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ORIGINAL ARTICLE

Feeding habits of *Boana raniceps* (Cope, 1862) in three mountains of the Brazilian semiarid

Nayla Letícia Assunção Rodrigues[1], Kássio Castro Araújo[1,2], Robson Waldemar Ávila[2], Etielle Barroso de Andrade*[1]

Edited by
Angela Johana Espejo Mojica
editorus@javeriana.edu.co

1. Grupo de Pesquisa em Biodiversidade e Biotecnologia do Centro-Norte Piauiense – BIOTECPI, Instituto Federal de Educação, Ciência e Tecnologia do Piauí – IFPI Campus Pedro II, 64255-000, Piauí, Brasil

2. Pós-Graduação em Ecologia e Recursos Naturais, Departamento de Biologia, Campus Pici, Universidade Federal do Ceará, 60440-900Fortaleza, Ceará, Brasil

*etlandrade@hotmail.com

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Abstract

Studying the trophic ecology of animals helps us understand their life history, their relationship with the environment and other species, and their role in ecosystems. In this sense, we describe the feeding habits of the hyalid frog *Boana raniceps* in three high-altitude mountain ranges of Northeastern Brazil, investigating intersex differences in the diet and the relationship between the size with the volume of prey consumed. Furthermore, we investigated prey-predator interactions in the Boana genus with an ecological network approach. We analyzed the stomach contents of 62 B. raniceps specimens collected in three mountains in the state of Ceará (Northeastern Brazil) and consulted data available in the literature for information on the diet of other Boana species. We identified 82 prey items distributed in eleven categories. Overall, there were no differences in the composition of *B. raniceps* diet among the three mountains. Although males and females shared the majority of prey items consumed, they tended to consume prey volumetrically differently, and predator size did not influence prey volume. In addition, predator-prey interactions in the genus *Boana* revealed low modularity, complementary specialization, and nestedness. Therefore, species of the genus *Boana* follow the general pattern for the diet of most Brazilian frog species (generalist and opportunistic habits), being likely influenced by the availability of prey in the habitat. Overall, the present study constitutes a complete review of the prey items consumed by the genus *Boana* in Brazil, describing the general pattern of anuran-prey networks in these hylids

Keywords: Trophic ecology; diet; Hylidae; Chaco Treefrog

1. Introduction

Food webs are networks of interactions, determined by food resources, between a small group of organisms or populations (Winemiller and Polis, 1996). These interactions act directly on the ecological processes of an ecosystem since they influence energy flow and matter cycling across trophic levels (Nunez *et al.*, 2021). In addition, an organism's diet composition may reflect its species' food preference in a given habitat and time (Vitt and Caldwell, 2014). Therefore, studying the feeding habits of animals is a central tool for understanding their species' life histories and grasping their relationship with the environment and other species and their role in ecosystems (Moser *et al.*, 2017).

Among terrestrial vertebrates, amphibians are considered one of the most diverse groups (Frost, 2021), featuring a moist and permeable integument, which is the main derived characteristic of this group (Pough *et al.*, 2013). Due to this characteristic and their biphasic cycle, amphibians depend on aquatic environments or humid places to reproduce and complete their life cycle (Haddad *et*

al., 2008; Wells, 2010), whereby playing a central role in ecosystems, driving energy flow and nutrient cycling between aquatic and terrestrial environments (Huckembeck *et al.*, 2014) since they represent a significant portion of the biomass in the habitat and occupy an important position in food webs (Vitt *et al.*, 1990; Lima *et al.*, 2019).

In general, amphibians are generalist predators and opportunistic foragers (Rodrigues *et al.*, 2004; Costa *et al.*, 2016), although some species show degrees of specialization to capture specific prey (Luría-Manzano and Ramírez-Bautista, 2017). The amphibian diet follows morphological characteristics such as predator size (Silva *et al.*, 2009), physiological aspects (Sugai *et al.*, 2012), ontogeny (Lima and Magnusson, 2000), different reproductive efforts between males and females (Carvalho *et al.*, 2008), and microhabitat characteristics related to prey availability (Toft, 1981). Therefore, a species' diet composition can reveal the predator's biological characteristics and reflect foraging strategies (Solé and Rodder, 2010; Blanco-Torres *et al.*, 2020).

