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Trophic ecology of small to large hylids from an Amazonia-Cerrado transitional zone in Brazil

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ABSTRACT

The diet of an organism is related to its intrinsic characteristics, such as morphology, physiology, and behavior, and those of the prey it consumes. For species occurring in sympatry, the knowledge of the mechanisms that favor the co-occurrence of morphologically and ecologically similar species may be important to understand the resource partition in the assemblage. In this study, we analyze the diet of small to large hylids (i.e., *Scinax fuscomarginatus*, *Dendropsophus anataliasiasi*, *Boana caiapo,* and *B. raniceps*) in an Amazonia-Cerrado transitional zone, verifying if the diet of species with different body sizes is similar and if species diet is explained by the availability of prey in the environment. We found that the dietary patterns of the studied hylids were not driven by prey availability in the environment, with species feeding preys in an opportunistic way. In addition, the diet composition was similar among species, however, the volume of consumed prey varied according to the body size, with large species feeding more prey volume than the small ones. This pattern is predicted by the optimal foraging theory, in which larger predators tend to maximize their energy intake by consuming large prey. Altogether, the segregation depending on the body size can play a key role in trophic resource partitioning, with small species feeding small prey and larger species consuming small to large prey, but preferring the larger ones when there is an option, avoiding interspecific competition.

1. Introduction

Understanding the diets of anurans is paramount to unveil their natural history and ecosystem services, in both terrestrial and aquatic environments associated with them (Duellman and Trueb, 1986). In this sense, the diet of an organism is related to its intrinsic characteristics, such as morphology, physiology, and behavior, and those of the prey it consumes. Thus, the diet of a species can vary according to the season (Michelin et al., 2020), body size/sex (Diaz et al., 2020), morphology (Moroti et al., 2020), habitat (Luría-Manzano and Ramírez-Bautista, 2017), prey availability (Ceron et al., 2022), and individual preferences (Araújo et al., 2007).

Ecological communities may be shaped by how species use resources, including food (Pianka, 1973). Furthermore, for species occurring in syntropy, the knowledge of the mechanisms that favor the co-occurrence of morphologically and ecologically similar species may be important to the resource partition in the assemblage. In this sense, the degree of trophic differentiation among species depends on many factors, with prey availability being one of the most relevant (Schoener, 1974). By analyzing it coupled with the species' diet, we can infer selectivity in dietary patterns, accessing trends from an active selection toward a rejection in diet, and being able to dissociate the influence of dietary preferences from the prey availability, which can blur our knowledge about the trophic ecology of anurans. Basic trophic ecology data remains poorly explored for most of the world's richest anuran fauna, in the Neotropical region (Ceron et al., 2019), where this situation is especially true for Brazil, with few studies using a comparative approach (Moser et al., 2017).

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Table 1
Prey categories found in the stomachs of *Boana caiapo, Boana raniceps, Dendropsophus anataliasiasi* and *Scinax fuscomarginatus* in an Amazonia-Cerrado transitional zone, Brazil. N'' = number of individuals registered (absolute number and %); FO = frequency of occurrence of prey category (absolute number and %); V = volume occupied by prey item in the entire sample (in mm^3 and %); IRI = Index of Relative Importance; Ei = Ivlev's eletivity index.

