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ANIMAL SCIENCE

Feeding ecology of six sympatric hylids (anura, hylidae) in a seasonally floodable environment in the brazilian Amazon

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Abstract: The knowledge of diet is essential to understanding species biology and thus fostering conservation strategies. This study described and compared the diet of six species of anurans in the family Hylidae (*Boana punctata, B. raniceps, Dendropsophus leucophyllatus, D. walfordi, Lysapsus bolivianus,* and *Sphaenorhyncus lacteus*), from a floodplain environment in the Brazilian Amazon. Research was conducted in the Lake Maicá complex, in Santarém municipality, Pará state, between April and August 2023. The diet of the six species was composed mainly of arthropods, with the order Diptera being the most common prey category, except in *B. raniceps* (Orthoptera) and *S. lacteus* (Formicidae). We observed a weak correlation between individual body size and the volume of prey consumed. Overall, niche overlap between species was high, with most having a broad trophic niche and generalist diets. The exception was *S. lacteus*, which had a diet which specialized on ants. Additionally, these findings emphasize the ecological role of hylid frogs in regulating some arthropods populations, reinforcing their significance in maintaining trophic dynamics in floodplain ecosystems.

Key words: Amazon floodplain, *Boana*, *Dendropsophus*, *Lysapsus*, *Sphenorhynchus*, trophic ecology.

INTRODUCTION

Assessing diet is an important aspect of understanding the biology of amphibian species (Duellman & Trueb 1994). Providing studies that describe the trophic ecology of organisms can be considered one of the first steps in studying the basic ecology of a group, and are therefore essential to understanding their ecological niches (Sih & Christensen 2001). Furthermore, studying trophic ecology enables the understanding of ecological interactions between organisms and of the processes that sustain biodiversity in ecosystems (Oliveira et al. 2015, Begon & Townsend 2021).

Anurans are considered the most ecologically diverse lineage of living amphibians (Duellman & Trueb 1994). They play a crucial role in the ecosystems in which they are found and can act both as predators, regulating the populations of insects and other arthropods, and as prey, sustain the food chain and promote biodiversity (Valencia-Aguilar et al. 2013, Pankaj & Nath 2023). In general, the diet of anurans are composed mainly of invertebrates, with some groups considered opportunistic, showing high dietary diversity, while others display varying degrees of specialization in prey selection (Toft 1980, Duellman & Trueb 1994, Solé & Rödder 2010, Sant'Anna et al. 2022, Rodrigues et al. 2023). For this reason, anurans are considered important organisms for studying the mechanisms of segregation promoting species coexistence (Duré & Kehr 2001, Baia et al. 2020).

Several factors can influence anuran diet composition, including seasonal variation in food availability, intra and interspecific competitive relationships, individual body size, prey size and volume, individual specializations, prey preferences and ecological tolerances of different species, and phylogenetic proximity (Woodward & Hildrew 2002, Cianciaruso et al. 2009, Oliveira & Haddad 2015, Rebouças & Solé 2015, Moser et al. 2022, Ceron et al. 2022, 2023). Theoretically, if two or more species coexist using the same limiting resource and this coexistence is not stable, niche overlap and resource competition is expected, and the less efficient competitor will have its niche reduced, altered or even excluded (Hardin 1960, Hiscock et al. 2023). Additionally, diet is one of the limiting factors that can generate interspecific competition due to trophic niche overlap in an assemblage of organisms (Begon & Townsend 2021). In this context, niche overlap can be understood as the extent to which species share those factors which regulate their population growth (Pastore et al. 2021). Understanding these concepts is central for analyzing inter-species competition, especially when developing hypotheses on how species deal with potentially conflicting ecological interactions, such as competition for food resources. Studies of ecological interactions involving anuran diets have been conducted in a variety of ecosystems and biomes, like Brazilian Cerrado, Atlantic Forest and Amazon (Brandão et al. 2020, Oliveira et al. 2021, Ceron et al. 2023, Moreira-Demarco et al. 2023), but rarely in tropical floodplain environments (Pedroso-Santos et al. 2022, Matos et al. 2022).

Amazonian floodplains (also called "*várzeas*") occur in areas periodically flooded by the overflow of rivers or lakes (Junk 1997). These recurrent flood pulses not only define the nature of the ecosystem, but also play a crucial role in the dynamics of the communities that inhabit it (Junk et al. 1989, Petsch et al. 2023). Knowledge of how the flood cycle structures amphibian communities in these environments is essential for a deeper understanding of the ecological processes involved (Ramalho et al. 2018, Fonte et al. 2021, Ganança et al. 2021). The interconnection between factors influencing anuran diets and the adaptation of these animals to predictable floodplain disturbances, highlights the complex relationship between the biological characteristics of anurans and the ecological patterns of the environment they inhabit (Schiesari et al. 2003, Upton et al. 2014).

Floodplain lakes generally have a substantial covering of aquatic macrophytes (Junk 1997). Such plants are important as they increase habitat heterogeneity, so enhancing the diversity of organisms that can persist in these aquatic systems (Thomaz et al. 2008). These environments are used as dispersal, reproduction, foraging and refuge sites by a wide variety of anuran taxa (Schiesari et al. 2003, Upton et al. 2014), and features of the macrophyte beds such as height, morphotype, connectivity and water depth provides environmental heterogeneity that can influence strongly the distribution of anuran species (Fonte et al. 2021, Ganança et al. 2021, Matos et al. 2022). In the Neotropical regions Hylidae are the anuran family most frequently encountered during ecological studies of macrophyte banks (Upton et al. 2014, Ramalho et al. 2018, Fonte et al. 2021, Ganança et al. 2021, Matos et al. 2022). This family has 1051 known species (Frost 2024), with approximately 400 of them occurring in Brazil (Segalla et al. 2021).