Brazil has the highest diversity of anuran amphibians on the planet, with more than 1.188 described species, and Hylidae being the most specious family (Segalla *et al.*, 2021). *Boana raniceps* (Cope, 1862) is a Neotropical hylid widely distributed in South America, from the Colombian Amazon to northern Argentina (Frost, 2021). Despite being considered a common species with a wide distribution, there are still gaps in the knowledge of its trophic ecology since it has only been studied in low-altitude regions in the Brazilian northeast and midwest regions (Leite Filho, 2015; Caldas *et al.*, 2019; Sabagh *et al.*, 2010). Northeastern Brazil has a semi-arid region marked by high temperatures and low and irregular rainfall, with a predominance of xeromorphic vegetation (Ab'Saber, 1974). Within this semi-arid landscape, high-altitude areas with milder temperatures and higher humidity harbor forests (Lima and Cascon, 2008). Since these forests are isolated systems, they have high biodiversity and a physiognomy distinct from their surrounding landscape (Tabarelli and Santos, 2004). Despite their role in maintaining ecological processes, studies of the trophic dynamics of amphibians in these forests are still scarce.

In this sense, the present study aimed to describe the feeding habits of *B. raniceps* in the humid mountain forest in Northeastern Brazil, investigating sex-related diet differences and the relationship between predator size and the volume of prey consumed. In addition, we also compile information on the trophic ecology of the genus, and, using an ecological network approach, we investigate the prey-predator interactions between the different species of the genus *Boana* in Brazil. We assumed that anuran diet composition can be influenced and directed by three aspects: changes in the composition of the landscape, which in turn determines prey availability (Das, 1996; Rosa *et al.*, 2011); sexual dimorphism (Juncá and Eterovick, 2007); and the predator-prey size relationship, in which larger individuals are expected to be able to consume larger prey (Maneyro *et al.*, 2004). These considerations led us to pose the following questions: (i) Does diet composition vary in space (i.e., among the studied mountains)? (ii) Do males and females differ in feeding habits? (iii) Do larger individuals tend to eat larger prey? (iv) How similar is the diet composition of the *Boana* genus in Brazil? The answers to these questions will contribute to the understanding of the trophic dynamics of *B. raniceps*, as well as grasping the influence of different landscapes on the diet composition of the species. Furthermore, the present work represents the first study of this nature for *B. raniceps* in high-altitude areas of northeastern Brazil.

2. Materials and methods

2.1. Study area

The present study was conducted in three high-altitude formations located in the state of Ceará (the Baturité, Maranguape, and Meruoca mountains), in Northeastern Brazil (Figure 1). These areas are crystalline residual massifs, considered humid forest islands in the Northeastern semi-arid region (Andrade-Lima, 1982). The climate in these regions is milder (mean temperatures ranging from 21.9 °C to 24.4 °C) compared to the Sertaneja Depression drylands ("Depressão Sertaneja") (mean temperature ranging from 26 °C to 28 °C) that surround them (Júnior and Souza, 2012). Additionally, the maximum altitude of these mountains varies from 600 m to 1200 m above sea level (Bétard et al., 2007), experiencing an annual rainfall higher than 1200 mm (Tabarelli and Santos, 2004; Lima and Cascon, 2008).

The Baturité Mountain is located in the North Cearense Mesoregion (4°12′19.7″S and 38°57′37.7″W), with an altitude of approximately 900 m, encompassing 10 municipalities in the state (Bétard *et al.*, 2007; Batista *et al.*, 2011). The Maranguape Mountain (3°54′16.7″S and 38°43′13.7″W) is located in the Metropolitan Mesoregion of Fortaleza, between the municipalities of Maranguape, Maracanau, and Caucaia, reaching more than 900 m in altitude (**?**Barbosa *et al.*, 2014). Finally, the Meruoca Mountain is located in the Northwest Cearense Mesoregion (3°3251.8′S and 40°26′55.1″W), with a maximum altitude of 700 m, spanning four municipalities: Alcântaras, Massapé, Meruoca, and Sobral (Diniz, 2013; Lima *et al.*, 2019). These areas are characterized by their distinct plant physiognomies: on their lowlands, the Caatinga vegetation is predominant whereas at high elevations, rainforest enclaves are predominant (Moro *et al.*, 2015).