Species	N	N%	FO	FO%	V (mm^3)	V%	IRI	Ei
Boana caiapo								
Acari	1	12.50	1	20.00	0.01	0.01	250.20	1.00
Araneae	1	12.50	1	20.00	32.22	32.29	895.82	0.25
Blattodea	2	25.00	2	40.00	2	2.00	**1080.18**	0.79
Coleoptera	1	12.50	1	20.00	31.94	32.01	890.21	0.12
Formicidae	2	25.00	2	40.00	1.67	1.67	1066.95	0.12
Orthoptera	1	12.50	1	20.00	31.94	32.01	890.21	0.47
Boana raniceps								
Acari	4	20.00	2	14.29	2.65	0.06	286.52	1.00
Araneae	1	5.00	1	7.14	89.89	1.92	49.42	−0.2
Coleoptera	6	30.00	4	28.57	1120.16	23.91	**1540.39**	0.51
Diptera	2	10.00	2	14.29	415.73	8.88	269.65	−0.1
Formicidae	2	10.00	2	14.29	1267.36	27.06	529.37	−0.3
Hemiptera	1	5.00	1	7.14	118.55	2.53	53.79	−0.6
Hymenoptera	3	15.00	3	21.43	1525.21	32.56	1019.16	−0.2
Lepidoptera	1	5.00	1	7.14	144.62	3.09	57.77	0.38
Dendropsophus anataliasiasi								
Araneae	2	10.53	2	14.29	5.12	4.99	221.72	0.49
Coleoptera	1	5.26	1	7.14	19.01	18.54	170.04	0.06
Formicidae	3	15.79	3	21.43	5.93	5.78	462.29	0.26
Hemiptera	2	10.53	2	14.29	16.63	16.22	382.11	0.06
Hymenoptera	4	21.05	4	28.57	20.08	19.59	**1161.12**	0.19
NI	6	31.58	6	42.86	34.87	34.01	2811.08	–
Orthoptera	1	5.26	1	7.14	0.88	0.86	43.73	0.42
Scinax fuscomarginatus								
Acari	1	7.69	1	12.50	0.32	0.10	97.46	1.00
Araneae	2	15.38	2	25.00	24.78	8.08	586.56	0.45
Blattaria	2	15.38	2	25.00	84.57	27.57	**1073.81**	0.74
Coleoptera	2	15.38	1	12.50	4.84	1.58	212.03	0.34
Diptera	1	7.69	1	12.50	11.87	3.87	144.52	−0.1
Hemiptera	1	7.69	1	12.50	4.13	1.35	112.98	−0.3
Hymenoptera	1	7.69	1	12.50	10.94	3.57	140.73	−0.4
NI	3	23.08	3	37.50	165.32	53.89	2886.28	–

Table 2
Prey categories sampled in the environment in an Amazonia-Cerrado transitional zone, Brazil. N = number of individuals registered (absolute number and %) and, V = volume occupied by prey item in the entire sample (in mm^3 and %).

Prey categories	N	%N	V	%V
Araneae	10	7.52	242.77	1.40
Blattodeaa	4	3.01	978.67	5.64
Coleoptera	13	9.77	1284.81	7.41
Collembola	1	0.75	0.01	0.00
Diptera	15	11.28	215.52	1.24
Formicidae	26	19.55	854.84	4.93
Hemiptera	26	19.55	10,849.78	62.57
Hymenoptera	28	21.05	457.71	2.64
Lepidoptera	3	2.26	1128.67	6.51
Orthoptera	6	4.51	1323.79	7.63
Thysanoptera	1	0.75	3.51	0.02

The western Tocantins state, northern Brazil, comprehends a vast transitional area between two highly diversified and endangered biomes, Amazonia and Cerrado (Haidar et al., 2013). This region also harbors a conspicuous anuran community composed by both Amazonian and Cerrado lineages (Silva et al., 2020). As observed in different regions of the Neotropics, the western Tocantins also present a high richness and abundance of hylids (Silva et al., 2020), which makes hylids good study models for ecological research. Examples of common hylids from the western Tocantins include the small-sized species *Dendropsophus anataliasiasi* (Bokermann, 1972) and *Scinax fuscomarginatus* (Lutz, 1925), and the large medium-sized species *Boana caiapo* Pinheiro, Cintra, Valdujo, Silva, Martins, Silva, and Garcia, 2018 and *Boana raniceps* (Cope, 1862). *Scinax fuscomarginatus* and *B. raniceps* are widely distributed species in South America (Brusquetti et al., 2014; Camurugi et al., 2021), whereas the remaining species show more restricted ranges. *Boana caiapo* was recently described and confirmed for different localities along the Araguaia River basin (Pinheiro et al., 2018; Silva et al., 2020), while *D. anataliasiasi* is a Cerrado endemic species, ranging mainly in Central Brazil (e.g., Teixeira and Giaretta, 2015; Vaz-Silva et al., 2020). Despite the distinctiveness in geographic distribution and size, these species occupy similar environments, mainly marginal vegetation of temporary ponds (personal observation; present study). This condition raises interesting questions about how these species partition food resources.

