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Smooth, striated, or rough: how substrate textures affect the feeding performance of tadpoles with different oral morphologies

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Abstract

For grazing animals that share spatial and alimentary resources, the relationship between differences in oral morphology and the physical properties of substrates can help explain how and where species forage. The substrates may require different efforts from animals to access and remove food from their surfaces. Variation in oral morphology may produce differences in animals' feeding efficiency. We tested whether one substrate characteristic, the surface texture (i.e., smooth, striated and rough), influences the growth and food consumption rates of anuran larvae from nine species with different oral morphologies. Tadpoles with few keratinized oral structures and those with more gaps in the marginal papillae row were more efficient grazing on smooth and rough surfaces, respectively. This may indicate possible feeding specializations. Conversely, tadpoles with a high number of labial tooth rows, regardless of the number of gaps in these structures, and those with only a dorsal gap in the marginal papillae row were equally efficient feeding upon all substrate textures. Tadpoles with the generalized labial tooth row formula 2(2)/3(1), had higher growth rates than the other species, suggesting an adaptive significance for this common oral morphology. We demonstrated that species differ in feeding efficiency when grazing on substrates with different textures. This can help elucidate the adaptive significance of variation in tadpole oral morphology. We also provide insights on resource selection and niche partitioning among species, especially for those whose diets do not differ in quantity or quality, as it is common in anuran larval assemblages.

Keywords Anuran larvae · Ecomorphology · Feeding behavior · Foraging surfaces · Niche breadth

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Introduction

Variation in oral morphology can produce differences in animals' efficiency to acquire, handle and prepare food for digestion (Wainwright and Richard 1995; Higham 2007). A classic example is the variation in mammalian tooth shape, which increases the ability of different species to obtain and process certain foods (in Evans and Pineda-Munoz 2018). Consequently, selection and adaptation to different alimentary resources can vary among species, allowing their coexistence—e.g., insectivorous warbler finches and granivorous ground finches (Grant and Grant 2003).

Among anuran larvae, variation in oral structures can reflect feeding specializations (Vera Candioti 2005; Haas et al. 2014). However, similarly to some cichlid fishes, tadpoles of many lentic species can co-occur and feed in the same area sharing alimentary resources (Rupp and Hulsey 2014). Consequently, for many species, there can be a high overlap in trophic habits among species, regardless of their

oral morphologies (Rossa-Feres et al. 2004; Vera Candioti 2007). This leads us to question (1) whether other environmental factors can influence the feeding of grazing tadpoles and (2) whether differences in oral structures among species influence tadpoles' feeding ability.

For grazing animals, characteristics of the substrates where they feed upon can influence feeding (e.g., Rupp and Hulsey 2014; Hanlon et al. 2015; Ramamonjisoa et al. 2017; Annibale et al. 2019). That may be due to a trade-off between the nutritional gain and the foraging effort in animals and their food sources (Ramamonjisoa et al. 2017). For example, substrate textures can influence the feeding efficiency of grazing animals by constraining species ability to reach and remove food from crevices (Dudley and D'Antonio 1991). Surface textures determine the friction and adherence between anatomical structures (adhesive disc in fishes, Wainwright et al. 2013; Ditsche et al. 2014; oral disc in tadpoles, Gradwell 1975) to the substrates, influencing the animals' ability to hold on to surfaces.

For tadpoles of most species, the oral apparatus is comprised of an oral disc with keratinized jaw sheaths and rows of labial teeth, surrounded by soft tissue and marginal papillae (McDiarmid and Altig 1999). When feeding, the labial teeth help to anchor the oral disc to the substrate as the tadpole begins to close its' jaw sheaths against the substrate (Wassersug and Yamashita 2001; Venesky et al. 2010). This movement, coupled with the release of the keratinized jaw sheaths as the tadpole closes its mouth, lifts organic material off the substrate. The material removed from the surface is then drawn into the oral cavity as the tadpole opens its' mouth during the next gape cycle (Venesky et al. 2010). The soft tissue of the oral disc thus helps hold the keratinized structures on the substrate. It has also been hypothesized that the marginal papillae have as well a sensory role (Van Dijk 1981; Wassersug and Yamashita 2001).

When tadpoles feed on relatively smooth substrates, the labial tooth rows can easily rake the surface and aid the jaw sheaths in removing food material. However, the teeth may be ineffective in anchoring the oral disc to smooth surfaces, due to the low friction (Wassersug and Yamashita 2001), and the jaws may lose effectiveness to bite off food. On rough substrates, the labial teeth may gain a purchase on the surface and the marginal papillae possibly increase adhesion between the oral disc and the substrate irregularities (McDiarmid and Altig 1999). However, the efficiency of keratinized structures to reach and extract food into crevices may be diminished (Dudley and D'Antonio 1991).

Interspecific differences in tadpoles' oral morphology—e.g., number of labial tooth rows (McDiarmid and Altig 1999) may affect tadpoles' ability to acquire food from substrates. This could represent a dimension of niche partitioning among species (Wainwright 1991). Moreover, differences in tadpole feeding performance could have cascading

effects on growth rates and on interspecific interactions. This could explain why one can find multi-species tadpole assemblages where gut contents suggest that there is major overlap in diet (Rossa-Feres et al. 2004).

We designed experiments to test the hypothesis that tadpoles with different oral morphologies differ in feeding performance when grazing upon substrates with different surface textures. Specifically, we tested three hypotheses: tadpoles from species with differences in the (1) number of labial tooth rows (2) number of gaps in the labial tooth rows, and (3) oral disc configuration (i.e., emarginations in the oral disc and gaps in the marginal papillae row) differ in growth and food consumption rates when feeding either on smooth, striated or rough substrates. Our study reveals how subtle variation in tadpole oral morphology correlates with the ability of tadpoles to acquire food from surfaces of different textures.