Given the strong influence of flood dynamics on amphibian assemblages (Matos et al. 2022), studies focusing on trophic ecology of hylids in these environments are particularly valuable. Therefore current study aimed to describe and compare the diet composition of six sympatric species of hylids in a Brazilian Amazon floodplain environment: *Boana punctata* (Schneider, 1799), *Boana raniceps* (Cope, 1862), *Dendropsophus leucophyllatus* (Beireis, 1783), *Dendropsophus walfordi* (Bokermann, 1962), *Lysapsus bolivianus* Gallardo, 1961 and *Sphaenorhyncus lacteus* (Daudin, 1800). The study aimed to: (1) identify the most important preys consumed by each study anuran; (2) analyze the niche breadth and the level of niche overlap between the six species; (3) verify the degree of specialization occurred in the diet of the species; (4) Test whether there is a relationship between predator size and the size of their consumed prey.

MATERIAL AND METHODS

Study area

Our study was carried out on the margins of the Lake Maicá complex, within the lower Amazon River floodplain, Santarém municipality, Pará, Brazil (2°27'44.51"S 54°39'34.26"W) (Figure 1). Lake Maicá is located within a lake system influenced by the waters of several streams, as well as by cyclic hydrological pulse of the Amazon River, itself influenced by the Tapajós River and local rainfall (Pinheiro et al. 2016). The banks of aquatic macrophytes that grow on the lake shores are composed mainly of grasses *Paspalum repens* P.J. Bergius and *Echinochloa polystachya* (Kunth) Hitchc, and by floating plants such as *Eichhornia crassipes* (Mart.) Solms, *Pistia stratiotes* L. and *Salvinia* spp (Pinheiro et al. 2016). The region has a hot and humid climate; Am according to the Köppen classification (Alvares et al. 2013). Precipitation is seasonal, with a rainy season between December and June, and a dry period between July and November (Silva et al. 2016). During the study months (April to August), mean monthly rainfall varied between 0.38 mm and 0.05 mm, while mean temperature had a maximum of 28°C and minimum of 25.8°C (INMET – Instituto Nacional de Meteorologia). Changes in mean water level in Lake Maicá can be divided into annual four phases: a flood period from December to March; the high water period, from April to June; the low water period, from July to September; and the dry period, between October and November (Bentes et al. 2018).

Sampling and data collection

Samplings were carried out between April and August 2023, with three sampling days each month. Nocturnal surveys took place from 6:00 p.m. 9:00 p.m. using simultaneous visual and auditory sampling methods to locate anurans (Rödel & Ernst 2004). Four people participated in each sampling effort. Aquatic macrophyte banks along the lakeshore and in the lake vegetation were sampled for hylid species. Captured specimens were placed in plastic bags, then euthanized with benzocaine-based anesthetic cream applied to the skin (Sebben 2007), then fixed in 10% formalin for later preservation in 70% alcohol. This procedure was performed immediately after collection to stop digestion. Collection and euthanasia procedures were authorized by the appropriate agencies (IBAMA/ICMBio/SISBIO License – 24072-3; CEUA UFOPA – 0320230242). All specimens used in the study (Supplementary table) are housed into the Herpetological Collection of the Universidade Federal do Oeste do Pará, Santarém, Pará, Brazil. For each specimen snout-vent length (SVL) was measured with digital calipers (precision, 0.01 mm). Stomach contents were accessed by dissecting the specimens using a longitudinal incision in the ventral region of each animal to remove the stomach. Specimens

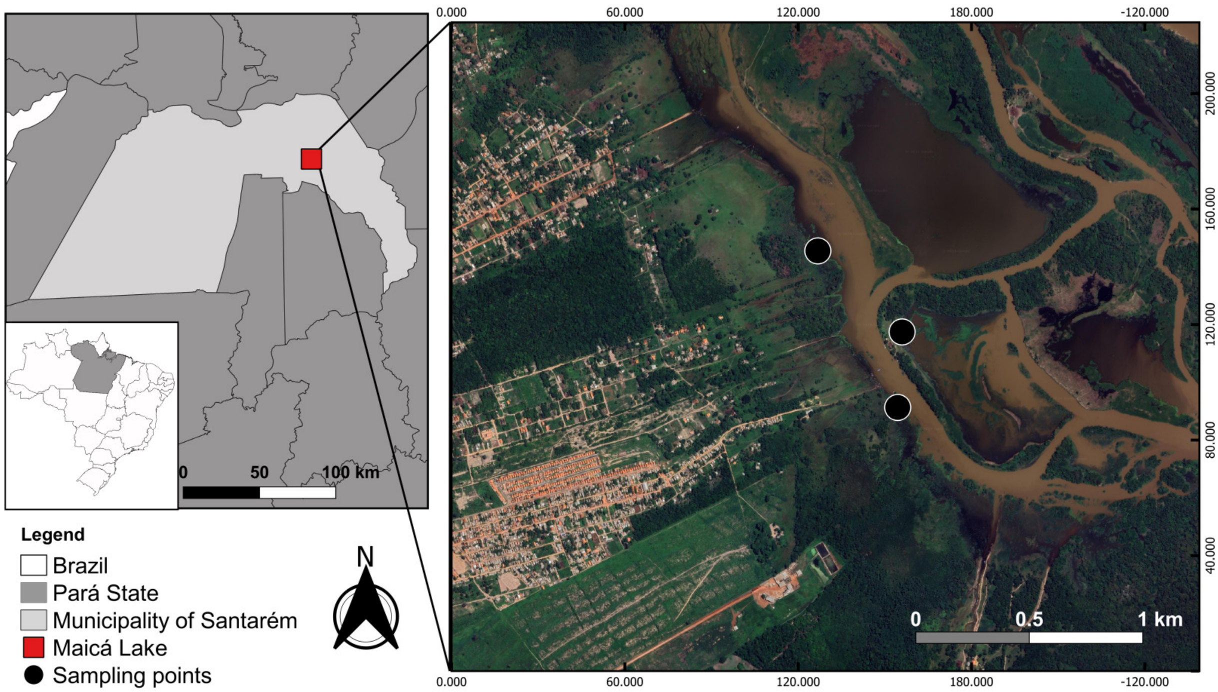

Figure 1. Study area on Maica Lake, lower Amazon River, Santarém municipality, Pará State, Brazil.

