RESEARCH ARTICLE

Ecological Society of Australia

Description and shaping factors of diet and feeding ecology of neotropical tadpoles: A case study and a comprehensive review

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 309513/2020-0

Abstract

Tadpoles are important components of many aquatic food webs as they influence populations at other trophic levels and, ultimately, energy transfer between aquatic and terrestrial ecosystems. What tadpoles consume is a key factor to their ecological functions. Neotropical anuran assemblages include many species with a larval stage, however, the diets of neotropical tadpoles are relatively poorly known. We performed a systematic review on the available literature on in situ studies of neotropical tadpole diets and found out that most studies are descriptive and temporally restricted, failing to consider seasonal variations. Studies frequently also fail to consider possible ontogenetic dietary variations or tadpoles' capacity to select food based on what is available to them in their habitats. We contributed to this topic by investigating seasonal variations and comparing the diets of two developmental stages of Scinax curicica tadpoles. Tadpole diet varied between dry and rainy seasons, but not between the studied developmental stages. These results, together with published studies, suggest that multiple ecological/physiological factors are likely to influence tadpole food intake and should not be overlooked. Studies on neotropical tadpole feeding ecology, digestion capacity, physiological effects of different diets and microbiome versus diet interactions are highly desirable but largely unexplored. Such studies are likely to add valuable information to understand tadpole roles in aquatic food webs, their growth and development performance resulting from food acquisition and assimilation, and consequently their effects on other species in aquatic and terrestrial ecosystems.

KEYWORDS

diet, food selectivity, neotropical region, ontogenetic variation, seasonality, tadpole

INTRODUCTION

Tadpoles play important roles in nutrient cycling, energy flow and bioturbation (Montaña et al., 2019). They are important components of aquatic ecosystems (Iwai & Kagaya, 2005) and influence nutrient transfer between aquatic and terrestrial food webs (Costa & Vonesh, 2013; Hite et al., 2018). As tadpoles show trophic plasticity in response to biotic (Arribas et al., 2015; Caut et al., 2013) and abiotic factors (Carreira et al., 2016), it is also important to take these into account to understand their trophic roles (Montaña et al., 2019). Tadpoles can be herbivores, omnivores, carnivores or detritivores (Altig et al., 2007;

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Schiesari, 2006), but their diets usually include both autotrophic and heterotrophic organisms (Vera Candioti, 2007).

Temperature changes, for instance, may make herbivory more advantageous than omnivory (Carreira et al., 2016) and alter food availability, leading to seasonal diet variations, which are known to exist for some tadpole species (Kloh et al., 2018). Food availability also varies among microhabitats and tadpoles occupying specific microhabitats that are favoured by their ecomorphotypes will be exposed to the food available there (Kloh et al., 2019).

Like the food ingested by tadpoles (Kupferberg, 1997), the microbial communities in animal guts have important implications to animal physiology and development (Tuddenham & Sears, 2015). These microbial communities are affected by the host's genetic background, immune system, age and diet (Tuddenham & Sears, 2015). This association allowed animals to successfully explore a variety of food sources that would not be available otherwise, and to amplify their metabolic potential intertwining their genomes with their microbiome (McFall-Ngai et al., 2013). Besides, animal microbiomes are associated with the habitats occupied by their hosts and may influence tadpole development (Vences et al., 2016).

Considering the great diversity of anuran species with a tadpole stage in the neotropics (Provete et al., 2012), studies on tadpole natural history and ecology are still scarce, despite their ecological importance (Andrade et al., 2007; Rossa-Feres et al., 2015). Here, we summarize knowledge on neotropical tadpole diets and describe the diet of tadpoles of *Scinax curicica* (Hylidae) addressing two knowledge gaps: seasonal variability and developmental-stage-related variability in food ingestion. We chose *Scinax curicica* as a model because it has a nektonic tadpole, and nektonic tadpoles have a diversified diet compared to other ecomorphotypes (e.g. Antoniazzi et al., 2020). Besides, *S. curicica* tadpoles can be found at different seasons and developmental stages.