Materials and methods

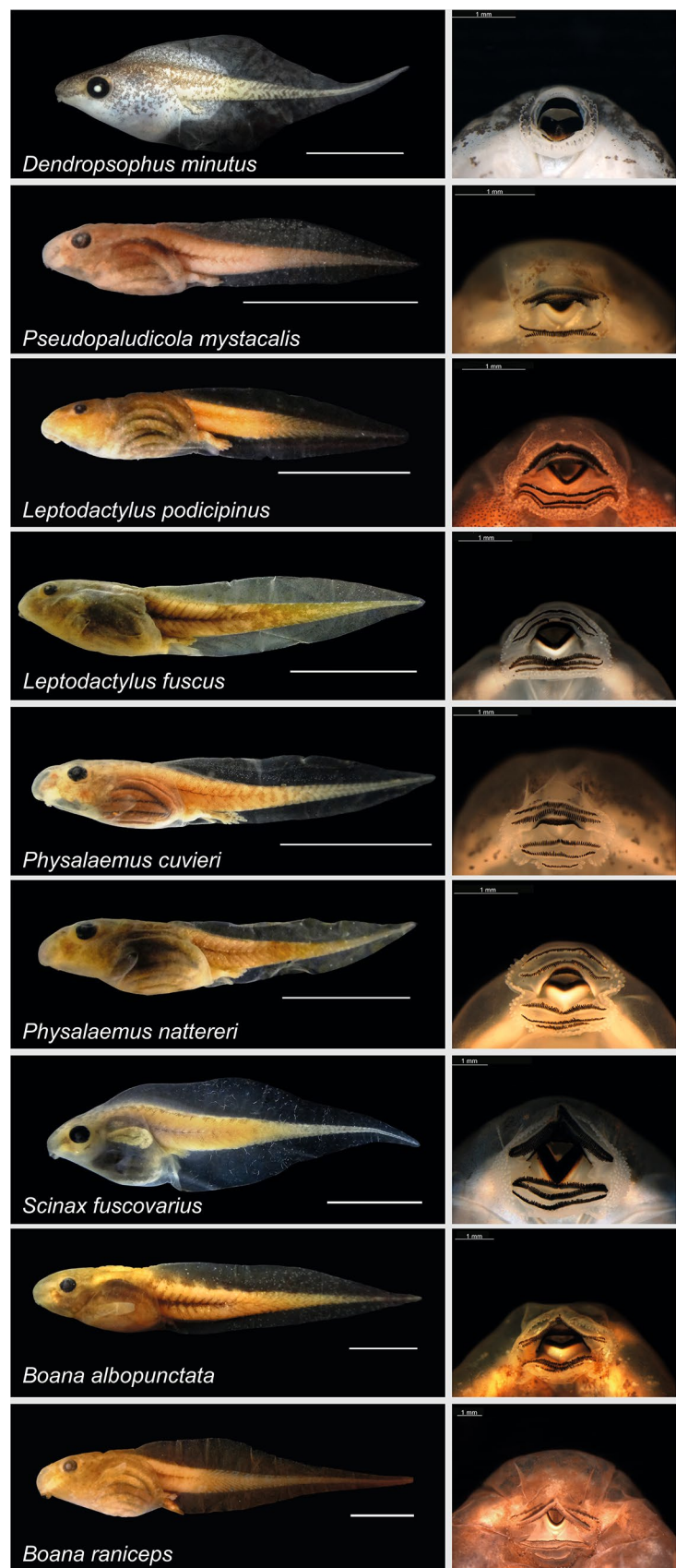
Species

We selected pond-dwelling tadpoles from nine anuran species: *Boana albopunctata* (Spix, 1824), *Boana raniceps* (Cope, 1862), *Dendropsophus minutus* (Peters, 1872), *Leptodactylus fuscus* (Schneider, 1799), *Leptodactylus podicipinus* (Cope, 1862), *Physalaemus cuvieri* Fitzinger, 1826, *Physalaemus nattereri* (Steindachner, 1863), *Pseudopaludicola mystacalis* (Cope, 1887), and *Scinax fuscovarius* (Lutz, 1925). Tadpoles varied in the number of (1) labial tooth rows, (2) gaps in the labial tooth rows and (3) emarginations in the oral disc and gaps in the marginal papillae row (Rossa-Feres and Nomura 2006). Emarginations and gaps could be equal to 0 (when absent), 1 (e.g., only lateral), 2 (e.g., both lateral and ventral) or 3 (for gaps only: dorsal, lateral and ventral) (Online Resource 1, Fig. 1).

Although the jaws have the main function of removing food from substrates (Wassersug and Yamashita 2001), we did not consider the jaws as a variable in our study. Instead, we focused on variables that are primarily related to the attachment of the oral disc to the substrate. This reflects the key role that the oral disc plays in holding the mouth on the substrate allowing the jaws to work effectively. In addition, the variables that we selected can be easily quantified among species.

The nine species are commonly found in the same habitats and often consume the same resources, even those that occupy different microhabitats (as noted for *P. nattereri* and *S. fuscovarius*; Rossa-Feres et al. 2004; Prado et al. 2009; Vasconcelos et al. 2011). Despite microhabitat difference, tadpoles of all the species feed and grow well by grazing

Fig. 1 Lateral view (left) and external oral morphology (right) of the species tested. Note the differences in the number of labial tooth rows, gaps in labial tooth rows, emarginations in oral disc, and gaps in marginal papillae row among species. Credit: Katiuce O. R. Picheli



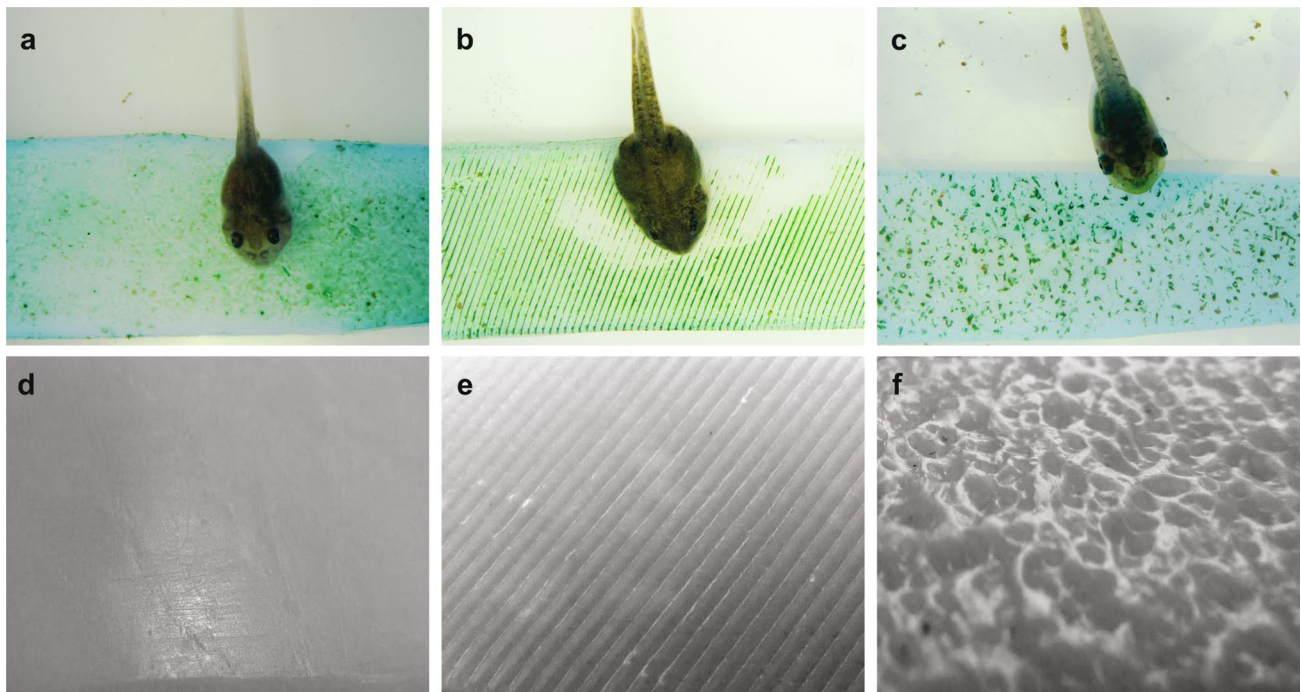


Fig. 2 Experiment treatments. Tadpole of **a** *P. nattereri* **b** *L. fuscus* and **c** *S. fuscovarius* grazing on **a** and **d** smooth, **b** and **e** striated, and **c** and **f** rough plastic plates coated with Sera Micron (in green, **a–c**)

upon solid substrates (F.S. Annibale, per. obs.; see *D. minutus* in Annibale et al. 2019).