were then dissected to access their contents, with extracted materials preserved in cryogenic tubes with 70% alcohol.

Diet analysis

Food item analysis was performed with a stereomicroscope. Identification was made to Order level, with the exception of Hymenoptera, which was categorized to family level (Formicidae). Taxonomic guides and an identification key (Hamada et al. 2014) were used to identify the groups of invertebrates present in the anuran diet (Griffiths & Mylotte 1987). We quantified the volume of each prey item using the equation:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right)x\left(\frac{w}{2}\right)^2$$

Where V represents the volume of the prey, l = length of the item and w = width of the item. Very fragmented prey, where it was not possible to estimate volume accurately, were disregarded and used only for richness data (Garda et al. 2012, 2014, Mesquita et al. 2016). To measure the importance of each prey category, the Relative Importance Index (IRI) was used, calculated with the formula:

$$IRI = (N\% + V\%)\ FO\%$$

Where N% = relative abundance of each prey item in the diet, V% = percentage volume of each prey item in the diet and FO% = percentage frequency of prey item occurrence (Pinkas et al. 1971). The higher the IRI value of a prey item, the greater its importance in the diet.

The trophic niche breadth of the species was calculated using the Levins index (B) (Krebs 1999). This index is defined as:

$$B = 1 / \sum_{i=1}^{n} pi^2$$

Where B = Levins index (breadth of the trophic niche), *i* = prey category, n = number of categories and *pi* is the individual proportion of a given resource *i* found in the diet. The standardized measure of the Levins index (B*sta*) was also calculated on a scale from 0 to 1.

$$Bsta = \frac{(B - 1)}{(n - 1)}$$

Where *n* represents the number of resources (prey categories) recorded and *B* represents the Levins measure of niche breadth. Values closer to 0 represent a more specialized diet (narrow niche breadth), while values closer to 1 indicate a more generalist diet (broad niche breadth) (Krebs 1999). We constructed rarefaction curves to estimate the sample representativeness of the prey set for each anuran species (Sanders 1968); and to compare per species diet diversity via a null model of rarefaction (Krebs 1999, Magurran 1988), since trophic breadth and species richness are strongly associated with the number of observations (Rosa et al. 2002).

To quantify diet diversity, we used the Shannon Diversity Index, given by:

$$H = - - \sum pi \;\; ln \;\; pi,$$

Where *pi* is the numerical proportion of prey item *i* in the numerical sum of *n* prey items (Krebs 1999).

To analyze the degree of trophic niche overlap between species, in terms of the degree of similarity between their diets, Pianka's Trophic Niche Overlap Index (O_{jk}) (Pianka 1973) was calculated, defined by the equation:

$$O_{jk} = \frac{\sum_{n=1}^{0} p_{ij} \times p_{ik}}{\sqrt{\sum_{n=1}^{0} p_{ij}^2 \times \sum_{n=1}^{0} p_{ik}^2}}$$

Where O_{jk} is the niche overlap index between species j and k; P_{ij} is the proportion of resource type i in relation to the total resources used by species j; P_{ik} is the proportion of resource i in relation to the total resources used by species k; and n is the total number of resource categories used by species j and k. The index ranges from 0 (no diet overlap) to 1 (complete diet overlap) (Krebs 1999).

To test whether between species differences in consumed prey volume and length were present, a nonparametric Kruskal-Wallis analysis was performed, and Dunn's post-hoc test was used to compare pairs of species. To test a correlation between SVL and the prey mean length, and between the SVL and the mean prey volume per anuran stomach, a simple regression analysis was performed. All tests were performed using PAST 4.03 software (Hammer et al. 2001).

RESULTS

The stomach contents of 334 specimens of six sympatric hylids (Figure 2, Table SI – Supplementary Material) were analyzed: *Boana punctata* (n = 19), *Boana raniceps* (n = 15), *Dendropsophus leucophyllatus* (n = 10), *Dendropsophus walfordi* (n = 20), *Lysapsus bolivianus* (n = 228) and

Sphaenorhyncus lacteus (n = 32). Of these, 254 (78.4%) contained some form of biological material (Table I). In total, 17 different prey categories recorded in the study individuals, these being mainly arthropods (Table II). Per species rarefaction curves showed that (except in *L. bolivianus*) prey richness did not show a tendency to stabilize as the number of analyzed stomachs increased (Figure 3), suggesting that by increased sampling would add new diet items, either via new prey taxa a greater abundance. The higherest richness (Figure 3) and greatest taxonomic diversity (H') were recorded in the diet of *B. raniceps* and *L. bolivianus* (Table I).