In this study, we (i) analyze the diet of *Scinax fuscomarginatus*, *Dendropsophus anataliasiasi*, *Boana caiapo* and *Boana raniceps* in an Amazonia-Cerrado transitional zone; (ii) test if the species diet is explained by the availability of prey in the environment and; (iii) verify if aspects of their diet (composition, volume, and the number of consumed items) are related with different body sizes. Once anurans are gape-limited predators (Duellman and Trueb, 1986) we hypothesized that anurans with different body sizes would have a different diet, in terms of volume and number of prey, but the composition of diet would be driven by the prey availability in the environment (Michelin et al., 2020; Moroti et al., 2020), thus, being similar among the species.

2. Material and methods

2.1. Study area

We studied the diet of *Scinax fuscomarginatus*, *Dendropsophus anataliasiasi*, *Boana caiapo* and *Boana raniceps* in an Amazonia-Cerrado Transitional Zone in Caseara municipality, Tocantins state, Brazil (9°24′56" S, 49°58′28" W, 177 m above sea level [a.s.l.]; *datum* WGS84). The sampled pond is inserted in a matrix of pasture and soybean monoculture in the Canadá farm. Despite this depauperate surrounding,

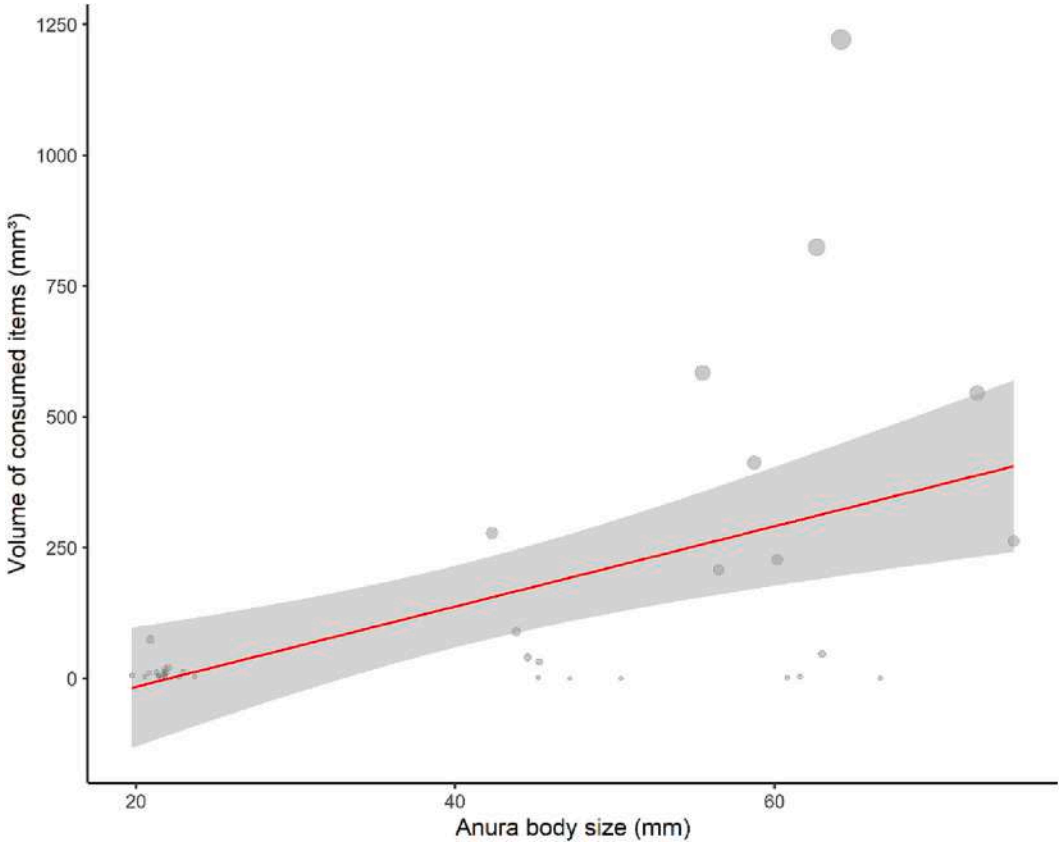

Fig. 1. Relationship between the volume of consumed items (mm^3) and anuran body size (mm, $F = 14.23$, $r^2 = 0.27$, $df = 34$, $p < 0.01$). The circle size represents the volume of consumed prey.

the area is nearby by three protected areas, the Reserva Particular do Patrimônio Natural (RPPN) Canto do Obrieni, the Cantão State Park, and Parque Nacional do Araguaia, which harbor a high diversity of amphibians to the state (Silva et al., 2020).