Collection and acclimation of tadpoles

Tadpoles were collected between January and April 2017 from ponds located in open areas on the northwestern region of São Paulo state, southeastern, Brazil (Online Resource 2). They were housed in polyethylene aquaria containing dechlorinated water, which was gently and constantly aerated. We used a 12:12 light:dark photoperiod and air room temperature of approximately 28 °C, which maintained water at approximately 25.5 °C. Prior to being tested in an experiment, we fed tadpoles *ad libitum* with Sera Micron®, a commercial powdered food consisting of phytoplankton (51% spirulina) and zooplankton (16% krill). Tadpoles were acclimatized in these conditions for at least three days before being tested in feeding experiments.

Experiment

During the experiments, temperature and photoperiod were maintained the same as in the acclimation period. We used glass aquaria (15 × 10 × 13 cm) filled with dechlorinated water and one tadpole per aquarium. We covered the aquaria walls with a blue adhesive to reduce the stress that other background colors and movements outside the aquaria might cause to the tadpoles (based on fishes, Maia and Volpato

2013). We arranged the aquaria in rows on the laboratory bench and randomized the order of treatment that each aquarium would represent.

We offered food to the tadpoles on plates (3.2 × 17.5 cm) made of a moldable plastic (TermoMorph®). The surfaces of the plates were either (1) smooth, with no recesses on their surfaces (Fig. 2a, d), (2) grooved in a single direction to give a striated surface with a clear pattern to their roughness (Fig. 2b, e) or (3) abraded in such a way that they were irregularly rough (Fig. 2c, f). These plates represented three treatments with increasing order of complexity in the surface texture: smooth, striated and rough, respectively. The three surface textures reflect stylized surface contours that can be found in natural ponds; e.g., smooth leaves and striated stems of aquatic plants, rough surfaces of woody substrates.

In each plate, we spread 3 ml of a liquid mixture of water and Sera Micron® (concentration of 80 mg·ml⁻¹). We allowed the plates to air dry for at least 6 h so the mixture would be firmly attached to the surfaces (adapted from Venesky et al. 2013). Next, we placed one plate per aquarium (smooth, striated or rough, respective to each treatment), horizontally and at the bottom of the aquaria. We changed the plates twice a day to guarantee that food would be available *ad libitum* throughout the experiment.

Within species, we selected only tadpoles with similar total length (Online Resource 3) and Gosner stages; i.e., all were between stages 28–32 (Gosner 1960) which are stages where most tadpole growth is in the size of the trunk and

tail (McDiarmid and Altig 1999). Due to some limitation on the availability of specimens in those stages, some species differed in sample size (Online Resource 3). On average though, we tested 12 tadpoles of each species per treatment ($n_{\text{total}} = 308$). Each tadpole received food on plates with the same type of texture during the entire experiment, which lasted 5 days for all species. We assumed that the development of tadpoles would be similar among species because the experiment lasted only 5 days and we controlled other factors known to influence anurans' developmental time—e.g., photoperiod, temperature and tadpoles' density (Denver 1997; Richter-Boix et al. 2011).

At the beginning and at the end of the experiments each tadpole was weighed with an analytical balance (A&D, GR-200) with the readability of 0.1 mg then photographed in lateral view with a digital camera (Sony Cyber Shot DCS TX 10 and TX20). The photographs were analyzed with the software ImageJ® (<https://imagej.nih.gov/ij/>) to obtain measures of tadpole's body and total length—i.e., body + tail length. With the initial and final measures of tadpoles' mass and length we inferred their relative growth by the formula:

$$\text{rg}(x) = \frac{\Delta x}{x_i},$$

where rg = relative growth, Δ = difference between the final and initial measures, x = mass or length measures, and i = initial measure.

We captured digital images of all the plastic plates using a scanner (HP, LaserJet M1132) and used the particle analysis tool in the software ImageJ® to quantify the percentage of food removed from each plate ($n = 10$ per tadpole). We used the mean percentage of food scraped by each tadpole as a measure of food consumption.

After each experiment, tadpoles were immersed in an anesthetic solution of 2% lidocaine. Then they were preserved in a solution of half 70% ethanol and half 15% formalin, and deposited in the Scientific Collection DZSJRP—Amphibia Tadpoles, of Universidade Estadual Paulista (UNESP), Campus São José do Rio Preto, Brazil.

Statistical analyses

Because all tested tadpoles feed by rasping organic material from surfaces (F.S. Annibale, pers. obs.), we considered differences in external oral morphology as the main factor to produce variation in the tadpoles' ability to feed on substrates with different textures. We used species taxonomic names as a surrogate for the variation in the oral structures tested in each analysis. We also used the term oral disc configuration in reference to variation in both emarginations in the oral disc margin and gaps in the marginal papillae row.

We used the growth rates of the tadpoles as a measure of their efficiency to graze and consume food from surfaces, and then invest it in growth. Mechanical processing of food, like grazing, and physiological adaptations, such as digestive enzymes, influence the ingestion, digestion, and assimilation of nutrients (McDiarmid and Altig 1999; Altig et al. 2007). Because we were not able to distinguish these effects, we used the relative increase in mass (not the absolute values) to reduce the effects inherent to the species. We also used food consumption as a covariate to control its effect on the relative mass gained by tadpoles when testing our hypotheses. We did not use food consumption as the covariate in the analyses of tadpoles' length (body and total length) because tadpoles that gain more mass do not necessarily increase more in length (Annibale et al. 2019).

We log-transformed the relative mass for every analysis performed with this variable and the total length of species with different numbers of gaps in labial tooth rows (Hypothesis 2) in order to meet the assumptions of normality and homoscedasticity. We used the post hoc Tukey's test (Honestly Significant Difference, HSD) to identify differences among groups when necessary. When the interaction between factors was significant, we analyzed the results by interpreting the graphs instead of using a post hoc test. All analyses were performed in R software version 1.0.143 (R Development Core Team 2017).