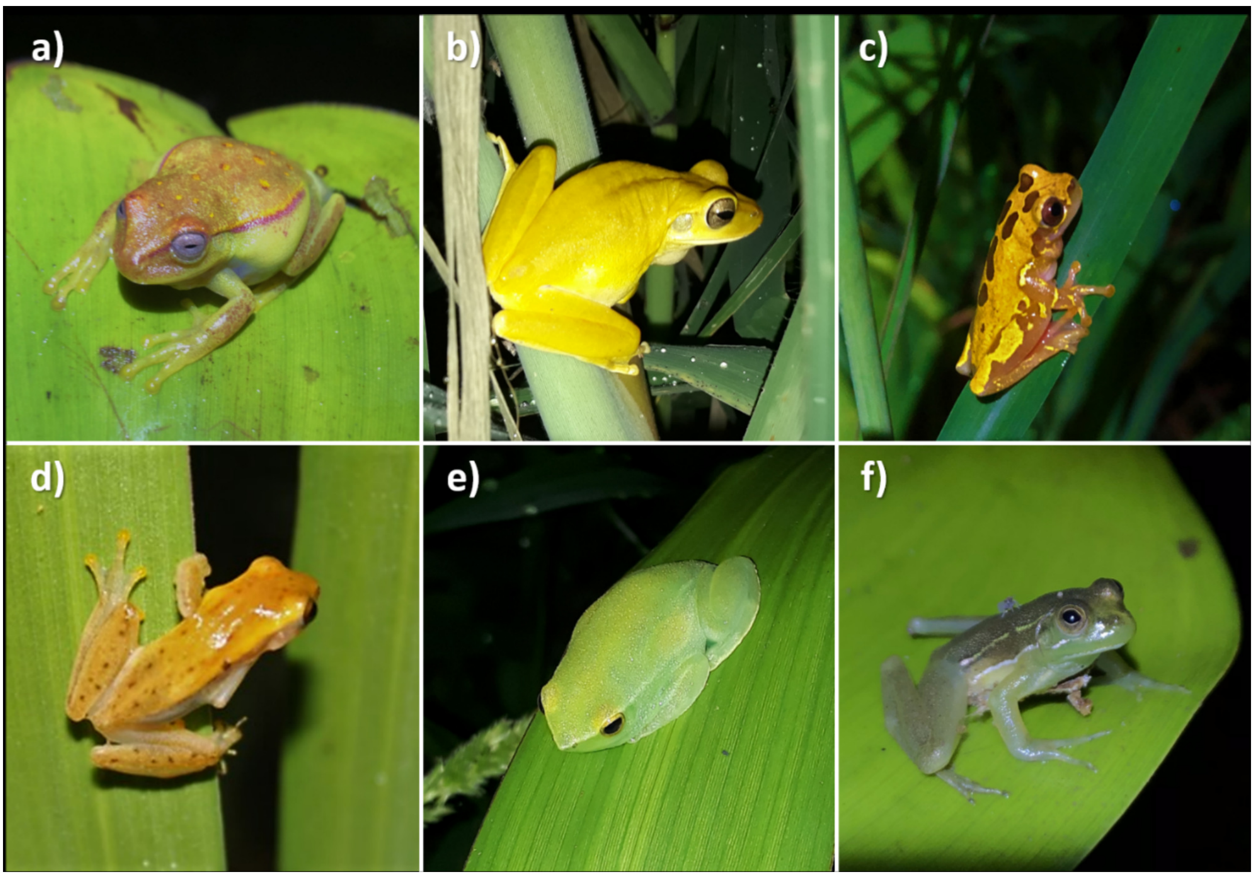

Figure 2. Species of anurans found in a floodplain habitat of Lake Maicá, lower Amazon River, Santarém Pará, Brazil. a: *Boana punctata,* b: *Boana raniceps;* c: *Dendropsophus leucophyllatus;* d: *Dendropsophus walfordi;* e: *Sphaenorhyncus lacteus;* f: *Lysapsus bolivianus.*

Table I. Species, total number of specimens collected (N), number of specimens with stomach content, total richness of prey consumed, dominant (most frequent) prey category, mean snout-vent length (SVL) and trophic diversity (H'), for anurans collected from a floodplain environment, Santarém municipality, Pará state, Brazil.

Species	N	Number of specimens with stomach content	Richness of prey consumed	Dominant prey category	SVL (mm)	H'
Boana punctata	19	9	7	Diptera	21.24	1.71
Boana raniceps	15	13	11	Orthoptera	44.27	2.12
Dendropsophus leucophylatus	10	9	9	Diptera	19.69	1.88
Dendropsophus walfordi	20	15	6	Diptera	16.82	0.84
Lysapsus bolivianus	228	181	16	Diptera	17.61	1.79
Sphaenorhyncus lacteus	32	27	7	Formicidae	31.24	0.56
Total	**324**	**254**	**56**			

Table II. Prey categories found in the stomach contents of six species of sympatric hylids collected from a floodplain environment in Santarém municipality, Pará state, Brazil. N%: number of items consumed; F%: frequency of items; V%: volume of prey (mm³); IRI%: Index of Relative Importance. *Bsta*: breadth of the trophic niche.

