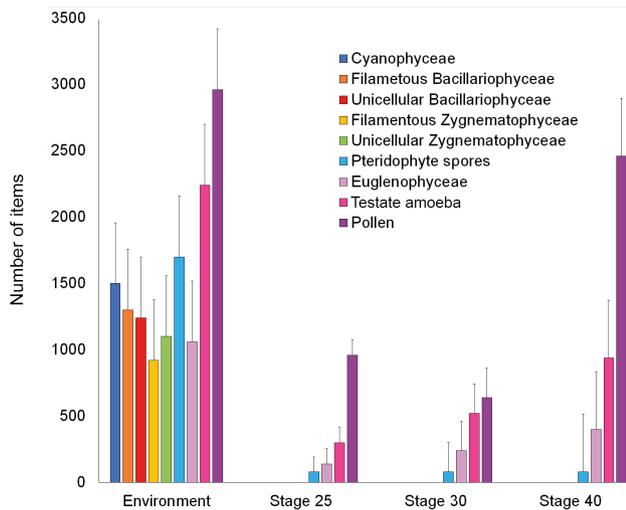


Figure 3. Food item availability and consumption by *Phasmahyla jandaia* tadpoles in developmental stages 25, 30 and 40 (sensu GOSNER, 1960), in a stream at the Serra do Cipó, Southeastern Brazil.

Discussion

The majority of the diet of *Phasmahyla jandaia* tadpoles was composed of pollen. Although the anatomy of the oral disc of these tadpoles favors pollen consumption at the water surface and its availability in the sampled stream was great, tadpoles in all developmental stages still showed a positive, high electivity for this food item, meaning a remarkable preference for it. Several groups of vertebrates have pollen as an important component of their diets as

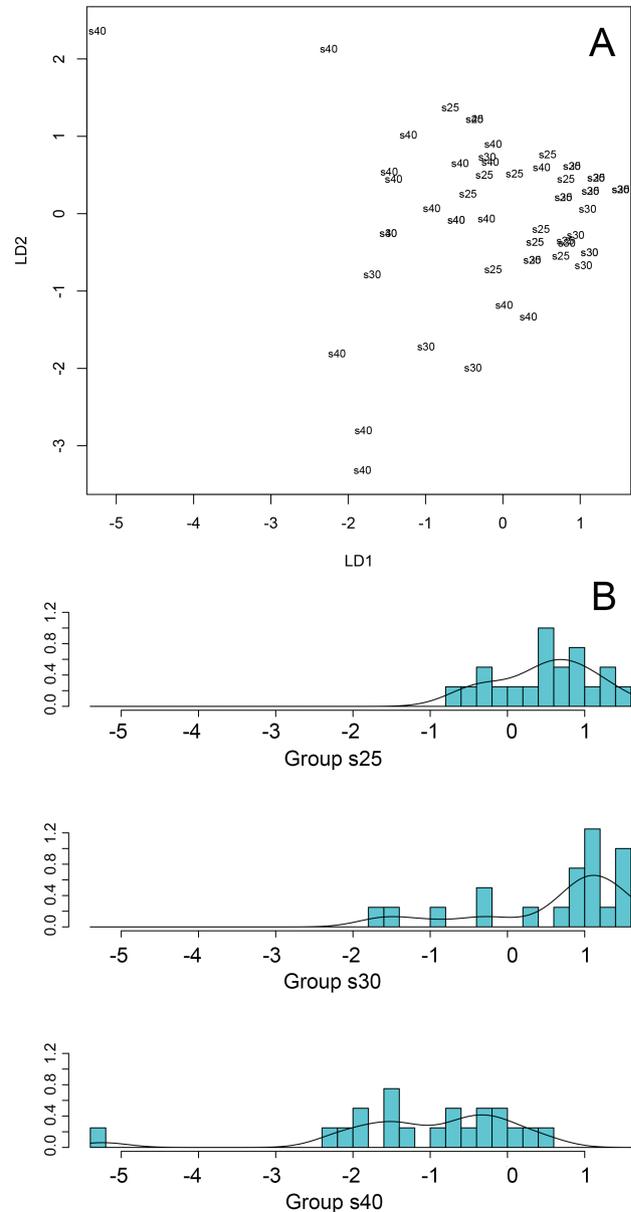


Figure 4. Representation of (A) the two first axes of the discriminant analyses to compare diet composition of three developmental stages of *Phasmahyla jandaia* tadpoles (25, 30 and 40; sensu GOSNER, 1960) and (B) the linear distribution of groups in the first axis, that explained 95.24% of the variation.

Table 3. Niche overlap results for the composition of the diet of *Phasmahyla jandaia* tadpoles in stages 25, 30, and 40 (sensu GOSNER, 1960). Expected value based on 1000 simulations (RA3 algorithm): 0.754.

Niche overlap	Stage 25	Stage 30	Stage 40
Stage 25	1	0.899	0.993
Stage 30		1	0.928
Stage 40			1

it provides lipids, proteins, vitamins, and mineral salts, among other essential elements for their development (ROULSTON & CANE 2000, FRIAS et al. 2016).