2.2. Anuran sampling

We collected both anurans and invertebrate specimens (potential prey) simultaneously on November 18, 2017. Anurans were collected by visual encounter surveys (Crump and Scott Jr, 1994) along a swamp in the area. The anuran specimens were euthanized using a topical anesthetic (Xylocaine 5%) and then fixed with 10% formaldehyde before the analysis of the stomach content. We removed stomachs through a small abdominal incision and stored the contents in separate vials. We preserved the frog individuals in 70% alcohol and deposited the specimens in the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul, Campo Grande municipality, Mato Grosso do Sul state, Brazil (ZUFMS-AMP).

2.3. Prey availability

To estimate prey relative abundance, we installed 20 pitfall traps (plastic cups 300 ml) in random locations around the swamp at the soil level. Hydrated ethyl alcohol 70% was used as a preservative, plus some drops of detergent to break the surface tension of the solution. Pitfalls traps were opened at sunset and were removed at sunrise. Pitfall traps may underestimate some groups such as sedentary prey, flying insects, or Orthoptera. In order to avoid bias in the sampling, we used an entomological umbrella method for 30 min to capture arboreal prey. Once invertebrates obtained in diet are partly digested, we assigned the items to operational taxonomic units (OTUs; Sneath and Sokal, 1973), usually at the level of Order, except for Formicidae. This family was separated from other Hymenoptera because of their particular morphological and ecological characteristics. Larvae were usually included in the same OTU (e.g., Lepidoptera larvae). Highly digested prey unable to be properly identified were assigned as non-identified (NI). Invertebrates were identified based on available literature (e.g., Rafael et al., 2012).

2.4. Diet analysis

To investigate the influence of anuran body size on the dietary pattern we measured the body size of mature individuals (snout to vent length – SVL) using a digital caliper (nearest 0.01 mm). After measuring the length and width of each prey, we estimated their volumes using the formula of the ellipsoid: $V = \frac{4}{3}\pi \times 2\left(\frac{w}{2}\right)^2 \times \left(\frac{l}{2}\right)$, where, V = volume, W = width and L = length (Magnusson et al., 2003). For each item (prey category) we calculated the number, volume, and frequency of occurrence in both absolute and percentage values. We then calculated the Index of Relative Importance (IRI) (Pinkas et al., 1971) to determine the relative importance of each prey item in the diet using the following formula: $IRI = (\%N + \%V)\%FO$. This formula effectively shows the main and rare food items, where FO% is the mean percentage of prey occurrence, N% is the numerical percentage of prey and V% is the volumetric percentage of prey. FO% was calculated as the ratio between the number of stomachs that contain the specific prey and the total number of stomachs accessed. Higher values of IRI regarding other prey items indicate greater importance of the prey category in the diet.

