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Trophic ecology of a Pantanal treefrog assemblage during a severe drought

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ABSTRACT

We investigated herein the diet of an assembly of anurans, specifically tree frogs belonging to the species *Scinax acuminatus*, *Boana raniceps*, and *Trachycephalus typhonius*, under extremely adverse conditions in the Pantanal, a region of great ecological importance that experiences cycles of flooding and drought. Recently, the region suffered an extreme and unusual drought, drastically reducing the availability of wet habitats. Data collection occurred in the Passo do Lontra region, Southern Pantanal, in November 2021. Anuran sampling was conducted through nocturnal searches, and collected specimens were subsequently subjected to stomach content analysis through animal dissection. Additionally, pitfall traps were used to estimate the relative abundance of anuran prey in the environment. Results revealed that the diet composition of the three tree frog species was similar, but bigger species consumed more prey volume than smaller species. The hylids exhibited dietary generalism, the prey categories most consumed by *S. acuminatus* was Orthoptera and Hemiptera, while *B. raniceps* and *T. typhonius* mostly consumed Coleoptera and Formicidae. Also, the electivity index shows that *S. acuminatus* and *B. raniceps* selected Coleoptera and Hemiptera, while *T. typhonius* selected Coleoptera and Araneae. Our study suggests that extreme climatic events, such as severe droughts, can alter the ecological processes of this group of hylids.

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Introduction

The dynamics of ecosystems are often shaped by an intricate association of biotic and abiotic interactions (Limberger et al. 2017). Understanding these complex relationships is fundamental for biodiversity conservation and maintaining ecosystem stability (Schoener 1974). Among various aspects of biological interactions, trophic ecology emerges as one of the most direct ways to assess how living organisms relate to each other (Pianka 1973). In this context, the diet of organisms stands out as a key variable reflecting the connections between organisms and available resources in the environment, a relationship particularly sensitive in amphibians (Ceron et al. 2019).

Amphibian diets can be highly variable, influenced by factors such as prey availability and morphology, leading to variations in trophic niche (Moroti et al. 2021). Therefore, anurans are generally considered diet generalists (Vignoli and Luiselli 2012). However, recent studies have revealed that the diet of these animals may be more specific than previously thought, with adaptations to ecoregions and seasonal variations in prey availability (Ceron et al. 2019). Consequently, although amphibians are widely recognized for their ecological and behavioral adaptations, they are also considered sensitive indicators of environmental change (Duellman and Trueb 1986).

The Pantanal, an ecoregion characterized as one of the largest temporary floodplain areas in the world (Alho et al. 2019), is known to harbor a high abundance of amphibians (Junk et al. 2006), mainly due to the vast expanse of wetlands that provide ideal habitats for these organisms. However, the Pantanal is also characterized by its multi-year flood cycles, with years of flooding followed by years of drought (Marengo et al. 2021). Recently, between 2018 and 2021, the Pantanal experienced an extreme drought, accompanied by forest fires that resulted in significant declines in animal populations (Tomas et al. 2021). Furthermore, the large flooded areas were restricted to small temporary lakes, drastically reducing the availability of moist environments, essential for the survival

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of many amphibian species. There is evidence that some Pantanal frog species exhibit traits that provide a degree of adaptability to droughts or fire/post-fire conditions, such as burrowing behavior and estivation (e.g. Van Buskirk 2005), supporting the hypothesis thatamphibian abundance in this ecoregion is mainly influenced by landscape characteristics and the availability of breeding habitats (Strüssmann et al. 2011). Factors such as lagoon hydroperiod and predator presence also play significant roles in shaping toad populations (Van Buskirk 2005).

In contrast, tree frogs (Hylidae) do not exhibit clear adaptations for burrowing or estivation (Uetanabaro et al. 2008). Commonly found hylids in the Pantanal plain include small-sized species such as *Scinax acuminatus* (Cope, 1862), medium sized such as *Boana raniceps* (Cope, 1862), and large sized such as *Trachycephalus typhonius* (Linnaeus, 1758), all widely distributed in South America (Sabagh et al. 2010; Ron et al. 2016; Camurugi et al. 2021). In the Pantanal, these three species occur in sympatry, occupying similar temporary water bodies. Consequently, their dependence on suitable aquatic habitats around makes them excellent study subjects for evaluating trophic ecology during periods of intense aggregation caused by severe droughts (Evans et al. 2020).