Hypothesis 1: variation in the number of labial tooth rows influences the growth rate of species grazing upon substrates with different textures To test this hypothesis, we selected the species *D. minutus*, *L. podicipinus* and *P. mystacalis*, because they represented a progression in the number of posterior labial tooth rows; i.e. from 1 to 3 (Fig. 3a–c). Also, only these tadpoles from our pool of species have complete posterior labial tooth rows. Thus, in selecting them, we removed the effect of gaps in these structures for the following analyses.

We performed the analyses separately for relative mass, body length and total length. When tadpole relative mass was the response variable, we used a two-way ANCOVA with the percentage of food consumed by tadpoles as a covariate. Either when tadpole body length or total length was the response variable, we used a two-way ANOVA. For all analyses, we used the substrate textures (three levels: smooth, striated, and rough) and the species (three levels: *D. minutus*, *L. podicipinus*, and *P. mystacalis*) as explanatory variables.

Hypothesis 2: variation in the number of gaps in the labial tooth rows influences the growth rate of species grazing upon substrates with different textures For this hypothesis, we tested the species *L. fuscus*, *L. podicipinus*, *P. cuvieri*, *P.*

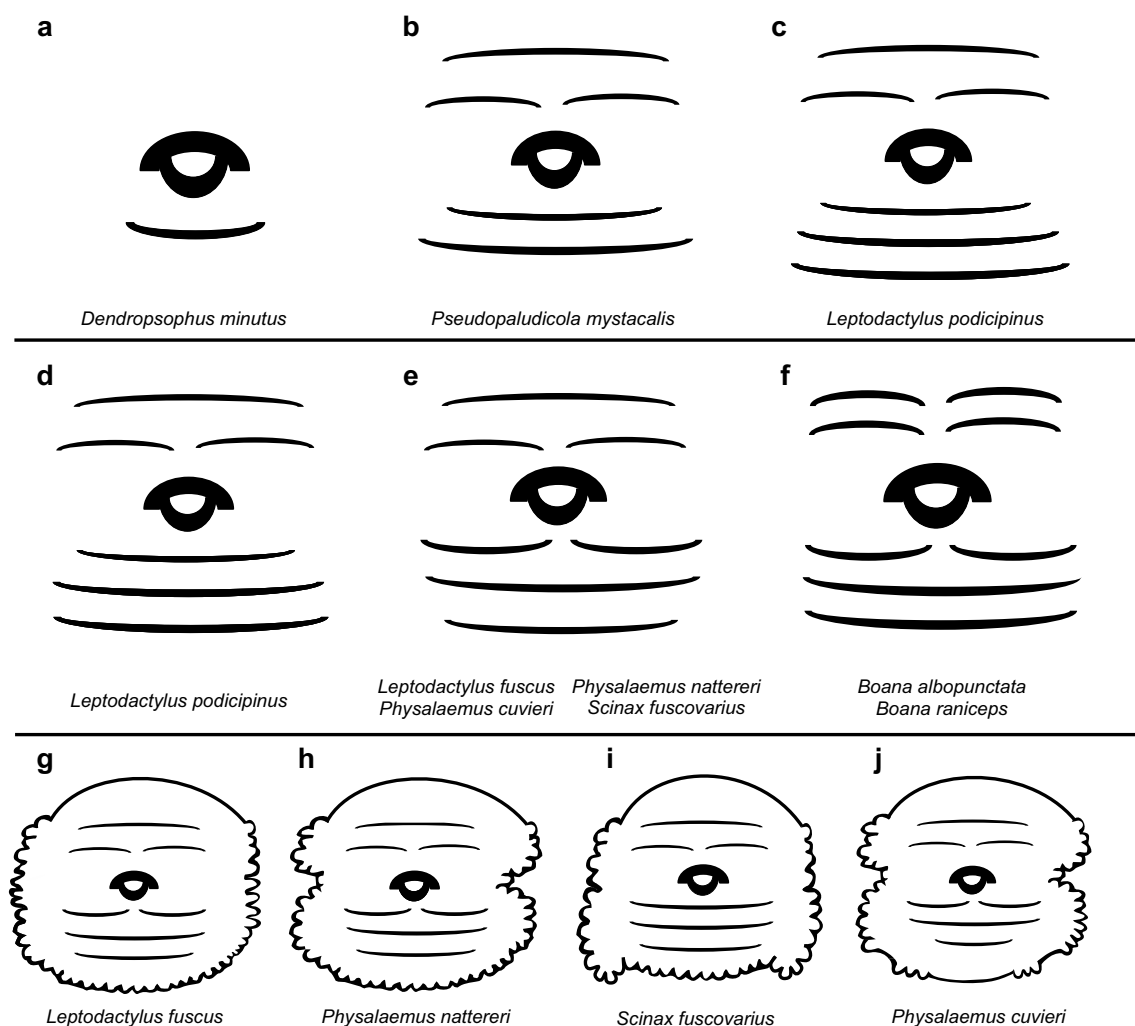


Fig. 3 Schematic illustration (not to scale) for variation in the tadpole's oral morphology. Hypothesis 1 **a–c**: tadpoles with 1–3 complete posterior labial tooth rows. Hypothesis 2 **d–f**: tadpoles with the same number of labial tooth rows, but with 1–3 gaps in these structures. Hypothesis 3 **g–j**: tadpoles with the same number of labial

tooth rows and gaps in these structures, but different oral disc configuration. Tadpoles with only a dorsal gap in the marginal papillae row and with an oral disc **g** not emarginated **h** laterally emarginated, or **i** ventrally emarginated. Tadpoles with **j** dorsal, lateral and ventral gaps in the marginal papillae row and an oral disc laterally emarginated

nattereri, *S. fuscovarius*, *B. albopunctata*, and *B. raniceps*. Tadpoles of these species have the same number of labial tooth rows, two anterior and three posteriors, but differ in the number of gaps in these keratinized structures; i.e., from 1 to 3 (Fig. 3d–f).

We conducted separate analyses for relative mass, body length, and total length. When analyzing tadpole relative mass, we used a two-way ANCOVA with food consumption as a covariate. For each length analysis (body and total length), we used a two-way ANOVA. The substrate textures (three levels: smooth, striated, and rough) and the species (seven levels: *L. fuscus*, *L. podicipinus*, *P. cuvieri*, *P. nattereri*, *S. fuscovarius*, *B. albopunctata*, and *B. raniceps*) were used as explanatory variables for all analyses.

Hypothesis 3: variation in the oral disc configuration influences the food consumption of species grazing upon substrates with different textures For this hypothesis, we tested four species that corresponded to a subset of the group of species tested in Hypothesis 2 (*L. fuscus*, *P. cuvieri*, *P. nattereri*, and *S. fuscovarius*). They represented differences only in the oral disc configuration, which we envisioned as a series of increasing complexity; i.e., from species with no emarginations in the oral disc and only a dorsal gap in the marginal papillae row to species with an emarginated oral disc and dorsal, lateral, and ventral gaps in the marginal papillae row (Fig. 3g–j).