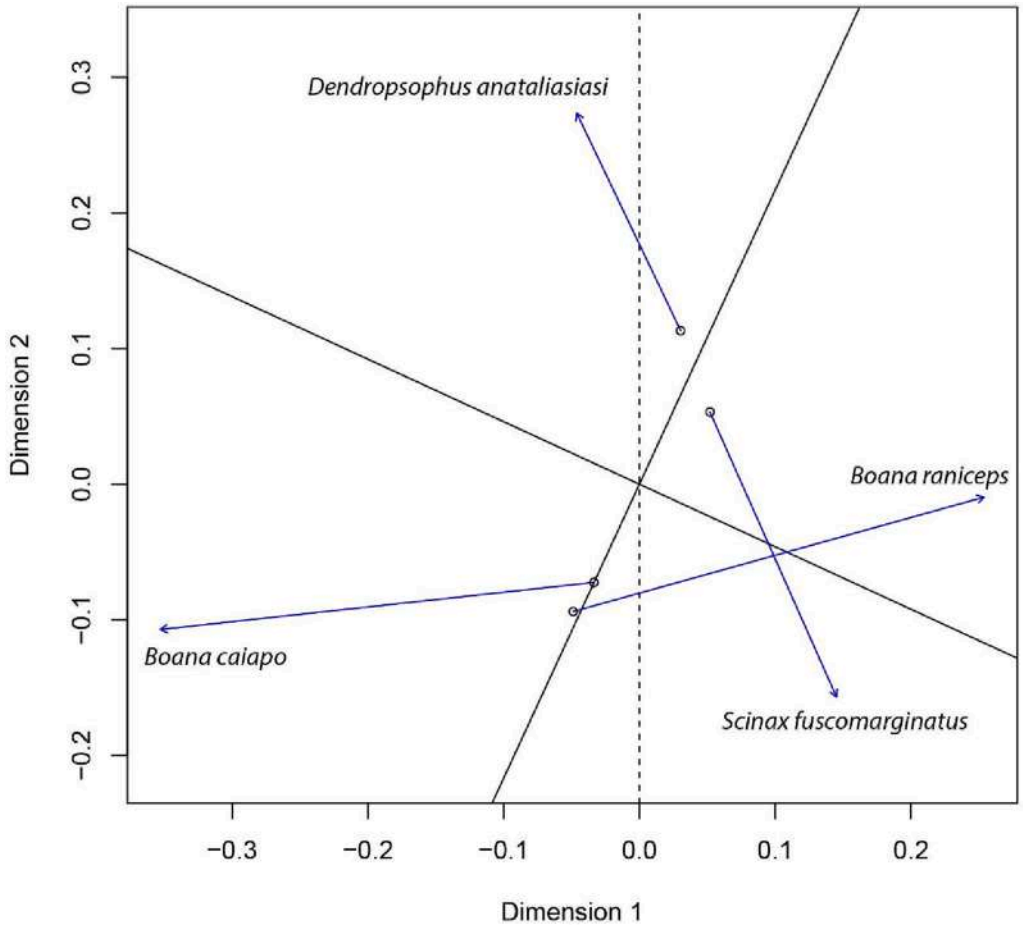

Fig. 2. Species diet demonstrated by the dispersion diagram of the Procrustes analysis ($P = 0.28$, sum of squares (ss) = 0.748, t0 = 0.5, $p = 0.91$). For each species: circles represent the matrix with prey availability that fits species mouth size; arrows represent the matrix of species diet; the line between both represents the size of congruence between matrices.

2.5. Statistical analysis

To determine species orderings according to morphometric data (i.e., SVL) we used K-means partitioning (Legendre and Legendre, 2012). The optimal number of clusters for the k-means analysis was determined using the statistical gap method (Tibshirani et al., 2001). The k-means analysis was carried out using the package *factoextra* (Kassambara and Mundt, 2017) in the R environment (R Core Team, 2022). To investigate similarities and differences in the diet of anuran species, a matrix of similarities between each pair of all individuals was calculated using a Hellinger-transformed Bray-Curtis similarity coefficient (Legendre and Gallagher, 2001). The one-way ANOSIM analysis was used to assess possible statistically significant differences in the diet composition between the species with different sizes (Clarke, 1993). In addition, to access the relation of anuran body size and prey number and volume, we carried out a linear regression, using anuran body size as a predictor and prey number (number of consumed items) and volume (sum of volumes) as a response variable. Analysis was performed using the package *vegan* (Oksanen et al., 2017) in the R environment (R Core Team, 2022).

Anuran feeding selectively was examined by comparing the similarity among stomach contents and prey availability sampled in the same area and time using Ivlev's index: $Ei = (r_i - p_i)/(r_i + p_i)$, where r_i is the relative abundance of food category in the stomach (as a proportion or percentage of all stomach contents) and p_i is the relative abundance of this prey in the environment. Values range from −1 to +1, with negative values indicating rejection or inaccessibility of the prey, zero indicates random feeding, and positive values for active selection (Ivlev, 1975). We preferred Ivlev's index of electivity because other electivity indices give similar results (Lechowicz, 1982) and the output from Ivlev's index is easily interpreted.