During a field expedition in the Pantanal, at the peak of the last extreme drought, we observed the phenomenon of a cluster of hylids in a small, isolated pool resembling an aquatic island amidst a dry and hostile environment. Motivated by the unusual aggregation of tree frogs species in an isolated pool during extreme drought, this study aims to (I) describe their diet under these challenging conditions, (II) evaluate the role of body size in resource partitioning among species, and (III) assess prey selection relative to environmental availability.

Material and methods

Study area

The Pantanal is recognized as one of the world's largest wetland areas, featuring prominent vegetation formations, including flood-free ridges (called old dikes) adorned with trees, seasonally flooded plains with grasslands, and water bodies harboring aquatic macrophytes (Pott and Pott 2004). Although the region does not have particularly high species diversity and endemism is virtually absent, it remains notable for its abundant wildlife populations (Harris et al. 2005). It is important to note that the annual precipitation in the studied area of the Pantanal averages approximately 1,177 mm (Fick and Hijmans 2017). We studied the diet of a hylid assemblage in a pond (−19.55251–-57.03885) located in the southern Pantanal, in the

Figure 1. Studied pond in the Miranda-Abobral Pantanal, municipality of Corumbá, Mato Grosso do Sul, Brazil.

Passo do Lontra region, municipality of Corumbá, Mato Grosso do Sul, Brazil. The pond was approximately 5 m in diameter, surrounded by dry vegetation, with some still green emerging grass, in a matrix of burned native grasslands (Figure 1).

Anuran sampling

During nocturnal amphibian surveys at the pond on 18 November 2021, only hylid species were encountered, none of which were vocalizing. We collected anurans only using visual encounter surveys (Scott et al. 1994) along and around the pond. We euthanized the anurans with a topical anesthetic (5% lidocaine) and then fixed with 10% formaldehyde (SISBIO license 49,080–5). Afterward, we removed the stomachs through a small abdominal incision and stored the contents in separate jars. We preserved the tree frogs and their stomachs in 70% alcohol and deposited them in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS-AMP), municipality of Campo Grande, Mato Grosso do Sul, Brazil.

Prey availability

To estimate the relative abundance of prey, we installed 20 pitfall traps (300 ml plastic cups) evenly spaced around the marsh at ground level, maintaining a minimum distance of 50 cm from the water margin. The pitfall traps were opened at sunset (around 6:00 pm) and removed at sunrise (around 05:30 am), which coincides with the hylids activity in the Pantanal, especially the three species evaluated in the present study (Uetanabaro et al. 2008). For invertebrates obtained in the diet, we assigned these items to operational taxonomic units (OTUs; Sneath and Sokal 1973), generally at the Order level, except for Formicidae family, where separated from other Hymenoptera due to its distinct morphological and ecological characteristics. Larvae were usually included in the same OTU (e.g. Lepidoptera larvae). Highly digested prey that could not be properly identified were classified as unidentified (UN). We identified invertebrates based on available literature (e.g. Rafael et al. 2024).

Diet analysis

To investigate the influence of anuran body size on feeding patterns, we measured the snout-vent length (SVL) of mature individuals using a digital caliper (0.01 mm precision). Regarding prey, we measured their length and width and estimated their volumes using the ellipsoid formula: $V = \frac{4}{3}\pi \times 2\left(\frac{w}{2}\right)^2 \times \left(\frac{l}{2}\right)$, where V is volume of prey in the stomachs, W is width of prey, and L is length of prey (Magnusson et al. 2003). For each prey item (category), we calculated the number of individuals, volume, and frequency of occurrence in absolute and percentage values. Then, we calculated the Index of Relative Importance (IRI) (Pinkas 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 average occurrence percentage of the prey for each anuran species, N% is the numerical percentage of the prey, and V% is the volumetric percentage of the prey. FO% was calculated as the ratio of the number of stomachs containing the specific prey to the total number of stomachs analyzed. Higher IRI values relative to other prey items with lower values indicate greater importance of the prey category in the diet.