Because differences in growth rate among these species were already known (from Hypothesis 2), we used a two-way ANOVA with the percentage of food consumed by

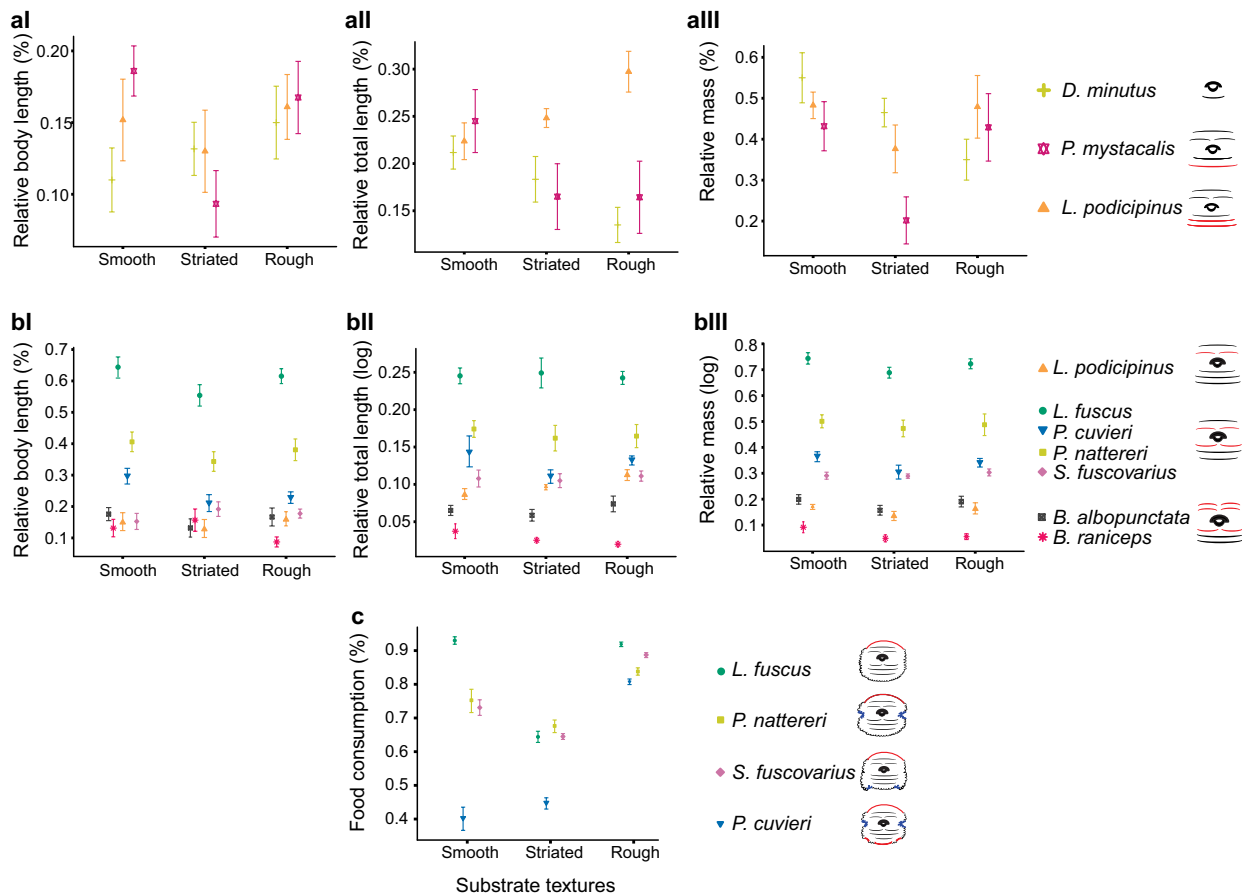


Fig. 4 Effect of differences in substrate textures and in tadpoles' external oral morphology on the mean values of growth and food consumption rates. **aI** Tadpoles with a different number of labial tooth rows had a similar increase in relative body length among all treatments. The interaction between species and substrates affected tadpole **aII** relative total length and **aIII** mass gain. **bI** Tadpoles with a different number of gaps in labial tooth rows had a lower increase in body length and **bIII** gained less mass feeding on striated surfaces. **bII** Substrate textures did not affect tadpoles' relative total length.

tadpoles as the response variable. We also used the substrate textures (three levels: smooth, striated, and rough) and the species (four levels: *L. fuscus*, *P. cuvieri*, *P. nattereri*, and *S. fuscovarius*) as explanatory variables.

Results

All tadpoles were able to feed upon all the three substrates tested despite the pattern of surface irregularity, but some species performed better in terms of feeding on specific substrates than others. Overall, tadpoles of most species, regardless of the groups tested for each hypothesis, feeding on

Species with two gaps had the best performances compared to the other species. **c** The interaction between substrates and differences in oral disc configuration produced variation in the percentage of food consumed by the tadpoles. Schematic illustrations of tadpole oral configurations are provided beside the species names in the graph's legend. Structures in red represent interspecific variation in gaps both in labial tooth and marginal papillae row of tadpoles. Structures in blue represent interspecific variation in emarginations in the oral disc

striated surfaces had lower growth rates in contrast to those feeding on smooth and rough substrates (Fig. 4).

Although we did not measure behavioral responses, we observed some tadpoles feeding in different directions of the texture patterns—e.g., positioning themselves either aligned, perpendicular or at other orientations to the substrates (Online Resource 4). The trails left on the plastic plates also reflected these observations (Online Resource 5).

Hypothesis 1: variation in the number of labial tooth rows influences the growth rate of species grazing upon substrates with different textures Tadpoles had a similar increase in body length regardless of the number of labial tooth rows on the oral disc of the species and the substrate texture upon which they grazed (Table 1, Fig. 4aI). However,

Table 1 Effect of the different types of substrates (smooth, striated and rough) on the growth rates of tadpoles with different number of labial tooth rows, different number of gaps in the labial tooth rows,

and on the percentage of food consumed by larvae of the species that varied in oral disc configuration