Prey Category	*Boana punctata*				*Boana raniceps*				*Dendropsophus leucophyllatus*			
	N%	F%	V%	IRI%	N%	F%	V%	IRI%	N%	F%	V%	IRI%
ARACHNIDA												
Acari	5.88	11.11	4.06	–	3.45	7.69	0.0007	0.74	5.26	11.11	0.2	1.36
Aranae	–	–	–	5.18	6.9	15.38	3.68	4.52	–	–	–	–
INSECTA												
Blattodea	–	–	–	–	3.45	7.69	31.04	7.37	–	–	–	–
Coleoptera	–	–	–	–	20.69	23.08	0.64	13.68	10.53	22.22	30.98	20.66
Coleoptera (larvae)	–	–	–	–	–	–	–	–	5.26	11.11	1.02	1.57
Collembola	23.53	11.11	0.05	12.28	–	–	–	–	–	–	–	–
Diptera	29.41	22.22	4.38	35.21	–	–	–	–	31.58	22.22	1.13	16.28
Diptera (larvae)	–	–	–	–	–	–	–	–	5.26	11.11	0.36	1.4
Diptera (pupae)	5.88	11.11	7.07	6.75	–	–	–	–	–	–	–	–
Hemiptera	5.88	11.11	9.27	7.9	3.45	7.69	3.78	1.55	5.26	11.11	39.76	11.21
Hymenoptera	–	–	–	–	3.45	7.69	0.03	0.74	5.26	11.11	9.87	3.77
Hymenoptera (Formicidae)	–	–	–	–	10.34	15.38	0.03	4.44	5.26	11.11	0.49	1.43
Hymenoptera (pupae)	–	–	–	–	–	–	–	–	–	–	–	–

Table II. Continuation.

Prey Category	*Boana punctata*				*Boana raniceps*				*Dendropsophus leucophyllatus*			
	N%	F%	V%	IRI%	N%	F%	V%	IRI%	N%	F%	V%	IRI%
Odonata	–	–	–	–	3.45	7.69	9.6	2.79	–	–	–	–
Orthoptera	5.88	11.11	25.22	16.21	20.69	46.15	17.04	48.39	–	–	–	–
Gastropoda	–	–	–	–	10.34	23.08	6.33	10.69	–	–	–	–
Plant Material	11.76	22.22	4.05	16.48	3.45	7.69	20.33	5.08	26.32	44.44	16.18	42.32
Unidentified	11.76	22.22	45.91	–	10.34	15.38	7.5	–	–	–	–	–
Bsta	0.6				0.58				0.51			
Prey Category	*Dendropsophus walfordi*				*Sphaenorhynchus lacteus*				*Lysapsus bolivianus*			
	N%	F%	V%	IRI%	N%	F%	V%	IRI%	N%	F%	V%	IRI%
ARACHNIDA												
Acari	6.76	13.33	0.19	–	0.37	3.7	0.003	0.02	6.4	6.63	0	0.99
Aranae	6.76	26.67	19.69	8.46	0.74	7.41	2.89	0.35	2.79	11.05	20.23	5.95
INSECTA												
Blattodea	–	–	–	–	–	–	–	–	–	–	–	–
Coleoptera	–	–	–	–	2.57	18.52	3.15	1.4	4.3	17.13	5.12	3.77
Coleoptera (larvae)	–	–	–	–	–	–	–	–	2.91	9.94	5.64	1.99
Collembola	–	–	–	–	–	–	–	–	3.02	6.08	0.02	0.43
Diptera	78.38	73.33	5.31	73.59	0.37	3.7	0.69	0.05	48.6	53.04	0.72	61.15
Diptera (larvae)	–	–	–	–	–	–	–	–	1.4	4.42	1.93	0.34
Diptera (pupae)	1.35	6.67	3.43	0.38	–	–	–	–	1.86	6.08	0.6	0.35
Hemiptera	–	–	–	–	–	–	–	–	14.53	29.28	3.07	12.05
Hymenoptera	–	–	–	–	0.37	3.7	0.2	0.03	0.47	2.21	0.43	0.05
Hymenoptera (Formicidae)	4.05	20	59.84	15.32	84.93	85.19	0.75	96.07	0.93	3.87	0.52	0.13
Hymenoptera (pupae)	–	–	–	–	–	–	–	–	0.23	1.1	0.73	0.02
Odonata	–	–	–	–	–	–	–	–	1.86	8.29	29.45	6.07
Orthoptera	–	–	–	–	–	–	–	–	1.4	6.63	29.03	4.72
Gastropoda	–	–	–	–	–	–	–	–	–	–	–	–
Plant Material	2.7	6.67	11.55	1.14	10.29	11.11	3.97	2.09	5.12	14.36	0.83	2
Unidentified	–	–	–	–	0.37	3.7	88.36	–	4.19	19.89	1.69	–
Bsta	0.12				0.06				0.17			

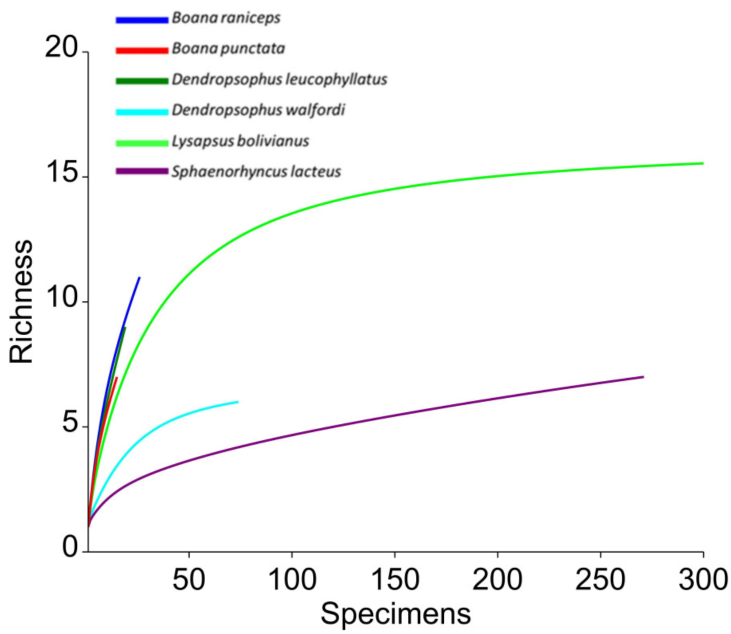

Figure 3. **Rarefaction curves based on prey richness for the six species of sympatric hylids studied in the Lake Maicá floodplain, lower Amazon River, Santarém Pará, Brazil.**