Prey electivity

To assess prey selection in the environment, we compared the relative abundance of each prey category in the diet with the relative abundance of the same prey sampled in the environment. For this purpose, we used the Vanderploeg and Scavia's Relativized Electivity Index (Vanderploeg and Scavia 1979). The index is calculated by first determining the selectivity coefficient for diet item $_i$ (W_i):

$$W_i = \frac{r/p_i}{\sum^{r_i}/p_i}$$

where r_i is the proportion in each category $_i$ and p_i is the proportional availability of the same prey category in the environment. The index W_i ranges from 0 (total avoidance) to 1 (total preference). The relativized index (E_i) is then calculated as:

$$E_i = \frac{w_i 1/n}{w_i + 1/n}$$

where n represents the number of diet categories available. This index ranges from −1 to 1, with 0 indicating random prey selection, negative values indicating avoidance or inaccessibility of the prey item and positive values showing active selection.

Statistical analysis

To determine species groupings based on morphometric data (i.e. SVL), we applied 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 2024).

To investigate similarities and differences in the diet of anuran species, we calculated a similarity matrix between individuals using a Hellinger-transformed Bray–Curtis similarity coefficient (Legendre and Gallagher 2001). We employed a one-way ANOSIM analysis to assess statistically significant differences in diet composition among species of different sizes (Clarke 1993). Analysis was perfomed using the package vegan (Oksanen et al. 2017) in the R environment (R Core Team, 2024).

We also calculated the prey diversity using Shannon index of diversity (H′) (hereafter Shannon index) $H' = -\Sigma p_i \log p_i$, where pi represents the proportion of each species/order in the species diet (Shannon and Weaver 1949). The use of this index enabled us to account for the generalism of predator's species.

Additionally, to evaluate the relationship between anuran body size and prey number and volume, we carried out a generalized linear model (GLM), using anuran body size as a predictor and prey number (number of consumed items) and volume (sum of volumes) as response variables. The model family were selected after inspecting the distributions of the response variables in the diagnostic plots generated in the DHARMa package (Hartig 2022) in the R environment (R Core Team 2024). The family model that best explained the data was Gaussian.

Results

We analyzed the stomach contents of 83 anurans from three species: *S. acuminatus* ($n = 19$), *B. raniceps* ($n = 32$), and *T. typhonius* ($n = 32$). Approximately, 40% of the stomachs (32 out of 83) were empty (*S. acuminatus* with *11, B. raniceps* with 09, and *T. typhonius* with 12 were empty). Among the 50 stomachs containing food, 12 prey categories were identified. Coleoptera (beetles) was the most abundant group (38%; *S. acuminatus* 20%, *B. raniceps* 45%, *T. typhonius* 39%), the most frequent prey category (FO% = 49%), and the most representative prey type (IRI = 63%) for the three species in total (Table 1). The diet of *S. acuminatus* included five prey categories, and Orthoptera being the most important (IRI = 19.54%) and Coleoptera being the dominant item (IRI = 53.62%). S. *acuminatus* and *B. raniceps* consumed six prey categories, with Coleoptera being the dominant item (IRI = 53.62%). *T. typhonius* consumed 10 prey categories, with Coleoptera dominating (IRI = 51.09%).

S. acuminatus selected Hemiptera (0.85), Coleoptera (0.39), and Orthoptera (0.19). *B. raniceps*

Table 1. Prey categories found in the stomachs of *Boana raniceps, Scinax acuminatus,* and *Trachycephalus typhonius* in the Pantanal, Brazil. *N* = number of individuals recorded; FO = frequency of occurrence of the prey category; V = volume occupied by the prey item in the entire sample (mm^3); UN = unidentified prey; IRI = relative importance Index; Ei = Vanderploeg and Scavia Relativized Electivity Index (%) indicate values in percentages.