MATERIALS AND METHODS

Literature review

We conducted a non-automated systematic literature review applying the PRISMA methodology (Page et al., 2021). We first used Clarivate Web of Science, (© Clarivate 2022) to search for publications containing "tadpole" and "diet" (considering all fields) and selected within the results only those studies conducted in South and Central America countries, as well as in Mexico, without timespan restrictions. This yielded 87 papers. After checking their titles and abstracts, we selected 26 papers that were performed with wild, native tadpoles, excluding experiments aimed at testing artificial diets for raising Lithobates catesbeianus (Ranidae) for commercial purposes or a few others that used artificial, manipulated diets to study their effects on tadpoles. After reading the full texts, we excluded one more paper that included tadpoles from South America but did not analyse their diet. We performed complementary searches in Scopus (© Elsevier 2022) using the same criteria, and retrieved 86 papers, from which we screened 24, all of them but one already obtained from Web of Science. We also searched SciELO (Scientific Electronic Library Online, Brazil) using "tadpole" and "diet", which resulted in five papers, two of which met our selection criteria and one of which was not previously found in Web of Science or Scopus (Figure 1). The searches were conducted during March 2022 and re-done on December 6, 2022, to check for eventual new publications. The literature review was led by P. C. Eterovick; the other authors also



FIGURE 1 PRISMA diagram (sensu Page et al., 2021) showing the steps of the systematic literature review performed on diets of neotropical tadpoles in their native habitats.

searched additional sources (i.e. Google Scholar, reference lists, personal communications) and checked whether selected papers were included in the results obtained from the systematic review. No additional papers fulfilling our criteria were found in these other sources.

Diet of Scinax curicica tadpoles

Scinax curicica is a treefrog endemic to the Espinhaço Mountain Range in southeastern Brazil (Eterovick et al., 2020). It breeds usually in puddles and ponds in high altitude areas from September to February. Tadpoles are diurnal, nektonic and can be found year-round (Eterovick et al., 2020). We collected tadpoles from a backwater of a temporary stream (19°17'28.7" S 43°34'39.8" W; 1374 m.a.s.l.) at the surroundings of the National Park Serra do Cipó on January 14 (rainy season) and September 21 (dry season) 2020. The rainy season in the area extends from October to March and the dry season from April to September. Rainfall varies between 1460 and 2490 mm and mean temperatures range from 13 to 29°C (Viveros, 2010). We collected 20 tadpoles in each period, 10 of them in Gosner (1960) stage 25 and the other 10 in stage 30. The tadpoles were immediately euthanized in xylocaine 10% (Pharlab Industria Farmaceutica SA) and then preserved in 10% formalin (Kloh et al., 2019). We confirmed tadpole stages under stereomicroscope at the laboratory. Next we removed the tadpole's guts and used material extracted from the anterior third of the gut to quantify ingested items. The material was diluted in 1 mL distilled water and placed in a Sedgewick Rafter counting chamber and examined under optic microscope (Olympus cx40) under 400× magnification (following Kloh et al., 2019). We identified ingested items based on specialized literature (Bicudo & Menezes, 2005; Silva et al., 2020).

We compared the gut contents of *S. curicica* tadpoles between the two developmental stages (25 and 30) and two seasons (rainy and dry; i.e., January and September). We adjusted the data on individual tadpole diets (numbers of items consumed for each food category) to two axes representing latent variables and built a model to test for effects of the studied developmental stages and seasons on the food items consumed by tadpoles. For the modelling we used the packages mvabund (Wang et al., 2022) and ecoCopula (Popovic et al., 2019) in R version 4.2.2. (R Core Team, 2021).

RESULTS

Literature review

The search for publications on neotropical tadpole diets resulted in 28 papers, 14 of which reporting on studies conducted in Brazil, 13 in Argentina (one of them also including species from Panama) and one in Mexico (Figure 2a, Appendix S1). Tadpoles of 63 species had their diets studied at least on one occasion/habitat (Figure 2b). Most studies focused only on the visual analyses of gut contents, just two included also stable isotope analyses. Only four studies considered temporal variability in tadpole diet composition, four searched for possible differences among tadpole developmental stages and seven evaluated food preferences based on food availability quantification. Just one study approached tadpole microbiomes but associated gut content analyses were not performed for the neotropical tadpoles included.