Lysapsus bolivianus had 181 individuals with stomach contents, with the most frequent and abundant prey types being Acari, Coleoptera, Diptera and Hemiptera. The most important prey categories for this species were Diptera (IRI% = 61.5) and Hemiptera (IRI% = 12.05) (Figure 4). For *Sphaenorhynchus lacteus*, 27 individuals had stomach contents, with the diet being dominated by Formicidae (IRI% = 96.07). For *Boana punctata*, the nine individuals' stomachs containing prey, had mostly Diptera (IRI% = 35.21), as did the 15 individuals of *Dendropsophus walfordi* (IRI% = 73.59). The nine specimens of *Dendropsophus leucophyllatus* with stomachs containing food items had Coleoptera as the main prey (IRI% = 20.66). The 13 individuals of *Boana raniceps* with food items as stomach content, collectively had Orthoptera as the main prey (IRI% = 48.39). *Boana raniceps* was also the only species to have Blattodea and Gastropoda in its diet (see Table II).

Boana punctata had the widest trophic niche breadth (Bsta = 0.60), followed by *B. raniceps* (Bsta = 0.58) and *D. leucophyllatus* (Bsta = 0.51). The lowest niche breadth values were obtaoned for *L. bolivianus* (Bsta = 0.17), *D. walfordi* (Bsta = 0.12) and *S. lacteus* (Bsta = 0.06). The species with the most similar diets were *B. punctata, D. walfordi, D. leucophyllatus and L. bolivianus*, with O_{jk} values above 0.70 indicating high levels of trophic niche overlap (Table III). In contrast, *Boana raniceps* and *S. lacteus* were the species had the lowest niche overlap indices (Table III). A significant difference was found between the mean volume ($p < 0.001$; Hc = 41.6) and mean length of prey ($p < 0.001$; Hc = 42.0) among the six species (Figure 5c and 5d, Table SII – Supplementary Material). Although statistically significant, the observed relationships between predator SVL and prey size (length and volume) explained only a small portion of the variance ($p < 0.005$; $r^2 < 0.30$), suggesting a weak trend (Figure 5a and 5b). When species were analyzed individually, a significant correlation was found only for *L. bolivianus* ($p = 0.02$), although with low explanatory power ($r^2 = 0.05$).

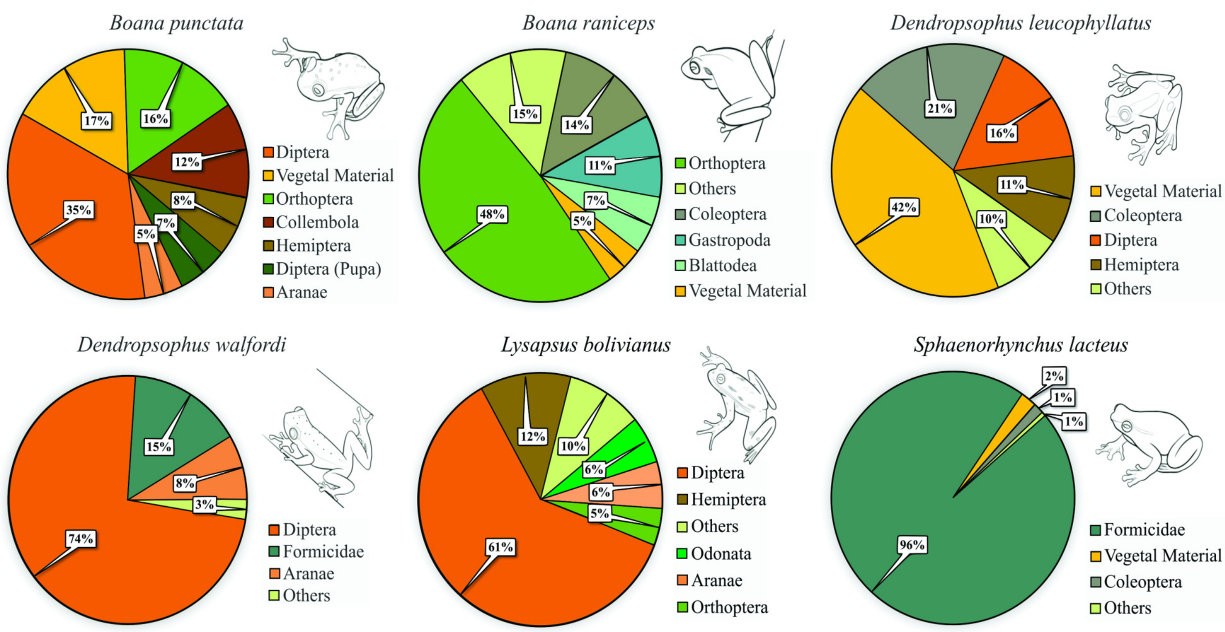

Figure 4. Diet composition for six species of sympatric hylids found in a floodplain environment in the municipality of Santarém Pará, Brazil. Percentages represent the Relative Importance Index (IRI).

Table III. Trophic niche overlap index (Ojk) between sympatric hylid species collected from a floodplain environment in the of Santarém municipality, Pará state, Brazil.