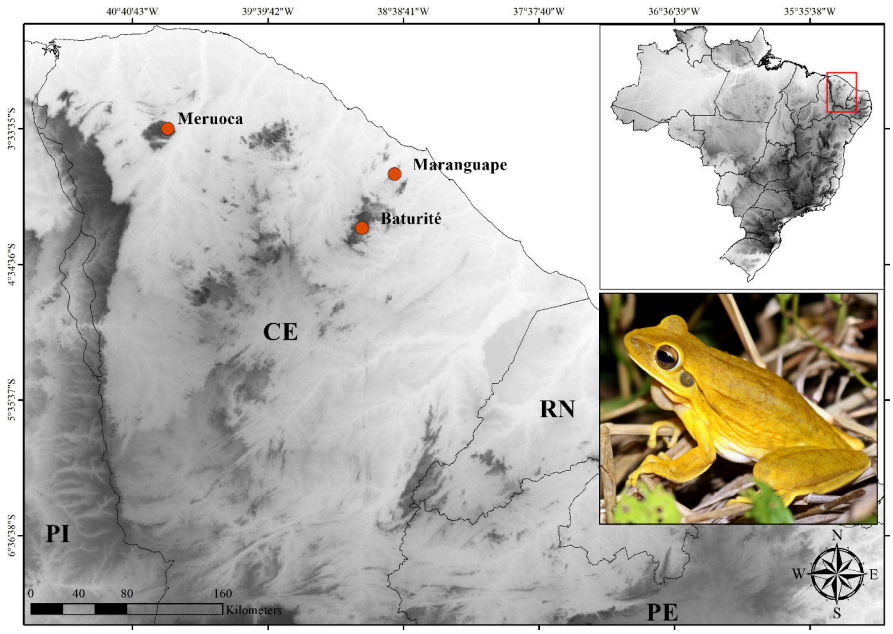

Figure 1. Map of the areas sampled in the three mountain ranges in the state of Ceará, Northeastern Brazil, featuring a *Boana raniceps* individual collected in the Meruoca mountain.

2.2. Sampling design

The specimens of *B. raniceps* (Figure 1) were collected during the rainy season in the region, between February and May 2019, with fifteen consecutive days of collection in each mountain, totaling 45 days of collection. The sampling sites were chosen depending on favorable environmental conditions for the reproduction of anurans, such as springs, streams, and ponds. The capture of individuals was performed through auditory and visual searches (Heyer *et al.*, 1994) at night (17:30 h to 00:00 h). Individuals were manually collected, euthanized with an injection of lidocaine (2 %), fixed in 10 % formalin, and preserved in 70 % alcohol. Voucher specimens were deposited at the Regional Center of Ophiology at Universidade Federal do Ceará, Fortaleza, Brazil.

2.3. Data analyses

In the laboratory, the stomachs of the specimens were removed and their contents were scrutinized under a stereomicroscope. The prey recorded were identified to the lowest possible taxonomic level, usually Order, using the specialized literature (Triplehorn and Johnson, 2010; Rafael *et al.*, 2012). We used a digital caliper (0.01 mm accuracy) to measure the snout-vent length (SVL) of the anurans collected (anuran body size estimator), besides the length and the width of the consumed prey. The volume of consumed prey was estimated using the ellipsoid formula:

$$V = \frac{4}{3}\pi \left(\frac{L}{2}\right)\left(\frac{W}{2}\right)^2 \tag{1}$$

where, V = volume, L = length, and W = prey width (Griffiths & Mylotte, 1987). We then calculated the Relative Importance Index (RII) to measure how much each food item contributed to the species' diet (Pinkas et al., 1971), using the following formula:

$$\text{RII} = \frac{F\% + N\% + V\%}{3} \tag{2}$$

where $F\%$, $N\%$, and $V\%$ are the proportions of the frequency of occurrence, numerical abundance, and volume of each prey, respectively (Powell, 1990). The frequency of plant material consumed by the specimens was accounted for but was not used in our statistical analyses. The volumetric trophic niche width (Bvol) was obtained through the inverse of the Simpson index (Simpson, 1949), while the prey diversity value was obtained through the Shannon-Wiener diversity index (Magurran, 2004). To investigate differences in the composition of the prey consumed by *B. raniceps* concerning the different mountains, we performed a permutational multivariate analysis of variance (PERMANOVA) followed by a permutational dispersion (PERMDISP) to investigate the groups' dispersion via post-hoc Tukey tests (pairwise analysis). Subsequently, we conducted a t-test to investigate differences in prey volumes consumed between males and females. In addition, linear mixed models (LMM) were used with the sex of the individuals as a random variable to investigate the influence of individual size (SVL) on the volume of each prey consumed.