To verify if a species' diet is explained by arthropod abundances that fit the species' diet size (i.e., prey able to be preyed by species according to its mouth gap), we performed a Procrustes analysis (Gower, 1975). We used Hellinger-transformed Bray-Curtis distance-based PCoA ordinations for each species (Legendre and Gallagher, 2001). This analysis allows us to evaluate the congruence between two data matrices through the rotation (or orthogonal transformation) of the ordering axes necessary for the overlap of the two data sets in the ordering space. From this rotation, a Procrustes correlation value (t0) is generated between the two matrices (which can be interpreted analogously to a Mantel matrix correlation), and an associated *p*-value based on null models from permutations (999 iterations) of the rotation and rearrangement events of the orthogonal axes (Gower, 1975). We used the matrix of the species' diet in opposition to the matrix of prey availability that fits the species' mouth size to each species. Thus, we consider that the species' diet is explained by the availability of prey that fit its mouth size if there was congruence between the two matrices. The Procrustes analysis was carried out using package *vegan* (Oksanen et al., 2017) in the R environment (R Core Team, 2022).

3. Results

We analyzed the stomach of 87 anurans, which were distributed among *Scinax fuscomarginatus* ($n = 15$ individuals), *Dendropsophus anataliasiasi* ($n = 29$), *Boana caiapo* ($n = 22$) and *Boana raniceps* ($n = 21$). Nearly 54% of the stomachs ($N = 47$) were empty. Among the 40