Diet of Scinax curicica tadpoles

Scinax curicica tadpoles ate unicellular and filamentous Bacillariophyceae and Zygnematophyceae, Euglenophyceae, Cyanophyceae, Fungi, Spermatophyta (pollen) and Testate Amoeba (Figure 3, Appendix S1). Some amorphous material could also be seen in tadpole guts and may have resulted from items that are quickly digested or most likely from ingestion of amorphous material itself. Tadpole diets differed between seasons (dev = 29.666, p = 0.001). Developmental stages did not explain diet variation (dev = 8.099, p = 0.201), nor interacted with seasons (dev = 11.963, p = 0.076). According to univariate tests, the food items that contributed to variability among tadpoles at different seasons were testate amoeba (dev = 13.276, p = 0.001) and Euglenophyceae (dev = 11.047, p = 0.001; Figures 3), both consumed at higher amounts in the rainy season.



FIGURE 2 Countries where studies on tadpole diets were conducted (and from where the tadpoles are native; a), and taxonomic distribution of studied tadpoles (b) based on a systematic review of the literature with no time restriction. Tadpoles of 63 species had their diets studied at least on one occasion/habitat, most of them in Brazil and Argentina. Taxa included six species in one genus from Bufonidae (*Rhinella arenarum*, *R. diptycha*, *R. fernandezae*, *R. jimi*, *R. rubescens* and *R. spinulosa*), four species in three genera from Ceratophryidae (*Chacophrys pierottii*, *Ceratophrys cranwelli*, *Lepidobatrachus laevis*, and *L. llanensis*), 34 species in 12 genera from Hylidae (*Aplastodiscus cavicola*, *A. sibilatus*, *Boana cordobae*, *B. pulchella*, *B. rosenbergi*, *Bokermannohyla alvarengai*, *B. capra*, *B. nanuzae*, *B. saxicola*, *Dendropsophus* sp., *D. microcephalus*, *D. nanus*, *Lysapsus limellum*, *Pithecopus hypochondrialis*, *P. megacephalus*, *P. nordestinus*, *Phasmahyla jandaia*, *Phyllomedusa sauvagii*, *Pseudis minuta*, *P. paradoxa*, *Scinax angrensis*, *S. boulengeri*, *S. fuscovarius*, *S. fuscomarginatus*, *S. granulatus*, *S. littoreus*, *S. machadoi*, *S. nasicus*, *S. perpusillus*, *S. x-signatus*, *S. similis*, *Trachycephalus cunauaru*, *T. typhonius* and *Triprion petasatus*), 13 species in three genera from Leptodactylidae (*Alsodes gargola*, *Leptodactylus ocellatus macrosternum*, *L. bolivianus*, *L. fuscus*, *L. natalensis*, *L. podicipinus*, *Physalaemus albonotatus*, *P. biligonigerus*, *P. centralis*, *P. cuvieri*, *P. fuscomaculatus*, *P. nattereri* and *P. santafecinus*), three species in two genera from Microhylidae (*Dermatonotus muelleri*, *Elaschistocleis bicolor* and *E. ovalis*), two species in two genera from Odontophrynidae (*Odontophrynus americanus*, *Macrogenioglotus alipioi*) and one species from Telmatobiidae (*Telmatobius* cf. *atacamensis*). Most studies were based in visual inspection of gut contents and did not approach seasonal or developmental st



FIGURE 3 Multivariate comparison of the diets of *S. curicica* tadpoles according to types and amounts of consumed items in two developmental stages (25 and 30, sensu Gosner, 1960) and in two seasons (rainy and dry). Testate amoeba and Euglenophyceae were more consumed in the rainy season than in the dry season, leading to seasonal variation in diet composition. Diet did not vary between developmental stages.

DISCUSSION

Neotropical tadpole diet composition

Most of the studies on neotropical tadpole diet analysed gut contents visually, as already noticed by Montaña et al. (2019). Only two studies employed stable isotope analyses (Antoniazzi et al., 2020; Huckembeck et al., 2014), a technique that gives a more realistic picture of what is