Additionally, we compiled information on prey items consumed by different *Boana* species in Brazil, identifying peer-reviewed scientific publications available in seven electronic databases (Google, Google Scholar, PubMed, Scielo, Science Direct, Scopus, and Web of Science) combining the following keywords in Portuguese and English: *Boana*, Brazil, diet, feeding habits, *Hyla*, Hylidae, *Hypsiboas*, and food webs. We used RII to produce anuran-prey interaction matrices and the graphic depiction of the food items most consumed by *Boana* species in Brazil. We used three network metrics to calculate the anuran-prey interaction networks: modularity, nestedness, and

complementary specialization (Ceron *et al.*, 2019; Dudczak *et al.*, 2021). We assessed modularity to verify the network of clusters because this metric identifies subgroups sharing similar resources or playing similar functional roles (Araujo *et al.*, 2018; Ceron *et al.*, 2019). Network nestedness allows us to understand whether species with low connections (specialists) interact with a subset of super-connected species (generalists), whereas complementary specialization reveals interaction exclusivity (Zanata *et al.*, 2017; Ceron *et al.*, 2019). All analyses were performed using Bipartite (Dormann *et al.*, 2009), Igraph (Csardi and Nepusz, 2006), and Vegan (Oksanen *et al.*, 2017) packages in R software (R core team, 2020).

3. Results

We collected 62 *B. raniceps* specimens in the three mountains studied, of which 12 individuals (10 males and two females) were found in the Baturité Mountain, 17 individuals (13 males and four females) in the Meruoca Mountain, and 14 individuals (9 males and five females) in the Maranguape Mountain, for a total of 51 males and 11 females. Nineteen individuals (30 %; three females and 16 males) had an empty stomach. Among the stomachs with food contents (70 %), 82 prey items were identified. These fell into 11 taxa within the arthropod classes Arachnida and Insecta. Other stomach contents included plant material (Table 1). The most frequent food items were Coleoptera, larvae, and Orthoptera, representing 57.1 % of the frogs' diet. Volumetrically, the most consumed prey were Orthopterans (33.9 %), larvae (25.7 %), and Coleopterans (23.3 %). Although we did not include plant material in the statistical analyses, plants had the highest frequency of occurrence in the diet composition (28.1 %). According to the RII (Table 1), the items that most contributed to the diet of *B. raniceps* were Coleoptera (29.4 %), Orthoptera (21.3 %), and larvae (17.0 %).

Table 1. *Boana raniceps* diet composition in three mountains in the state of Ceará, Northeastern Brazil. Absolute and relative values (%) of the number (N), frequency (F), volume (V) of prey, and the relative importance index (RII) of each one.

Items	N (%)	F (%)	V (%)	IRI
ARACHNIDA				
Acari	1.0 (1.6)	1.0 (2.2)	0.1 (0.0)	1.3
Araneae	3.0 (4.8)	3.0 (6.5)	514.3 (4.5)	5.2
INSECTA				
Coleoptera	19.0 (30.2)	16.0 (34.8)	2694.2 (23.3)	29.4
Dermaptera	2.0 (3.2)	2.0 (4.3)	104.3 (0.9)	2.8
Diptera	5.0 (7.9)	2.0 (4.3)	411.8 (3.6)	5.3
Formicidae	5.0 (7.9)	2.0 (4.3)	22.9 (0.2)	4.2
Hemiptera	6.0 (9.5)	3.0 (6.5)	507.4 (4.4)	6.8
Odonata	5.0 (7.9)	4.0 (8.7)	396.7 (3.4)	6.7
Orthoptera	8.0 (12.7)	8.0 (17.4)	3913.4 (33.9)	21.3
OTHER ITEMS				
Larvae	9.0 (14.3)	5.0 (10.9)	2974.6 (25.8)	17.0
Plant material	-	64	-	-
TOTAL	63.0 (100)	46.0 (100)	11539.7 (100)	100

Among the three studied mountains, we did not find significant differences in the prey composition consumed by *B. raniceps* (Figure 2) (R2 $= 0.20$, Pseudo-F $= 1.27$, P $= 0.23$). Likewise, there were no differences in group dispersion (Pseudo-F $= 3.14$; $P = 0.08$), nor were there following the pairwise mountain contrasts Maranguape – Baturité (P-adjusted $= 0.58$), Baturité – Meruoca (P-adjusted $= 0.07$), and Maranguape – Meruoca (P-adjusted $= 0.37$). Although males and females consumed similar prey items, they tended to consume prey volumetrically differently ($t = 2.27$; $p = 0.02$). Males displayed a volumetric trophic niche width (Bvol $= 3.83$) and a diversity of consumed prey ($H' = 1.98$) that were slightly larger than those of females (Bvol $= 3.34$ and $H' = 1.80$, respectively). According to the RII, Coleoptera was the most important prey item in the diet of males, while females consumed more Orthoptera and larvae (Table 2). In this study, the mean size of females (SVL $= 77.6 – 64.2$, Mean $= 75.6$) of *B. raniceps* was slightly larger than males (SVL $= 78.1 – 64.7$, Mean $= 72.1$). Nonetheless, our results do not support the hypothesis that larger anurans tend to eat volumetrically large prey items ($T = -1.78$; $P = 0.08$); however, the sex of the individuals explained almost 40 % of the observed variation (Intercept $= 2.09$, Residual $= 3.51$).