Species	Prediction	Response variable	Source	d.f	F	P
<i>D. minutus</i> <i>L. podicipinus</i> <i>P. mystacalis</i>	1. Number of labial tooth rows and textures	Relative body length ^a	Species	2	0.53	0.59
			Surfaces	2	1.46	0.23
			Species*surfaces	4	1.01	0.4
			Residuals	79		
		Relative total length ^a	Species	2	11.76	< 0.001*
			Surfaces	2	0.78	0.46
			Species*surfaces	4	4.24	0.003*
			Residuals	79		
		Relative mass ^b	Food consumption	1	1.12	0.29
			Species	2	2.11	0.12
			Surfaces	2	3.23	0.04*
			Species*surfaces	4	3.03	0.02*
<i>B. albopunctata</i> <i>B. raniceps</i> <i>L. fuscus</i> <i>L. podicipinus</i> <i>P. cuvieri</i> <i>P. nattereri</i> <i>S. fuscovarius</i>	2. Number of gaps in the labial tooth rows and textures	Relative body length ^a	Species	6	123.26	< 0.001*
			Surfaces	2	3.65	0.02*
			Species*surfaces	12	0.97	0.47
			Residuals	230		
		Relative total length ^a	Species	6	100.94	< 0.001*
			Surfaces	2	0.74	0.47
			Species*surfaces	12	0.54	0.88
			Residuals	227		
		Relative mass ^b	Food consumption	1	74.94	< 0.001*
			Species	6	283.81	< 0.001*
			Surfaces	2	4.04	0.02*
			Species*surfaces	12	0.57	0.86
<i>L. fuscus</i> <i>P. cuvieri</i> <i>P. nattereri</i> <i>S. fuscovarius</i>	3. Oral disc configuration and textures	Food consumption ^a	Residuals	229		
			Species	3	108.32	< 0.001*
			Surfaces	2	180.97	< 0.001*
			Species*surfaces	12	26.12	< 0.001*
			Residuals	149		

d.f. degrees of freedom, F F-ratio (observed F statistic value), P probability value (p value)

*p value statistically significant ($\alpha = 0.05$)^aANOVA test^bANCOVA test

the interaction between species and the surface texture produced variation in the relative total length of tadpoles (Table 1, Fig. 4aII). Both tadpoles with a low and an intermediate number of labial tooth rows (*D. minutus* and *P. mystacalis*, respectively) had the greatest increase in total length when grazing on smooth surfaces. Tadpoles with more labial tooth rows (*L. podicipinus*) had the opposite response: the rougher the surfaces, the greater the increase in total length.

The interaction between species and treatments also explained variation in the relative mass of the tadpoles (Table 1, Fig. 4aIII). Tadpoles with more labial tooth rows

(*L. podicipinus*) gained mass regardless of the substrate texture on which they grazed. Tadpoles with an intermediate number of labial tooth rows (*P. mystacalis*) had high growth rates on both smooth and rough substrates. On striated surfaces though, these tadpoles gained less mass than the other species (26% less than *D. minutus* and 17% less than *L. podicipinus*). When the surface was smooth, the tadpoles of *D. minutus* gained more mass than the other species (7% more than *L. podicipinus* and 12% more than *P. mystacalis*).

Therefore, tadpoles of *L. podicipinus* had good performances feeding on the three types of surfaces, *P. mystacalis*

performed well on both smooth and rough substrates, and *D. minutus* had high growth rates feeding on smooth substrates.

Hypothesis 2: variation in the number of gaps in the labial tooth rows influences the growth rate of species grazing upon substrates with different textures We found tadpoles to be overall more efficient grazing on smooth and rough substrates than on striated ones, regardless of their oral morphology (Table 1, Fig. 4bI, III). In comparison to the other substrates, tadpoles feeding on striated surfaces increased 3% less in body length and 15% less in mass. The tadpoles' relative total lengths were similar among species and treatments (Fig. 4bII).

Differences in the number of gaps in the labial tooth rows were important in explaining variation in species growth rates. Tadpoles with two gaps in the labial tooth rows (*L. fuscus*, *P. cuvieri*, *P. nattereri*, and *S. fuscovarius*) had the highest growth rates. Together, they grew two times larger in body length (Fig. 4bI, Online Resource 6a), and three times longer in total length (Fig. 4bII, Online Resource 6b) and doubled their mass (Fig. 4bIII, Online Resource 6c) compared to the other three species (in terms of the relative measures). Tadpoles with either one more (*B. albopunctata* and *B. raniceps*) or one less (*L. podicipinus*) gap in the labial tooth rows had a similar increase in body length and mass gain. They only differed in relative total length, where tadpoles with fewer gaps (*L. podicipinus*) grew almost three times larger than tadpoles of both species of *Boana*.

Hypothesis 3: variation in the oral disc configuration influences the food consumption of species grazing upon substrates with different textures The interaction between the substrate texture and species produced variation in the percentage of food consumed by tadpoles (Table 1, Fig. 4c). All species consumed from 80 to 90% of the food on rough surfaces, regardless of the number of emarginations in oral disc or gaps in marginal papillae row.

Species with an oral disc emarginated and with only a dorsal gap in marginal papillae row (*P. nattereri* and *S. fuscovarius*) showed the same response, being able to acquire food effectively from a relatively wide range of surface textures (Fig. 4c).

The simpler oral disc configuration of *L. fuscus* allowed tadpoles to acquire food equally well on all substrates tested (Fig. 4c). Comparatively, tadpoles of *P. cuvieri*, which have a more complex oral disc, grazed effectively only on rough substrates but consumed less than 50% of the food available on both smooth and striated surfaces (Fig. 4c).

Discussion

Gut content analyses can reveal much about what tadpoles ingest (e.g., Rossa-Feres et al. 2004; Prado et al. 2009; Santos et al. 2016; Kloh et al. 2019), but not necessarily elucidate what morphological specializations tadpoles have for acquiring and/or selecting food from different substrates. Physical properties of substrates upon which tadpoles graze can influence their survivorship (Hanlon et al. 2015), feeding preference (Ramamonjisoa et al. 2016, 2017) and feeding efficiency (Annibale et al. 2019). Thus, the substrate characteristics may be more significant than diet in revealing how species use and partition the environment, especially those that share similar resources.

In the aquatic habitat, tadpoles encounter food on a variety of substrates with different surface textures—e.g., from smooth leaves to rough rocks (Duellman and Trueb 1994; McDiarmid and Altig 1999). Even a single substrate may have more than one type of texture. For example, a rough rock can present smooth areas due to the development of biofilm. This changes the frictional properties of the substrates (Ditsche et al. 2014) and consequently, tadpoles may deal with different resistances while grazing on surfaces. This can help explain why all tadpoles tested here performed well feeding on all treatments.

However, we found that the overall growth rate of tadpoles grazing for food from striated substrates was lower than on other surface textures. This may be because we grooved the plastic plates to produce striated surfaces regularly spaced and with standardized topographic relief—i.e., regular width between crevices (of 1 mm) and uniform depth (of 0.5 mm). Although the margins of the striations were smooth and rounded, this particular pattern may hamper the tadpole's ability to access food in crevices. Tadpoles may try to position their oral discs on the substrate to better adjust to the direction of the striations. In contrast, a more irregular texture provides crevices that differ in width, depth and direction. These irregularities may allow tadpoles to reach more food with less constraints. In nature, uniformly striated surfaces may be uncommon though found on some vegetal substrates, such as the stems of some aquatic plants (e.g., *Cabomba* sp., de Lima et al. 2014). As such, tadpoles may be neither familiar nor well adapted to feeding on this particular surface texture.