actually assimilated by tadpoles. Based on available studies, diatoms (Bacillariophyta, Bacillariophyceae) were usually the numerically predominant items in the diets of most neotropical tadpoles (e.g. Baffico & Ubeda, 2006; Kloh et al., 2019; Protázio et al., 2020; Santos et al., 2016). The most remarkable exceptions were the predaceous tadpole of Ceratophryidae, which ate insects, crustaceans and tadpoles (Fabrezi & Cruz, 2020; Vera Candioti, 2005), the bromeliad-dwelling tadpoles of Scinax littoreus and S. perpusillus, which ate mainly Cyanophyceae and Zygnematophyceae respectively (Sabagh et al., 2012) and the tree hole breeder Trachycephalus cunauaru, which ate mainly conspecific eggs (Schiesari et al., 2003). Tadpoles also had other items besides algae in their guts, however, usually in small proportions, such as fungi (Protázio et al., 2020), testate amoeba (Kloh et al., 2018, 2019; Pollo et al., 2019; Sabagh et al., 2012; Vera Candioti, 2005; Vera Candioti, 2007), insect remains/eggs/larvae (Dutra & Callisto, 2005; Pollo et al., 2019; Protázio et al., 2020; Sabagh et al., 2012), Rotifera, Cilliophora, Nematoda, Crustacea, Oligochaeta (Verburg et al., 2007), pollen (Kloh et al., 2019; Protázio et al., 2020; Sabagh et al., 2012). The proportion of diatoms in tadpole diets may be overestimated because many studies analysed the whole digestive tract and the capsules of diatoms can be identified even after digestion, whereas other items are digested and not seen in posterior portions of the gut (Kloh et al., 2018). However, even in studies that considered just the first third of the gut (e.g. Babini et al., 2017; Baffico & Ubeda, 2006; Bionda et al., 2012, 2013; Kloh et al., 2018), where the proportions of ingested items can be observed with the least digestion (Kloh et al., 2018), diatoms were the main item in the diets of several species. Bacillariophyceae are periphytic algae and their consumption by benthic tadpoles is expected, as these tadpoles supposedly feed on the bottom (Altig & Johnston, 1989), although nektonic tadpoles have also been reported to consume large amounts of these algae (e.g. Pithecopus megacephalus; Kloh et al., 2019).

The role of tadpole ecomorphotypes and microbiome on diet

Tadpole ecomorphotypes are likely to have an important influence on what tadpoles consume (Antoniazzi et al., 2020), as they relate to the use of specific microhabitats which vary in food availability (Kloh et al., 2019). Microhabitats have different surfaces for periphyton attachment (e.g. Kloh et al., 2019), and substrate orientation can also influence food acquisition by scraping tadpoles (Annibale et al., 2019). Consequently, the diets of tadpoles reflect in a large extent the food availability and distribution in the microhabitats they use (Kloh et al., 2019). For instance, the neustonic tadpole of *Phasmahyla jandaia* has a diet largely differentiated from those of other sympatric and syntopic benthic/nektonic stream tadpoles (Kloh et al., 2019, 2021; Appendix S1). Isotopic signatures also differ among microbial feeders, herbivores and neuston feeders (Verburg et al., 2007).

Interestingly, the composition of diets of tadpoles around the world do not change considerably regarding the main taxonomic groups consumed (e.g. Chen et al., 2008; Ocock et al., 2018; Pryor, 2014). The gutassociated microbiota also showed similarities between tadpoles from Brazil and Madagascar, corroborating microbiome and diet association (Vences et al., 2016). Although Vences et al. (2016) did not analyse the diet of Brazilian tadpoles, the tadpoles from Madagascar consumed mainly diatoms, with smaller proportions of algae, plant fragments, fungi and insect fragments (Vences et al., 2016), a diet with similar composition to those of many neotropical tadpoles (Appendix S1).

Temporal and ontogenetic variation in diet composition

Most studies did not test nor consider variations among developmental stages, except for the study on the diets of Scinax angrensis (Sousa-Filho et al., 2007), Bokermannohyla saxicola (Kloh et al., 2018) and Phasmahyla jandaia tadpoles (Kloh et al., 2021). The diet of S. angrensis tadpoles varied between developmental stages (Sousa-Filho et al., 2007) as also did the diet of B. saxicola but, in this case, just considering number of ingested items and not biovolume (Kloh et al., 2018). However, P. jandaia tadpoles showed subtle variations in food preference among developmental stages, but they could not be precisely assigned to developmental stage based on their diets. This diet similarity throughout development may be related to the more specialist habits of these tadpoles (Kloh et al., 2021). Variation throughout tadpole developmental stages has also been recorded for temperate species (Schriever & Williams, 2013). Regarding seasonal variation in food consumption, only the tadpoles of B. saxicola were compared within the same developmental stage throughout the year, and showed different diets, what may be related to food availability (Kloh et al., 2018). Bromeliad-dwelling tadpoles of Scinax littoreus and S. perpusillus did not show diet variation between dry and rainy seasons, however, a broad range of developmental stages was pooled for the analyses (Sabagh et al., 2012).