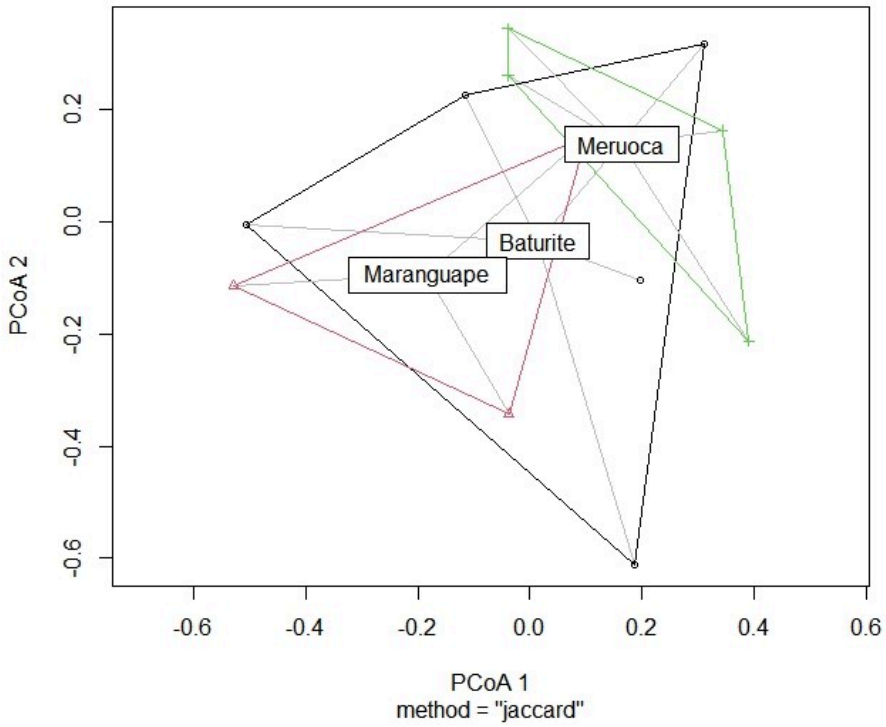

Figure 2. PERMANOVA graph evidencing little variation in the diet composition of *Boana raniceps* in the three (labeled) mountains studied.

Table 2. Male and female *Boana raniceps* diet composition in three mountains in the state of Ceará, Northeastern Brazil.

Item	Males				Females			
	F (%)	N (%)	V (%)	IRI	F (%)	N (%)	V (%)	IRI
ARACHNIDA								
Acari	-	-	-	-	1 (7.1)	1 (6.7)	0.1 (0.0)	4.6
Araneae	2 (6.3)	2 (4.2)	183 (2.1)	4.2	1 (7.1)	1 (6.7)	331.2 (12.0)	8.6
INSECTA								
Coleoptera	13 (40.6)	16 (33.3)	2430.7 (27.7)	33.9	3 (21.4)	3 (20.0)	263.4 (9.5)	17
Dermaptera	2 (6.3)	2 (4.2)	104.3 (1.2)	3.9	-	-	-	-
Diptera	2 (6.3)	5 (10.4)	411.8 (4.7)	7.1	-	-	-	-
Formicidae	2 (6.3)	5 (10.4)	22.9 (0.3)	5.6	-	-	-	-
Hemiptera	1 (3.1)	4 (8.3)	123.4 (1.4)	4.3	2 (14.3)	2 (13.3)	384.1 (13.9)	13.8
Odonata	3 (9.4)	4 (8.3)	340.1 (3.9)	7.2	1 (7.1)	1 (6.7)	56.5 (2.0)	5.3
Orthoptera	4 (12.5)	4 (8.3)	3091.5 (35.2)	18.7	4 (28.6)	4 (26.7)	821.9 (29.7)	28.3
OTHER ITEMS								
Larvae	3 (9.4)	6 (12.5)	2068.4 (23.6)	15.1	2 (14.3)	3 (20.0)	906.2 (32.8)	22.4
Total	32 (100)	48 (100)	8776.3 (100)	100	14 (100)	15 (100)	2763.4 (100)	100