The highest absolute food intake in Gosner stage 40 may be related to a higher energy demand for tadpoles in that stage. It is probably important to maximize nutrient intake in stage 40, as this is the last stage in which tadpoles can be considered as maintaining a normal tadpole diet, followed by atrophy of mouthparts from stage 41 on (ALTIG & JOHNSTON 1989). Besides, an increased oral disc (see Table 1) and gained experience may turn stage 40 tadpoles more efficient in pollen acquisition than smaller stage 30 and 25 tadpoles. Tadpoles in stage 25 can probably supply their nutritional needs with smaller pollen quantities due to their smaller size. On the other hand, stage 30 tadpoles may need a greater amount of pollen than stage 25 tadpoles, but they may not be efficient enough to acquire it before pollen availability decreases. As pollen becomes less profitable to harvest, stage 30 tadpoles may switch to other food items and complement their diets with proportionally

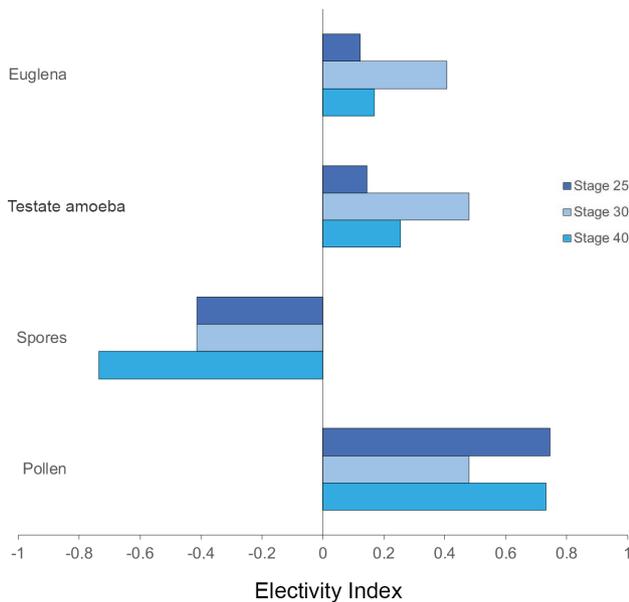


Figure 5. Electivity indexes of the food items consumed by *Phasmahyla jandaia* tadpoles in developmental stages 25, 30 and 40 (sensu GOSNER, 1960), in a stream at the Serra do Cipó, South-eastern Brazil.

larger amounts of Euglenophyta and testate amoeba, which could be easier to acquire as the amount of pollen available for consumption is gradually reduced at the vicinities of the tadpole group.

It is interesting to notice that the gut of *P. jandaia* tadpoles (107–163 cm total length through stages 25–40) is shorter than those of benthic hyloid tadpoles of similar size [*Bokermannohyla saxicola* (BOKERMANN, 1964): 230–290 cm in stages 25–30, *Scinax machadoi*: 180–250 cm in stages 25–30; J. S. KLOH, pers. obs.]. This could be related to a great consumption of pollen, whose high nutritional value (ROULSTON & CANE 2000) may supply tadpole needs with lower consumed amounts. Although pollen is considered to be difficult to digest (ROULSTON & CANE 2000), a shorter gut could reduce tadpole weight and minimize the energy needed to keep their bodies close to the surface, where they can easily eat pollen, in accordance with the optimal foraging theory (MACARTHUR & PIANKA, 1966).

Euglenophyceae also constituted an important component of the diet of *P. jandaia* tadpoles. As flagellates, they remain for more time close to the water surface (CHINDIA & FIGUEREDO 2018), where they can be easily captured by the tadpoles of *P. jandaia*. These tadpoles move the water with their tail tips (LEITE et al. 2008) and the water flow promoted by groups of tadpoles may facilitate acquisition of suspended food items. Testate amoeba are amoeboid protists with a test that partially encloses the cell. They usually occupy the water surface and are indicators of low habitat quality (SOUSA 2008). Their presence in the studied stream may be related to the occasional presence of cattle in its vicinities, as well as the increasing traffic at the road, sewage irregular disposal, and other human activities that lead to water pollution and eutrophication at the Serra do Cipó, although still with low intensity. The presence of testate amoeba as a preferential item in the diet of *P. jandaia* tadpoles in all developmental stages may relate to the high iron and manganese contents in their tests (SOUSA 2008), as these elements play important roles as nutrients for vertebrate immunity and metabolism (PINTO-COELHO, 2009). Pteridophyte spores, on the other hand, were not preferential items, although they may be easily available at the surface. Their nutritional value for tadpoles remains unknown.

We reported here that the diet of neustonic *P. jandaia* tadpoles is largely influenced by their ecomorphotype. They occupy the water surface and have a dorsal mouth with no denticles (COSTA & CARVALHO-E-SILVA 2008), resulting in the absence of periphyton in their diets. However, it does not mean that they do not select their food items, as even with a relatively specialized morphology, they showed differential selectivity for the potential food items available to them.

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