Food selectivity and other knowledge gaps

Food selectivity has rarely been tested for neotropical tadpoles. Tadpoles of *Phasmahyla jandaia* showed preference for pollen, testate amoeba and *Euglena* (Kloh et al., 2021), tadpoles of *Scinax littoreus* preferred algae and fungi, whereas *S. perpusillus*, in the same bromeliad phytotelmata habitat, showed no preferences, eating food items in the same proportions available (Sabagh et al., 2012). The diets of Brazilian stream tadpoles of five species reflected the availability of food items in the microhabitats they used, however, some items were consumed in larger proportions, whereas others were apparently avoided, the discrepancy between available and consumed proportions being larger for some species than others (e.g. *Bokermannohyla saxicola*; Kloh et al., 2019). Although tadpoles are broadly assumed to be non-selective feeders (e.g. Dutra & Callisto, 2005; Protázio et al., 2020), the available studies that accessed food availability and compared to consumption by tadpoles indicate that this should not be considered a general rule (e.g. Antoniazzi et al., 2020).

The data on diet composition of neotropical tadpoles are scarce considering their species diversity but relatively large compared to other regions (Montaña et al., 2019). However, there are still important gaps regarding feeding ecology, as previously noticed by Altig et al. (2007). Tadpole flexibility in food acquisition based on the exploitation of available resources and in response to varying nutritional needs throughout development is an interesting topic that needs to be further explored in the neotropics, as well as in other regions (Montaña et al., 2019). Also, digestibility of different food items was not accessed in any of the published articles reporting natural diets of neotropical tadpoles, indicating a huge knowledge gap. Some studies addressed assimilation efficiency under different temperatures and diets (Benavides et al., 2005) or effects of different diets on growth, development (Toledo et al., 2014) and morphological plasticity (Castañeda et al., 2006; Ruthsatz et al., 2019, 2022), but they all used manipulated/artificial diets that did not correspond to what tadpoles eat in situ. The investigation of natural diets is important because even if nutritional composition of artificial diets mirror natural ones, digestibility is likely to vary among food items (Pryor, 2014) and play a role on the benefits of each diet, as assimilation of consumed items vary (Schmidt et al., 2017).

Environmental impacts and tadpole diet composition

Besides natural sources of variation, environmental impacts may also influence tadpole food acquisition. A comparison of diets of *Rhinella arenarum* and *Physalaemus biligonigerus* tadpoles from preserved areas versus areas impacted by agriculture and livestock showed reduced food consumption and growth in impacted areas with increased representation of resistant taxa, suggesting that diet evaluation can also be an early indicator on how habitat quality may affect tadpole growth and development (Babini et al., 2017; Bionda et al., 2012, 2013). Testate amoebae are common in low-quality aquatic habitats (Sousa, 2008) and were found in the diets of many tadpoles (Babini et al., 2017; Kloh et al., 2018, 2021; Pollo et al., 2019; Sabagh et al., 2012; Vera Candioti, 2005; Vera Candioti, 2007). This suggests that, as a topic worth further exploration, increased consumption of testate amoeba could be an indicator of decreasing habitat quality.

Diet of Scinax curicica tadpoles

The diet of *Scinax curicica* tadpoles varied between rainy and dry seasons. This result differs from results obtained for *Bokermannohyla saxicola*, whose tadpoles had greater than expected niche overlap among seasons (Kloh et al., 2018). However, stage-specific nutritional needs did not seem to define diet composition for neither *S. curicica* nor *B. saxicola* as tadpoles from both stages 25 and 30 had similar diets within seasons (Kloh et al., 2018; this study). *Scinax angrensis* tadpoles also had similar diets in two studied developmental stages (Sousa-Filho et al., 2007).

Phasmahyla jandaia tadpoles had very similar diets at three developmental stages, however, analyses of food availability showed that they have strong food selectivity, and their diet reflects ecomorphotype related microhabitats (Kloh et al., 2021). Thus, it cannot be said that the seasonal diet variation for *S. curicica* is simply due to the combination of indiscriminate consumption and expected seasonal variations in available food items (e.g. Ferragut et al., 2010). The information available so far on tadpole feeding ecology, although limited, indicates that both differences in microhabitat use (Kloh et al., 2019) and food selectivity (e.g. Antoniazzi et al., 2020) are likely to be important. The diets of tadpoles are thus likely influenced by a complex combination of variables, which have frequently not been well controlled in previous studies.