We discuss our results in comparison to our expectations (Fig. 5) defining species as grazing generalists or specialists in terms of substrate surface texture. We considered tadpoles as generalists when they were able to gain mass and increase in length regardless of the texture of the substrates. Tadpoles were considered as specialists when they had high growth rates grazing upon specific substrate surface textures.

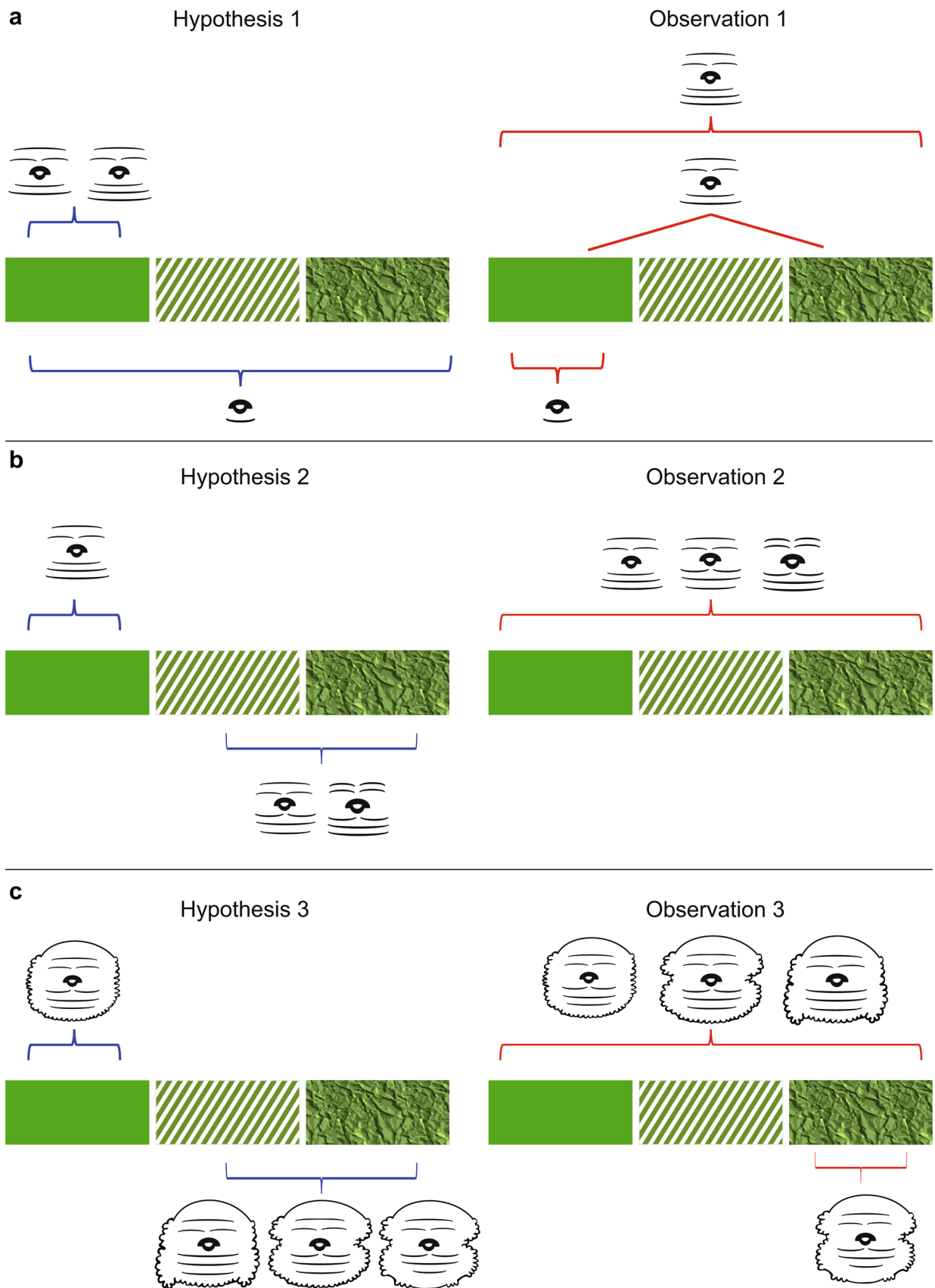


Fig. 5 Schematic illustration of our three hypotheses and their general results. **a** We expected that tadpoles with few keratinized structures would have high growth rates grazing on any type of surface texture. However, they were specialists on smooth substrates. Conversely, we expected that tadpoles with more keratinized structures would be specialists on smooth substrates. These tadpoles, though, were generalists. **b** We expected that species with more gaps in labial tooth rows would have high growth rates grazing on irregular surfaces (i.e., striated and rough), whereas those with complete labial tooth rows would be specialists on smooth surfaces. However, all these species were able to grow well despite the surface texture. **c** Lastly, we expected that tadpoles with no emargination in oral disc and with a single dorsal gap in the marginal papillae row would be specialists on smooth surfaces; i.e., those with emarginations in oral disc and more gaps in marginal papillae row would consume more food on irregular surfaces. Regardless of the presence of emarginations, species with only one gap in the marginal papillae row consumed high amounts of food despite the substrate texture. Tadpoles with more gaps in the marginal papillae row were specialists on rough substrates

Contrary to our hypothesis, tadpoles with the lowest number of labial tooth rows (*D. minutus*) were specialists on smooth surfaces (Fig. 5). The reduced number of labial tooth rows in *D. minutus* oral disc may have limited the tadpoles' ability to access food from substrates with irregularities. In contrast, we found that a higher number of labial tooth rows did not constrain a tadpole's performance on substrates with complex surface textures. Possibly, the number of labial tooth rows influence the effort of tadpoles to remove food from substrates with different textures. That is because a higher number of labial tooth rows in the oral disc implies a higher number of labial teeth. Consequently, tadpoles with more labial teeth are able to consume a greater amount of food with fewer gape cycles—i.e., biting movements (Venesky et al. 2010).

Higher growth rates on substrates with specific surface textures may indicate some level of specialization in feeding behavior. For example, tadpoles of *D. minutus* can feed by filtering planktonic organisms out of the water (Rossa-Feres et al. 2004). This feeding behavior is usually related to species with small oral discs that have few or no keratinized structures (Vera Candioti 2007). However, *D. minutus* tadpoles also forage on aquatic vegetation away from the bottom of ponds (Schulze et al. 2015). This can be an alternative, but efficient foraging behavior for this species. As such, they probably forage more often on smooth aquatic vegetation, such as leaves rather than rougher surfaces, such as sticks lying on the bottom.