Species	N	N%	FO	FO%	V(mm^3)	V%	IRI	IRI%	Ei
Boana raniceps									
Coleoptera	17.00	44.74	14.00	60.87	1598.89	17.10	3763.88	53.62	0.73
Diptera	1.00	2.63	1.00	4.35	41.70	0.45	13.38	0.19	0.21
Formicidae	6.00	15.79	6.00	26.09	41.14	0.44	423.38	6.03	−0.60
Hemiptera	4.00	10.53	2.00	8.70	2485.45	26.58	322.66	4.60	0.77
Hymenoptera	1.00	2.63	1.00	4.35	77.02	0.82	15.02	0.21	-
Odonata	1.00	2.63	1.00	4.35	498.60	5.33	34.62	0.49	-
UN	8.00	21.05	8.00	34.78	4608.33	49.28	2446.39	34.85	-
Scinax acuminatus									
Blattaria	1.00	6.67	1.00	12.50	0.04	0.00	83.37	1.02	-
Coleoptera	3.00	20.00	3.00	37.50	129.36	10.31	1136.53	13.94	0.39
Formicidae	1.00	6.67	1.00	12.50	0.55	0.04	83.88	1.03	−0.84
Hemiptera	3.00	20.00	3.00	37.50	183.69	14.64	1298.87	15.93	0.85
Orthoptera	3.00	20.00	3.00	37.50	282.34	22.50	1593.63	19.54	0.19
UN	4.00	26.67	4.00	50.00	659.04	52.51	3958.95	48.54	-
Trachycephalus typhonius									
Araneae	3.00	7.32	3.00	15.00	117.70	0.80	121.81	1.92	0.63
Blattaria	2.00	4.88	2.00	10.00	123.56	0.84	57.21	0.90	-
Coleoptera	16.00	39.02	10.00	50.00	3784.07	25.83	3242.70	51.09	0.68
Diptera	2.00	4.88	2.00	10.00	5.01	0.03	49.12	0.77	0.46
Formicidae	7.00	17.07	7.00	35.00	1977.38	13.50	1069.97	16.86	−0.59
Hemiptera	2.00	4.88	2.00	10.00	392.10	2.68	75.54	1.19	0.55
Hymenoptera	1.00	2.44	1.00	5.00	137.02	0.94	16.87	0.27	-
Nematoda	1.00	2.44	1.00	5.00	11.86	0.08	12.60	0.20	-
Odonata	1.00	2.44	1.00	5.00	81.73	0.56	14.98	0.24	-
Thysanoptera	1.00	2.44	1.00	5.00	0.07	0.00	12.20	0.19	-
UN	5.00	12.20	5.00	25.00	8019.64	54.74	1673.40	26.37	-

Table 2. Prey categories sampled in the environment in Pantanal, Brazil. *N* = number of individuals registered and V = volume occupied by prey items in the entire sample (%) indicate values in percentages.

Prey categories	N	N%	V(mm^3)	V%
Acari	3	0,43	148,3	1,85
Araneae	13	1,84	901,23	11,23
Coleoptera	58	8,66	2436,75	30,36
Diplopoda	1	0,14	36,86	0,46
Diptera	14	1,99	193,94	2,42
Formicidae	512	72,62	668,51	8,33
Hemiptera	11	1,56	926,33	11,54
Ixodida	2	0,28	0,72	0,01
Orthoptera	91	12,91	2714,44	33,82

selectively consumed Hemiptera (0.77), Coleoptera (0.73), and Diptera (0.21). *T. typhonius* selected Coleoptera (0.68), Araneae (0.63), Hemiptera (0.55), and Diptera (0.46) (Table 1, Figure 4). Prey availability sampling using pitfall traps we recorded 705 invertebrates across nine taxa: Acari, Aranae, Coleoptera, Diptera, Diplopoda, Formicidae, Hemiptera, Ixodida, and Orthoptera. Formicidae accounted for 72.6% of the total number of prey, followed by Orthoptera at 12.9%. In terms of volume, Orthoptera occupied the largest proportion (33.8%), followed by Hemiptera (11.5%). However, three prey categories (Acari, Diplopoda, and Ixodida) were present in the environment but absent from the analyzed stomachs (Table 2).

K-means analysis of morphological measurements identified three size groups: small, medium, and large. The small group included *S. acuminatus* and one juvenile individual of *B. raniceps*. The medium group consisted of *B. raniceps* and *T. typhonius*, while the large group comprised *T. typhonius* and two large individuals of *B. raniceps* (Figure 2). There was no significant difference in diet composition among the three anuran species (ANOSIM $p = 0.054$). The Shannon diversity index decreased with species size, with values of 0.94 for *S. acuminatus*, 1.16 for *B. raniceps*, and 1.73 for *T. typhonius*.

Additionally, we found no relationship between body size and the number of items consumed ($p > 0.05$), but we found a significant relationship between body size and the volume of prey ($z = 4.913$; $p < 0.005$, $df = 30$) (Figure 3). However, the anurans showed slight variations in how they utilized available resources, with some species selectively consuming certain prey items while avoiding others (Table 1, Figure 4).