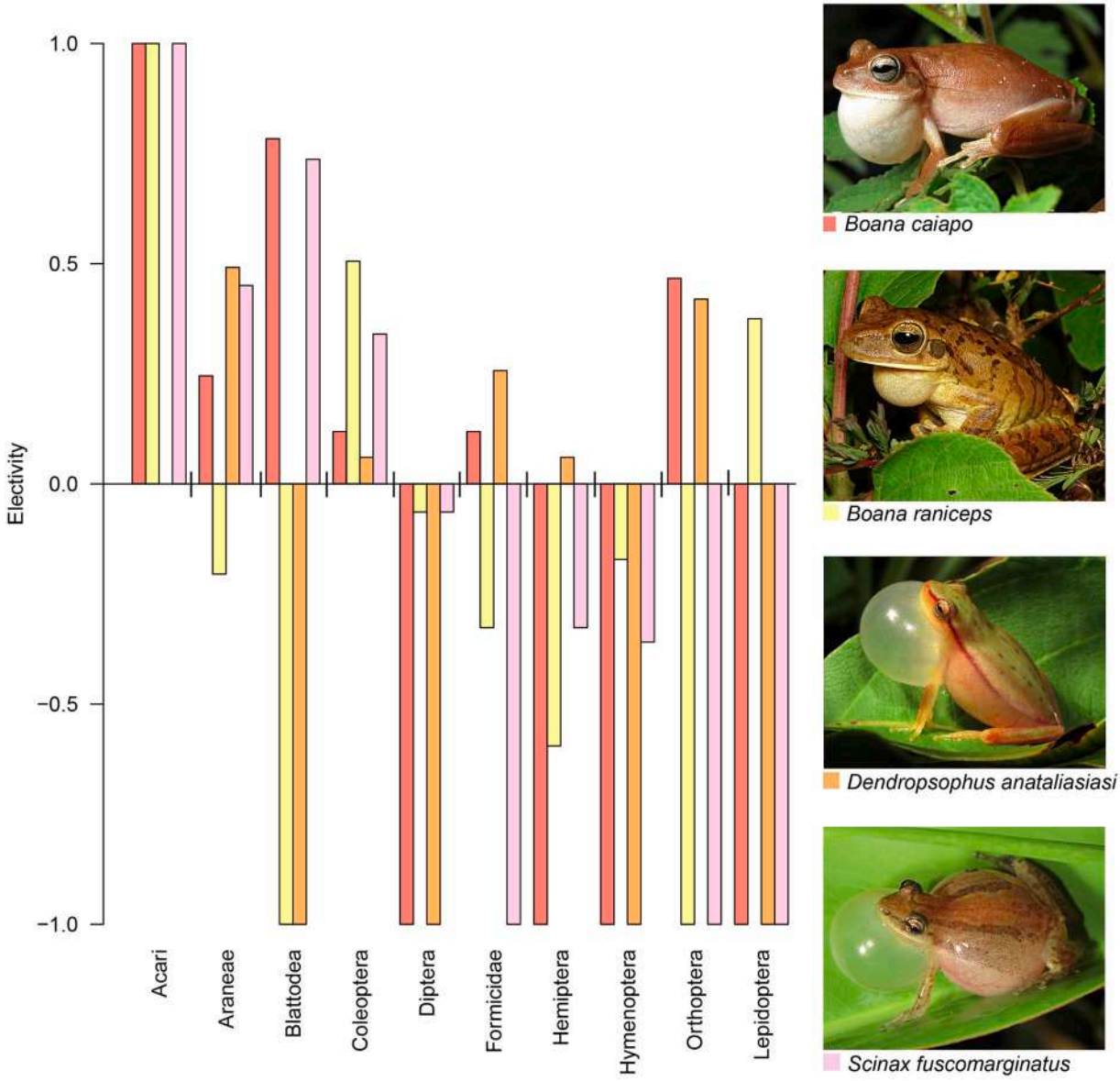

Fig. 3. Ivlev's (1979) electivity index for prey categories of *Boana caiapo*, *Boana raniceps*, *Dendropsophus anataliasiasi* and *Scinax fuscomarginatus* diets in an Amazonia-Cerrado transitional zone.

remaining stomachs, we found nine identified prey categories, of which Coleoptera was the most numerous group ($N = 16.95\%$), and the most representative prey category (IRI = 2812). Hymenoptera was the most frequent prey category (FO% = 19.05%), followed by Coleoptera and Formicidae (16.67%) (Table 1). The diet of *B. caiapo* comprised six prey categories, and Blattodea was the most important item (IRI = 1080). *Boana raniceps* presented a diet comprised of eight prey categories, of which Coleoptera was the most important item (IRI = 1540). The diet of *D. anataliasiasi* and *S. fuscomarginatus* encompassed seven and eight prey categories respectively, of which Hymenoptera (IRI = 1161) and Blattaria (IRI = 1073) were the most representative prey category within identified preys, respectively. Environmental sampling produced a total number of 133 individuals of invertebrates, representing 11 taxa (Table 2). Only two prey categories recorded in prey availability sampling were not found in the analyzed stomachs, Collembola and Thysanoptera.

Three size clusters (i.e., small, medium, and large frogs) were observed in the k-means analysis for morphological measures. The first cluster (large-sized) grouped *Boana raniceps*, the second one grouped *B. caiapo* (medium-sized), and the third grouped *Scinax fuscomarginatus* and *Dendropsophus anataliasiasi* (small-sized). There was no difference in the diet composition of anuran species (ANOSIM $p = 0.4$). However, there was a positive relationship between the volume of consumed items with anuran body size (Fig. 1, $F = 14.23$, $r^2 = 0.27$, $df = 34$, $p < 0.01$). On the contrary, we did not observe a relationship between the number of consumed items with anuran body size ($p > 0.05$). In addition, the anuran diet was not explained by the availability of prey that fit species mouth size, because there was a weak congruence between the matrices in the Procrustes analysis (Fig. 2, $P = 0.28$, sum of squares (ss) = 0.748, $t0 = 0.5$, $p = 0.91$). Anurans used the resources available in the environment in a slightly different way, with species selecting some items and avoiding others (Table 1, Fig. 3).

4. Discussion

We found that the dietary patterns of small to large hylids were not driven by prey availability in the environment, with species opportunistically feeding their prey. In addition, the diet composition and the

number of consumed prey were similar among species, whereas the volume of consumed prey varied according to the body size, with large species feeding a higher volume of prey than the small ones.