	B. punctata	*B. raniceps*	*D. leucophyllatus*	*D. walfordi*	*L. bolivianus*	*S. lacteus*
B. punctata	—	0.17	0.70	0.73	0.79	0.04
B. raniceps		—	0.27	0.04	0.13	0.33
D. leucophyllatus			—	0.74	0.81	0.20
D. walfordi				—	0.96	0.06
L. bolivianus					—	0.04
S. lacteus						—

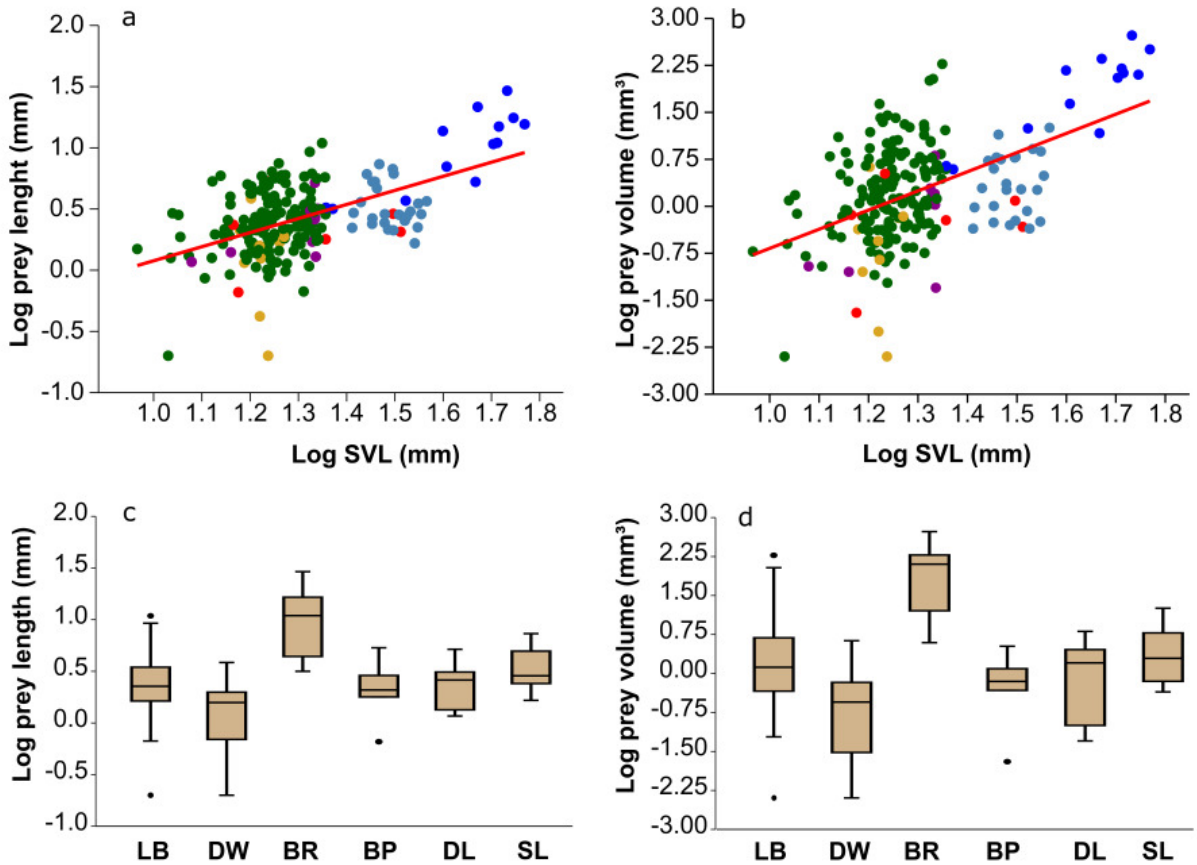

Figure 5. Relationship between snout-vent length (SVL) and mean prey length. b. Relationship between SVL and mean prey volume. c. Mean length (log) of prey consumed by each anuran species. d. Mean volume (log) of prey consumed by each anuran species. BP: *Boana punctata* (Red), BR: *Boana raniceps* (Blue), DL: *Dendropsophus leucophyllatus* (Purple), DW: *Dendropsophus walfordi* (Gold), LY: *Lysapsus bolivianus* (Green), SL: *Sphaenorhyncus lacteus* (Light blue).

DISCUSSION

The species analyzed here showed similarity in the composition of their diets, which are largely composed of arthropods. Diptera (mosquitoes and flies) were the most frequent and most important prey items in the diet of most species. However, in *B. raniceps* and *Sphaenorhynchus lacteus*, the most important prey were grasshoppers and ants, respectively. The importance of mosquitoes and flies in the diet of the studied anuran assemblage may reflect the great availability of this prey category in the sampled environment (Duellman & Trueb 1994). From our field observations, Diptera were certainly very abundant in the studied area, and could be found in large concentrations in emergent aquatic vegetation. However, it is not possible to infer whether this was the most abundant potential prey in the environment, since the food resources availability was not quantified in the current study. However, it is known that Diptera are among the most megadiverse orders of insects in the world (Carvalho et al. 2024), and that they are very abundant in lentic environments, using aquatic macrophytes as a habitat for reproduction and egg deposition (Nessimian & Henriques-de-Oliveira 2005, Silva & Henry 2013, Hamada et al. 2014).

Interestingly, plant material was shown to be relevant in the diet of the species studied here. The ingestion of plant material is generally considered accidental for anurans (Leite Filho et al. 2015, Protázio et al. 2017, Sabagh et al. 2010). However, when large volumes of this type of material are recorded in the diet, it may indicate intentional consumption by the species in the studied area (Rodrigues et al. 2023). Although uncommon for most anurans, intentional consumption of plant material has been recorded in some species (Severgnini et al. 2020, Schäfer et al. 2022, de-Oliveira-Nogueira et al. 2023). Though it is rarely a major component its inclusion may be related to facilitating exoskeletal digestion, eliminating parasites, absorbing nutrients or as an alternative source of hydration (Anderson et al. 1999, Mackenzie & Vladimirova 2022).