Discussion

In our analysis, we found that *S. acuminatus* mainly consumed Orthoptera and Hemiptera, while *B. raniceps* consumed Coleoptera and Formicidae. *T. typhonius* had a diet dominated by Coleoptera and Formicidae. Also, we found that the volume of prey consumed vary according to body size and that the composition of the diet was similar between species. Based on the electivity index, *S. acuminatus* selected the taxa Hemiptera, Coleoptera, and Orthoptera. *B. raniceps* selectively consumed Hemiptera, Coleoptera, and Diptera. *T. typhonius* selected a greater number of taxa such as Coleoptera, Araneae, Hemiptera, and Diptera.

We initially hypothesized that the diets of frogs in this assemblage might vary with body size, as demonstrated by Ceron et al. (2023). Our results demontrated this to be true for volume of prey in relation to the anuran body size, thus, despite the consumption of prey being similar among species, bigger species tended to have more volume in their stomachs than smaller species. Seasonality and rainfall, which are known to influence tree frog diets (Michelin et al. 2020), may help explain this finding. The extremely dry period in the Pantanal floodplain, characterized by reduced rainfall and harsh survival conditions (Marengo et al. 2021), likely constrained resource availability and could have affected body size and dietary flexibility in these individuals.

The diet pattern of *S. acuminatus*, which had Orthoptera and Hemiptera as the most important prey, followed the expected pattern observed in congeners in other regions, such as *Scinax fuscomarginatus* (Michelin et al. 2020), which preferred Hemiptera and Araneae. In the Pantanal, it was also reported that *S. acuminatus* mainly consumed Araneae and Orthoptera (Sabagh et al. 2010). A similar pattern was found for the diet of *B. raniceps* which is also in line with the findings of other congeners in the Pantanal, such as in Sabagh et al. 2010 who in their study observed a higher consumption of Coleoptera and Blattaria, while the individuals in our sample consumed Coleoptera and Formicidae. The similar diets of *B. raniceps* and *S. acuminatus* suggest a possible niche overlap, although there may be differences in prey