Tadpoles of *P. mystacalis* and *L. podicipinus* are both bottom-dwelling and probably forage on substrates with a broader range of textures than *D. minutus*. However, tadpoles of *L. podicipinus* are found in shallow areas of structurally complex ponds (Schulze et al. 2015) which present substrates that vary in surface texture—e.g., leaves, mud, and fallen tree branches (F.S. Annibale, pers. obs.). Tadpoles of *P. mystacalis* are commonly found in small puddles and

cow hoof prints close to ponds or swamps, or in very shallow areas on the margins of ponds (Schulze et al. 2015; Pelinson et al. 2016). These habits clearly have less diversity in substrate texture. This may help explain why these tadpoles were not as efficient generalists as *L. podicipinus*—i.e., they had lower performance feeding on striated substrates.

It should be pointed out that the irregularities that we produced on both striated and rough surfaces were smaller than all the tadpoles' oral discs. As such, tadpoles, even those with few keratinized structures, may not be able to reach with their jaws or oral discs the deepest crevices on our fabricated surfaces. If the size of crevices is closer to the size of tadpoles' oral discs, food acquisition may depend on the efficiency of their keratinized structures to reach and grasp the food. Notable, we observed that a high number of labial tooth rows was advantageous for tadpoles to graze on substrates with more complex textures. Future studies may yield different results when tadpoles are challenged to graze on surfaces with other patterns of abrasion and roughness of other scale.

The ability of tadpoles to graze on substrates with different textures may also depend on characteristics of oral structures not tested here, such as the width and shape of the jaws, the relative proportion between the size of the oral disc and the jaws, the length of labial tooth rows, and features of the teeth themselves. These characteristics may influence the ability of the tadpole's oral disc to adjust to, to attach to, and to remove food from surfaces. Future studies investigating the role of these oral structures in tadpole feeding efficiency will improve our understanding of tadpole functional morphology.

Differences in the configuration of gaps in labial tooth rows seem to be not enough to favor tadpoles to feed on specific substrate surface textures, at least for the range of variation that we tested. However, the high performances of tadpoles with the particular LTRF = 2(2)/3(1) (seen in *L. fuscus*, *P. nattereri*, *P. cuvieri*, and *S. fuscovarius* in our study) suggest a general selective advantage for this type of oral configuration. This can help explain why this oral configuration is widespread among anuran families and is found in tadpoles from a wide range of habitats, both lentic and lotic (Orton 1953; Altig and Johnston 1989; McDiarmid and Altig 1999). Other oral configurations, with either more or fewer gaps in the labial tooth rows, may represent specialization for feeding on other properties of substrates such as their overall shape (i.e., being more contoured versus flat).

Further studies using high-resolution videography of feeding tadpoles (following Wassersug and Yamashita 2001; Venesky et al. 2013; de Sousa et al. 2014) should help elucidate how tadpoles adjust their feeding behavior and oral structures when grazing on substrates with different textures. Such studies can advance our understanding

of how gaps in labial tooth rows function—e.g., adding mobility to the labial tooth rows while grazing, and/or modifying the oral disc shape. This, in turn, may help us understand how oral biomechanics influence the growth rates of tadpoles when feeding in different microhabitats.

Based on our results, we suggest that a simple oral disc, with no emargination and with less marginal papillae gaps (as seen in tadpoles of *L. fuscus*) can be effective in helping tadpoles to adhere to rough substrates (similarly to lotic species, Altig and Johnston 1989). It also may facilitate suction by the oral disc on both smooth and rough surfaces. In contrast, an increase in the number of gaps in the marginal papillae row probably reduces the adherence of the oral disc to smooth substrates, but may improve feeding on surfaces with more irregularities—e.g., *P. cuvieri*. In this case, gaps may allow the oral disc shape to conform to the irregular substrate (Gradwell 1975; McDiarmid and Altig 1999), increasing the ability of keratinized structures to reach and rake organic material from recesses on the substrates.

Some of our results, however, leave unresolved the role of variation in marginal papillae row and emarginations in the oral disc. For example, regardless of the oral disc configuration all species tested here were equally able to consume food on rough surfaces. Emarginations did not increase the tadpoles' efficiency in acquiring food from substrates with different textures. In addition, it remains unclear why tadpoles of *P. cuvieri* perform so well on rough substrates, but so poorly on the other surface textures such as the striated type. More effort is thus needed to understand the adaptive significance of the variation in the oral disc configuration of tadpoles.

Final considerations

Tadpoles are known to select food whose nutritional content, notably protein, permits greater growth (Kupferberg 1997b). However, if the toughness of substrates increases, tadpoles choose softer materials to feed upon even if the food is of lower nutritional value (Ramamonjisoa et al. 2017). As such, we envision that tadpoles select substrates by the nutritious content of the food, but also by the texture pattern upon which they can concurrently graze most effectively and grow well. Differences in feeding efficiency, when tadpoles graze on substrates with different surface textures, may thus represent specializations in feeding behavior.

Interspecific differences in feeding efficiency can also influence niche partitioning among tadpoles (Higham 2007; Rupp and Hulsey 2014; Glos et al. 2017) because more efficient species can change the availability of resources, especially high-quality food. This can affect tadpole growth rates, the timing of metamorphosis, and survivorship (Kupferberg 1997a, b) and may lead tadpoles to forage on other substrates

regardless of whether they perform well in terms of growth or not. Thus, variation in growth rates due to differences in resource use can elucidate the adaptive significance of variation in morphology (e.g., Losos 1990; Betz 2002).

Although we did not test resource selection or niche partitioning, our study provides a new perspective on how environmental factors (i.e., substrate texture) and interspecific variation in oral morphology influence the community ecology of anuran larvae. We encourage more studies on the functional morphology of tadpole oral structures, but also on tadpole feeding ecology and physiology in general. For example, we know a fair bit about how tadpoles in general capture food and what they ingest, but little about what really nourishes them and how they assimilate food (Altig et al. 2007). We also do not have enough information about the metabolic costs of grazing, nor how these costs vary in response to changes in substrate physical properties. Such data will enable us to better understand the adaptive design of tadpoles and the community ecology of anuran larvae overall.

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Authors' contributions FSA, RJW, FN, DCRF and MDV conceived the ideas and designed the experiments; FSA and CES conducted the fieldwork and the experiments; FSA and VTTS analyzed the data; FSA prepared the original draft; FSA, RJW, FN, DCRF, MDV and VTTS reviewed and edited the manuscript.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Collection of tadpoles was approved by the Institute of Environment and Natural Renewable Resources (IBAMA) and Chico Mendes Institute for Biodiversity Conservation (ICMBio): Authorization and Information System on Biodiversity (SISBIO—18163-1 to D. C. Rossa-Feres). All procedures with tadpoles in the laboratory (maintenance and experiments) were in accordance with the Ethics Commission on the Use of Animals of Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP)—Campus São José do Rio Preto, Brazil (CEUA—121-2015).

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