Lysapsus bolivianus was the most abundant species in our sampling, probably because it is a very common species in the studied area and it is reproductively active throughout the year (Furtado et al. 2014, Ganança et al. 2021). Diptera, followed by Hemiptera, were the most important prey categories for *L. bolivianus*, a pattern already reported in other species of the Pseudae group (Duré & Kehr 2001, Vaz-Silva et al. 2005, Garda et al. 2007, Downie et al. 2010, Furtado & Costa-Campos 2020). Our results corroborate other studies that classify the species as a generalist and passive forager, with a diet composition that reflects prey availability in the environment (Furtado & Costa-Campos 2020).

The species *B. punctata, B. raniceps* and *D. leucophyllatus* all had a broad trophic niche, indicative of a generalist diet. This same pattern has been found in other populations of *B. punctata* in Colombia and of *B. raniceps* in central Amazonia and the Caatinga (Caicedo-Moncada et al. 2022, Sant'Anna et al. 2022, Machado et al. 2024), and is also the common pattern for other hylid species from the genera *Boana* and *Dendropsophus* (Jiménez & Bolaños 2012, Pereira et al. 2023, Sanches et al. 2021, Soeiro et al. 2022). The larger sizes of such species as *B. punctata* and *B. raniceps*, may provide an advantage when in terms of prey diversity, since it allows a range sizes to be consumed, effectively increasing the number of prey categories they can available compared to smaller species which, as gape-limited predators, can feed only on small prey (Batista et al. 2011, Moser et al. 2022). This behavioral and ecological flexibility may reduce intraspecific and interspecific competition, promoting coexistence with other species with more restricted niches.

The relationship between size of consumed prey and that of the predator is well-known from several groups of amphibians (Santos-Pereira et al. 2015, Almeida-Santos et al. 2017, Ceron et al. 2023). Just as larger predators can eat larger prey (Moser et al. 2022), body size can also be considered a limiting factor for small predators and lead to specialized diets due to the possibility of taking advantage of a particular sub-section of what is available locally. Amphibians are animals that swallow their prey whole, so the size of the jaw (and, consequently, the SVL), are important factors in the predator/prey size relationship (Toft 1980). This pattern was not clearly observed in the present study. Although there was a tendency for larger predators to consume prey with proportionally greater sizes and higher total prey volumes in their stomachs, the statistical support for this trend was marginal. When each species was analyzed separately, no significant correlation was found between predator body size and mean prey volume (Figure 5). We attribute this result to factors related to the limited variability in both predator and prey sizes. For instance, if the environment does not offer sufficient variation in prey size, intraspecific prey size segregation may not be detectable. Additionally, although the study included juvenile individuals, which increase the variation in predator body size, this range may still have been insufficient to clearly detect the relationship between predator size and prey size, potentially contributing to type II errors. Finally, dietary specialization in certain prey groups—such as in ant-eating (formicivorous) species—may mask the influence of predator size (SVL) on prey volume or abundance.

Sphaenoryncus lacteus had the lowest trophic diversity and niche breadth among the species in our study, showing a strong preference for ants, with very few other invertebrates being recorded (Table I). This agrees with the suggestions of Rodriguez & Duellman (1994), that the species is a specialist in ants, which it captures with an active foraging strategy. This foraging method and emphasis on ants is also widespread in species of the Sphaenorhynchini tribe (Teixeira & Ferreira 2010, Araujo-Vieira et al. 2019, Corrêa et al. 2020, Carilo Filho et al. 2021). This specialized feeding pattern, known as myrmecophagy, is considered a synapomorphic characteristic of the Sphaenorhynchini tribe (Faivovich et al. 2005, Araujo-Vieira et al. 2019).

Overall, the trophic niche overlap was high between the species studied, except for *B. raniceps* and *S. lacteus* which had low overlap values with the other species (Table III). These species differ from the rest of the assemblage in their most important prey category; this is Orthoptera in the case of *B. raniceps*, and Formicidae for *S. lacteus*. The high overlap recorded between *B. punctata, D. leucophyllatus, D. walfordi* and *L. bolivianus* is mainly due to the high importance of Diptera in the diet of these species. Species of the genera *Boana* and *Dendropsophus* are arboreal (Torralvo et al. 2021), unlike *Lysapsus* species, which are generally found on the water surface, often associated with clusters of emergent aquatic vegetation (Vaz-Silva et al. 2005).

Coexistence in the same environment with high levels of trophic niche overlap may also be favored occupation by component species of different microenvironments. This may be achieved via variations in habitat preference, activity patterns or microclimatic niches. Such spatial segregation reduces direct competition for resources and contributes to successful coexistence, even when there is considerable overlap in the types of prey consumed (Brandão et al. 2020, Hiscock et al. 2023). Such microhabitat specialization has been reported by Ganança et al. (2021) for Amazonian floodplains, where the complex vegetation cover of macrophytes structures the anuran community, allowing spatial variation in the use and availability of shelters and dispersal corridors for adults and tadpoles.

The current study provides new information on the trophic ecology of Hylid anuran species in a floodplain habitat in the Brazilian Amazon. Our results highlight the importance of amphibians in regulating some ecosystem services, particularly as predators controlling mosquito populations and other invertebrate species (Pankaj & Nath 2023, Valencia-Aguilar et al. 2013). In general, the anuran species studied here had generalist feeding behaviors. Although *S. lacteus* specialized in ants, the studied assemblage showed high niche overlap values, mainly due to the high importance of Diptera in the diet of most component species.

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SUPPLEMENTARY MATERIAL

Tables SI and SII.

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