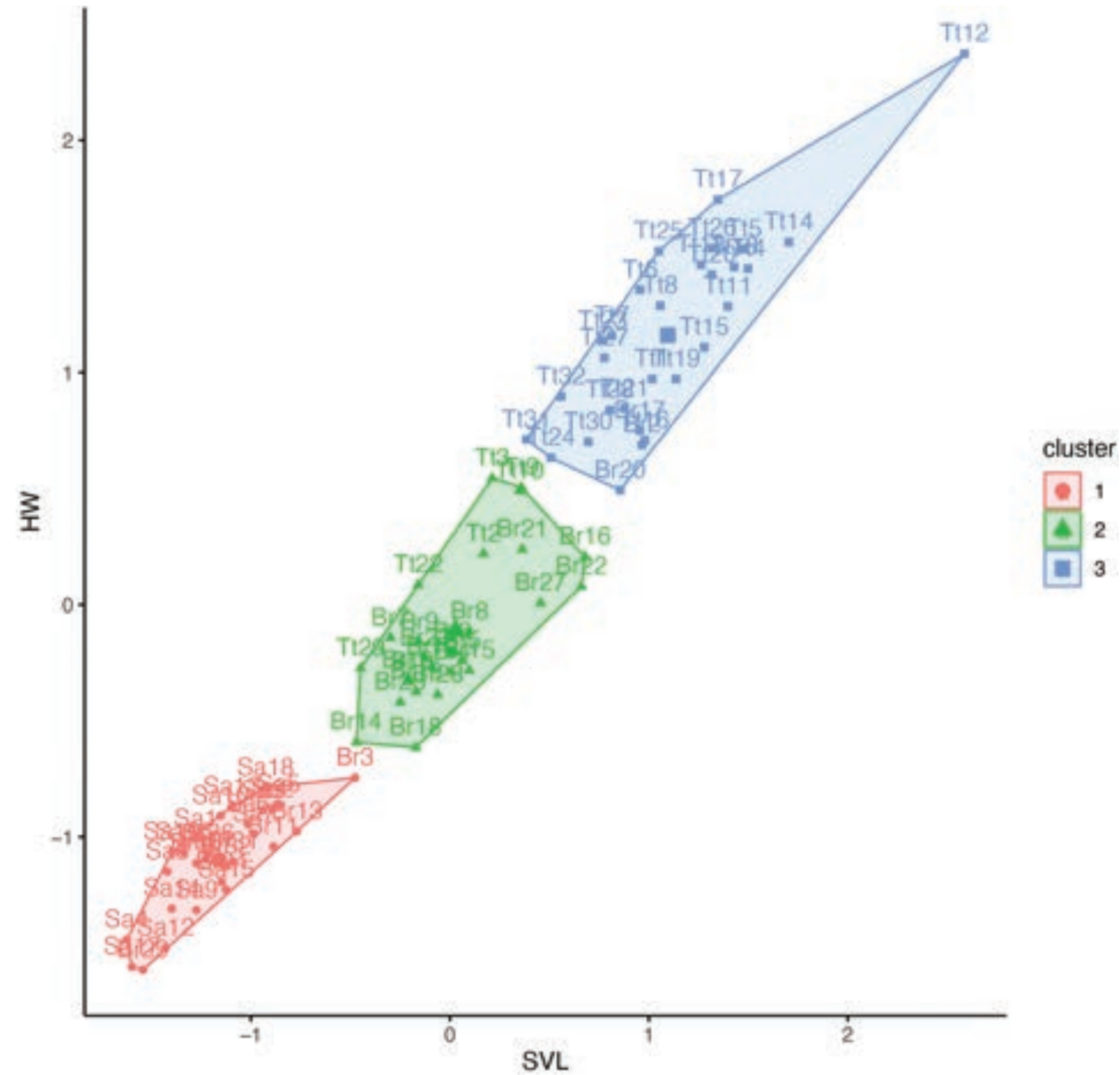

Figure 2. K-means analysis showing clusters based on anurans snout-vent length and head width, where: SA (*Scinax acuminatus*), BR (*Boana raniceps*), and TT (*Trachycephalus typhonius*).

volume (Sabagh et al. 2010). *T. typhonius* presented a diet composed primarily of Coleoptera which is consistent with the feeding patterns of the genus in other ecoregions and with populations of the species in the Pantanal (Muri 2005; de Araújo-Silva et al. 2024). Coleoptera was the most frequently consumed prey item across all species, consistent with the global dietary patterns observed in frogs (Ceron et al. 2019). This may be due to the high diversity of Coleoptera worldwide, which provides a range of prey sizes and forms (Rafael et al. 2024). Furthermore, the sit-and-wait foraging strategy of hylids likely facilitates predation of beetles inhabiting the arboreal strata where tree frogs forage (Toft 1981). The generalist diets of these three species, coupled with the challenging environmental conditions, resulted in a feeding pattern not driven by prey selectivity, as observed in other studies (Ceron et al. 2019, 2023). According to optimal foraging theory, generalist species consume prey that maximizes energy reserves relative to effort (Emlen 1966). In drought- and fire-affected environments, habitat homogenization may make prey more visible to predators, allowing them to forage for maximum energy gain (Bamford 1992). However, drought also reduces prey abundance and