Regarding the algae found in the guts of *S. curicica*, there is little specific information in the literature about their relevance for tadpoles. According to Lee (2008), the green algae (Chlorophyta and Charophyta) are relevant sources of carotenoids for animals that cannot synthesize these important antioxidant agents. Cyanobacteria is used as human and animal food supplements, and diatoms (Bacillariophyta) are preferred by some invertebrates (Lee, 2008), being highly nutritive due to their fatty acid content (Lavens & Sorgeloos, 1996). Although there are specific differences in the biochemical composition of different microalgal taxa, the protein fraction is

always the major organic constituent, commonly followed by lipid, and then by carbohydrate (Lavens & Sorgeloos, 1996).

Testate amoeba and Euglenophyceae were the food items that contributed the most to the seasonal variation in the composition of *S. curicica* tadpoles. The tests of testate amoeba are rich in iron and manganese (Sousa, 2008), which are important for vertebrate immunity and metabolism (Pinto-Coelho, 2009). Their consumption by *S. curicica* tadpoles was higher in the summer (rainy season). The cause of this increased consumption remains to be investigated, as it could include higher availability of this item in the habitat and/or higher selectivity by tadpoles, maybe due to an increase in metabolism in the warmer season.

The presence of some amorphous material in the guts may indicate other food sources with rapid digestion or organic material with no determined shape. For example, tadpoles can scrape the bodies of other dead tadpoles (PCE, pers. obs.) and eat their own faeces (Pryor, 2014). The proportion of amorphous material in relation to identifiable items increases through the end of the gut (Kloh et al., 2018, JSK pers. obs.). Thus, we optimized diet characterization by restricting our analyses to the first third of the gut.

Concluding remarks

Studies on the diet of neotropical tadpoles (Appendix S1) approached in just a few instances the effects of seasonality, developmental stage and food selectivity as natural sources of variability in diet composition, but the available data indicate none of these sources of variation should be overlooked. The dynamic of food acquisition by tadpoles is likely to reflect not only in their health but also in aquatic (Costa & Vonesh, 2013; Hite et al., 2018; Schmidt et al., 2017) and terrestrial food webs, as diet influences populations of aquatic prey (Costa & Vonesh, 2013) as well as time to metamorphosis (Díaz–Páez & Canales–Arévalo, 2018; Kupferberg, 1997).

In summary, studies on neotropical tadpole feeding ecology, digestion capacity, physiological effects of different diets, and microbiome versus diet interactions are highly desirable and still practically unexplored. Such studies are likely to add valuable information to understand tadpole roles in aquatic food webs, their growth and development performance. All these parameters result from food acquisition and assimilation and have consequent effects on other species in aquatic and terrestrial ecosystems.

AUTHOR CONTRIBUTIONS

lara Matias Gonçalves: Conceptualization (equal); data curation (equal); investigation (equal); writing – original draft (equal); writing – review and editing (supporting). **Jéssica S. Kloh:** Conceptualization (equal); data curation (equal); methodology (equal); project administration (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Katharina Ruthsatz:** Data curation (supporting); validation (equal); writing – review and editing (supporting). **Cleber Cunha Figueredo:** Data curation (supporting); investigation (equal); methodology (equal); resources (equal); supervision (equal); writing – review and editing (supporting). **Paula Eterovick:** Conceptualization (equal); data curation (equal); formal analysis (lead); methodology (equal); project administration (equal); supervision (equal); writing – review and editing (equal).

ACKNOWLEDGEMENTS

We are thankful to Yasmim Mossioli and Felipe S. F. Leite for suggestions in a previous version of this manuscript, the Parque Nacional da Serra do Cipó for support during the field trip, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a Scholarship for JSK and a Research Productivity grant for PCE. Collection permits were provided by Sisbio/ ICMBio (64500) according to ethical guidelines. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

This study was financed by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) through a Scholarship to JSK and a Research Productivity grant to PCE. Collection permits were provided by Sisbio/ICMBio (64500) according to ethical guidelines.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data sets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

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How to cite this article:

Gonçalves, I.M., Kloh, J.S., Ruthsatz, K., Figueredo, C.C. & Eterovick, P.C. (2023) Description and shaping factors of diet and feeding ecology of neotropical tadpoles: A case study and a comprehensive review. *Austral Ecology*, 00, 1–13. Available from: <u>https://doi. org/10.1111/aec.13302</u>