The anuran's diet followed the global trend, with Coleoptera as an important item to their diet (Ceron et al., 2019), which can be related to the worldwide elevated richness of Coleoptera, showing a broad number of shapes and sizes, and the shared habits of resource use, with coleopterans using plants as food resources and treefrogs using plants as a spatial resource to perching (Rafael et al., 2012). In relation to the diet of *Boana* species (*B. caiapo* and *B. raniceps*), they showed a similar diet composition, despite the more category of prey items fed by *B. raniceps*. The range of consumed prey by *Boana* species in this study was similar to other congeners in Brazil (e.g., Pacheco et al., 2017; Moser et al., 2018; Tupy et al., 2021), and to the diet of *B. raniceps* from the Pantanal (Sabagh et al., 2010). The diet of *D. anataliasiasi* was similar to the diet of its congeners like *D. branneri* (Castro et al., 2016), *D. microcephalus* (Fonseca-Pérez et al., 2017) and *D. minutus* (Leivas et al., 2018), showing a preference by Araneae and Orthoptera, common items in the diet of this genus. *Scinax fuscomarginatus* presented a diet composition similar to other populations of this species in the Cerrado (Michelin et al., 2020), showing a preference for Acari, Blattaria, and Araneae. The non-identified prey was presented only in small-sized species, which tended to consume small prey in relation to the larger treefrogs. The relatively small size of prey allied to the advanced stage of digestion turns them unable to be correctly identified, being categorized as non-identified material (e.g., Castro et al., 2016; Leivas et al., 2018).

Species' diet was not driven by prey availability in the environment. The electivity index showed that species used the resources available in the environment in a slightly different way, as in other studies carried out in Brazil (e.g., de Oliveira et al., 2019; Michelin et al., 2020). However, there is no clear pattern shown by species to select or avoid prey. For example, *Boana caiapo* selected Araneae, Orthoptera, and Formicidae, all of them common items in *Boana* species diet, but avoided Diptera, Hemiptera, Hymenoptera, and Lepidoptera, other common prey in dietary assessments of the genus (e.g., Pacheco et al., 2017; Moser et al., 2019). Given that anurans are opportunistic predators and that species were in the reproductive period (personal observation; present study) is reasonable to think that reproduction was the individuals' priority at that moment. It can be corroborated by the high number of empty stomachs (54%) and by the low number of prey present in stomachs (mean 1.46 prey by individual). Consequently, during the breeding period, anurans may opportunistically eat prey, without showing a clear pattern of selection or rejection of prey types. In addition, despite the differences in body size among species, with *Boana* species being larger than *Scinax* and *Dendropsophus* species, the first one also consumed small prey items such as Formicidae (*B. caiapo*) and Acari (*B caiapo* and *B. raniceps*), reinforcing the hypothesis of an opportunistic foraging mode (Dietl et al., 2009).

Species showed different body sizes, with *Boana raniceps* grouped as large-sized, the *B. caiapo* as medium-sized, and *Scinax fuscomarginatus* and *Dendropsophus anataliasiasi* as small-sized. Despite these differences, diet abundance was similar among species, but the volume of consumed prey varied according to body size. Vignoli and Luiselli (2012) found that prey volume is a better descriptor of community structure than the number of prey. The relationship between body size and prey volume is known in anurans (Toft, 1980; Parmelee, 1999), and in Neotropical communities it occurs in some species, such as *Ameerega braccata* (Forti et al., 2013), *Incilius mazatlanensis* (Smith et al., 2011) and *Boana albopunctata* (Pacheco et al., 2017). Once anurans were in their reproductive period and food was obtained opportunistically, each intake of energy is valorous. In this sense, species try to maximize their energy intake by consuming the largest prey they can (Emlen, 1966; Robinson and Wilson, 1998). This segregation depending on the body size can play a key role in trophic resource partitioning, with small species feeding small prey and larger species consuming all prey sizes, but preferring the larger ones when there is an option, avoiding interspecific competition (Moroti et al., 2020).

Altogether, we showed that the dietary pattern of related species is opportunistic, whit body size affecting the niche partitioning of species. Despite these findings being in line with those presumed by classical theories such as optimal foraging and niche partitioning, the driver of this finding is still a challenge to frog communities, once it can be attributed just to the capacity to catch and swallow bigger prey, or it can be related to an energetic approach, with species preferring to eat more caloric preys (Raubenheimer et al., 2009).

CRediT authorship contribution statement

Karoline Ceron: Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Supervision. **Tays Paula:** Data curation, Formal analysis, Investigation, Writing – original draft. **Paola Scheibler:** Data curation, Formal analysis, Investigation, Writing – original draft. **Renata Fadel:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition. **Carla da Silva Guimarães:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition. **Leandro Alves Silva:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition. **Diego José Santana:** Conceptualization, Resources, Writing – review & editing.

Declaration of Competing Interest

None.

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