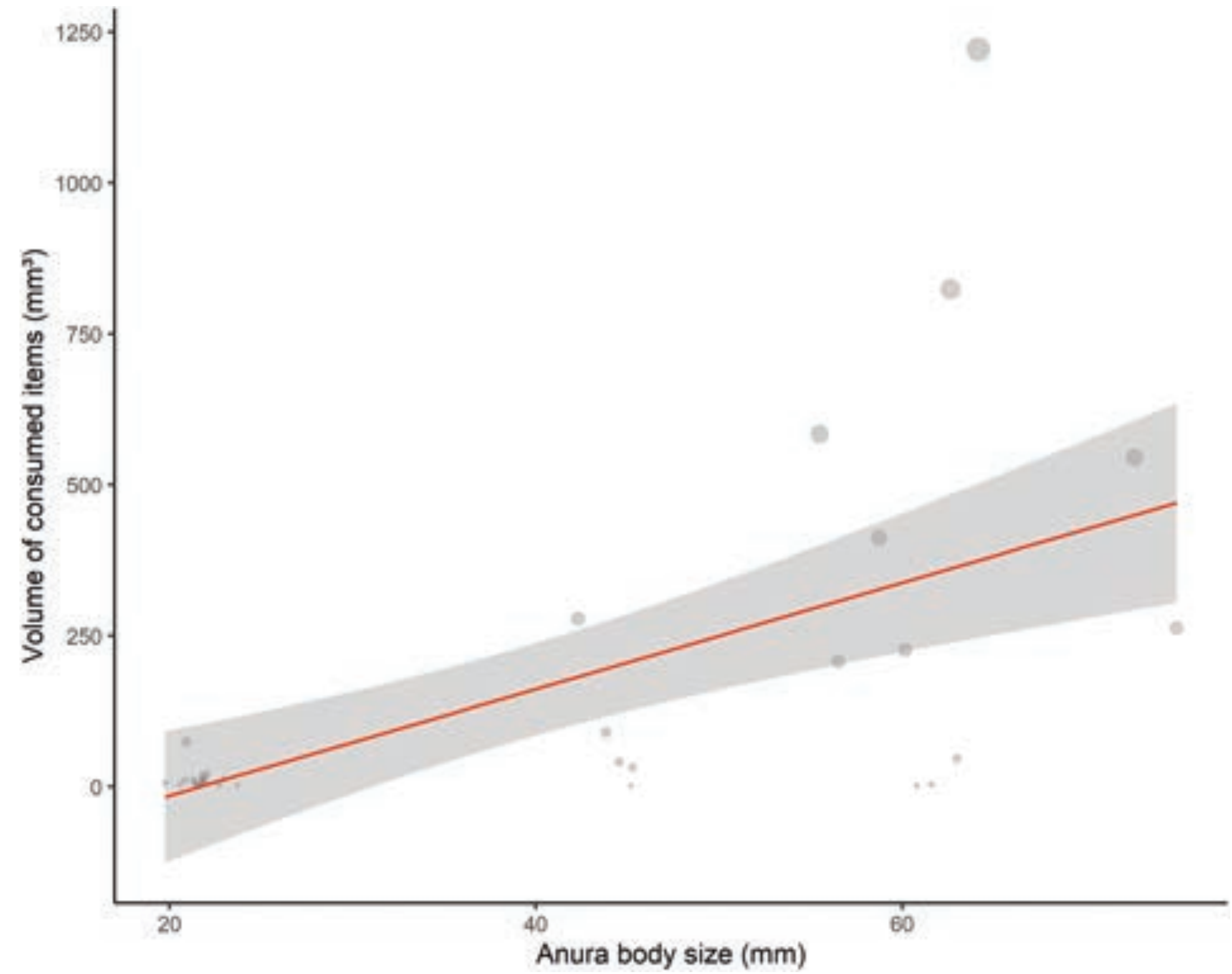

Figure 3. Relationship between the volume of consumed items (mm^3) and anuran body size (mm, $z = 4.913$; $p < 0.005$, $df = 30$). The circle size represents the volume of consumed prey.

capture opportunities (Saffarinia et al. 2022), which likely contributed to the high percentage of empty stomachs (40%) observed in this study.

During our survey, we noted that the hylids were not vocalizing. This behavior could indicate energy conservation, as calling is energetically costly for male anurans, especially during periods of resource scarcity (Wells and Schwartz 2007; Uetanabaro et al. 2008). The absence of vocalizations suggests that these individuals prioritized energy storage over reproduction, a common strategy in response to environmental stress (Ryan 1985). The feeding patterns observed in this hylid assemblage suggest that during adverse environmental conditions, these species adopt an opportunistic feeding strategy (Hirai and Matsui 2000). Survival and energy conservation appear to take precedence over prey selectivity (Robinson and Wilson 1998). The extreme drought and fire conditions likely drive these species to develop adaptive strategies to minimize energy expenditure, which may also impact their reproductive dynamics. Future research is needed to better understand how anuran populations respond and adapt to extreme environmental changes, particularly in light of increasing climate variability.

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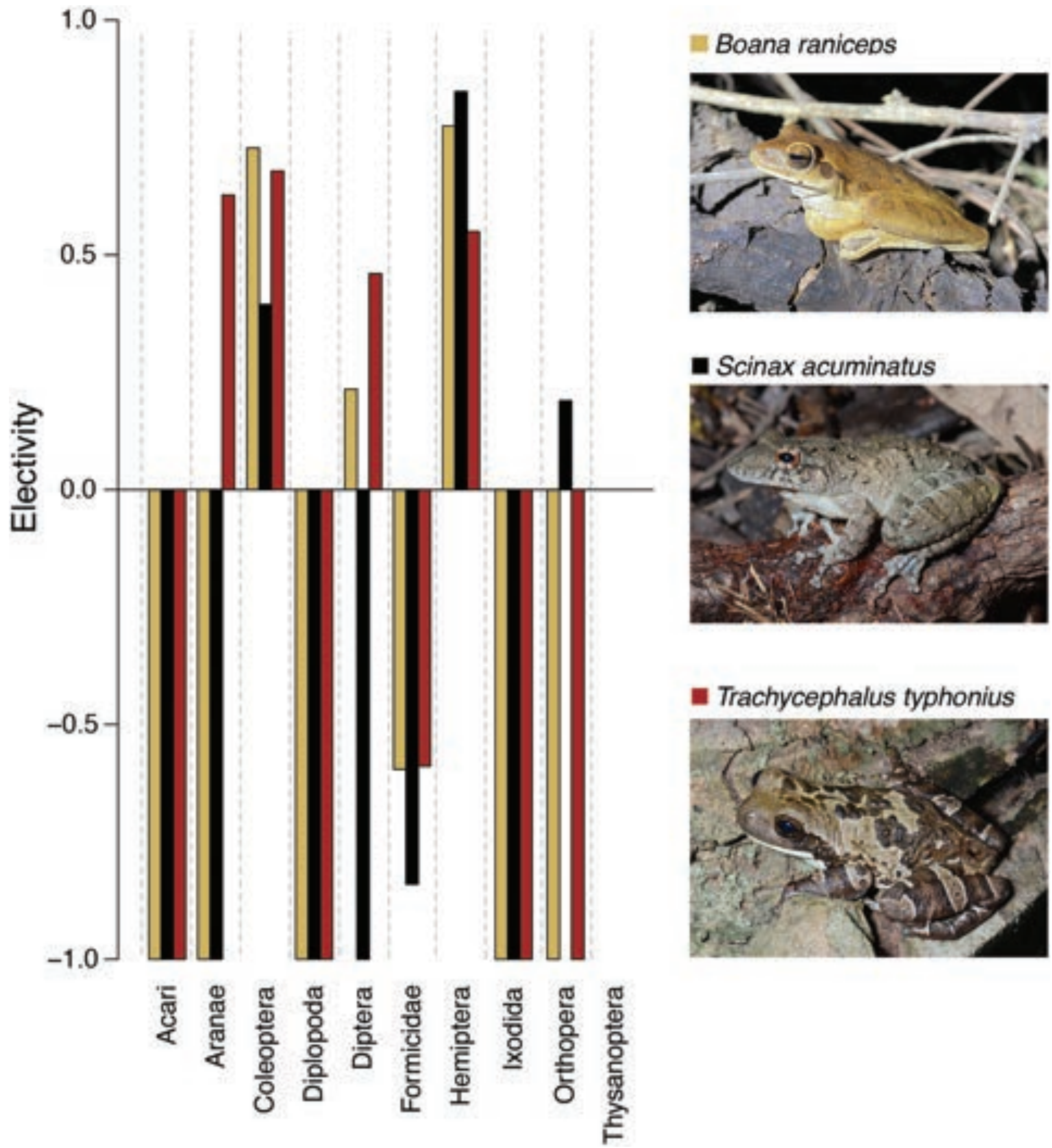

Figure 4. Vanderploeg and Scavia's Relativized Electivity Index for prey categories of *Boana raniceps, Scinax acuminatus*, and *Trachycephalus typhonius* in Pantanal, Brazil.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Authorship contribution

CRediT: Rafaela Machado: Data analysis, writing the manuscript, and reviewing the text. Ana Alice Cabral: Data analysis and reviewing the text. Lauany Serafim: Data analysis and reviewing the text. Diego Gomiero Cavalheri: Fieldwork and reviewing the text. Ibrahim Kamel Rodrigues Nehemy: Fieldwork and reviewing the text. Karoline Ceron: Conceptualization, data analysis, writing, and reviewing the final draft. Diego J. Santana: Conceptualization, fieldwork, resources, writing, and review & editing.

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