Among the different species of the genus *Boana*, *B. raniceps* had the highest diversity index ($H' = 2.11$), followed by *B. albopunctata* (see Table 3). These species also presented the largest trophic width among the genus *Boana* (Table 3). Considering the ecological network approach, despite some prey items being more consumed than others (*e.g.*, Coleoptera and Orthoptera; Figure 3), we observed that predator-prey interactions in the genus *Boana* tended to show low complementary specialization ($H2 = 0.35$), modularity ($M = 0.31$), and nesting (WNODF = 37.3).

Table 3. Species of the genus *Boana* and amount of prey categories consumed (N), Shannon-Wiener Diversity Index (H') and volumetric trophic niche width (Bvol), localities, federative units (Brazilian states), and data sources. Data not available (-).

Species	N	H'	Bvol	Locality	Brazilian State	Reference
Boana albomarginata	07	1.29	1.63	Parque Nacional da Serra de Itabaiana	Alagoas	Tupy et al. (2021)
Boana albopunctata 1	13	1.86	4.32	Fazenda Sucupira	Distrito Federal	Araújo et al. (2007)
Boana albopunctata 2	11	1.89	4.30	Ponte Nova	Minas Gerais	Pacheco et al. (2017)
Boana albopunctata 3	09	1.52	3.45	Gama	Distrito Federal	Guimarães et al. (2011)
Boana albopunctata 4	05	1.21	2.23	Parque Estadual Serra da Boa Esperança	Minas Gerais	Diniz et al. (2013)
Boana bischof	15	1.57	-	São Francisco de Paula	Rio Grande do Sul	Moser et al. (2018)
Boana cinerascens	07	1.63	-	Manaus	Amazonas	Telles et al. (2013)
Boana faber	04	1.02	2.35	Parque Estadual Serra da Boa Esperança	Minas Gerais	Diniz et al. (2013)
Boana leptolineata	11	2.06	5.20	Centro de Pesquisas e Conservação da Natureza	Rio Grande do Sul	Barbosa et al. (2014)
Boana lundii	03	0.89	1.73	Parque Estadual Serra da Boa Esperança	Minas Gerais	Diniz et al. (2013)
Boana marginata	12	1.16	-	São Francisco de Paula	Rio Grande do Sul	Moser et al. (2018)
Boana pombali 1	04	0.67	1.01	-	Bahia	Protázio et al. (2018)
Boana pombali 2	05	1.37	2.19	Parque Nacional da Serra de Itabaiana	Sergipe	Tupy et al. (2021)
Boana raniceps 1	10	1.95	4.13	Baturité, Maranguape, Meruoca	**Ceará**	**Present study**
Boana raniceps 2	11	1.96	-	Corumbá	Mato Grosso do Sul	Sabagh et al. (2010)
Boana raniceps 3	05	1.30	1.90	São João do Cariri	Paraíba	Leite Filho et al. (2015)
Boana semilineata	05	1.21	1.01	-	Bahia	Protázio et al. (2018)

4. Discussion

Although some anuran species specialize in certain types of prey, most have a generalist diet composed mainly of invertebrates (Toft, 1981; Wells, 2010). In general, species of the Hylidae family have a great diversity of spatial niches (Protázio *et al.*, 2015), favored by their generalist feeding habits (e.g., López *et al.* (2009); Moser *et al.* (2018). In this study, *B. raniceps* consumed a great diversity of prey items, stating its generalist habit, as already observed for this species in areas of Caatinga and Cerrado (Sabagh *et al.*, 2010; Leite Filho, 2015). The diet of hylids is usually composed of prey items with high modularity, which is a consequence of their sit-and-wait foraging strategy (Parmelee, 1999). We also found a great variety of mobile prey in the diet of *B. raniceps* (coleopterans, orthopterans, and hemipterans), exhibiting a sit-and-wait hunting strategy (Toft, 1981). This foraging mode was already observed for other *Boana* species, for instance, *B. semilineata* and *B. pombali*, in the Brazilian Atlantic Forest (Protázio *et al.*, 2018).

Coleopterans and orthopterans were the two items with the highest levels of importance in the *B. raniceps* diet, being also the most common category for the genus (*e.g.*, Telles *et al.* (2013); Leite Filho (2015); Protázio *et al.* (2018). These prey items usually belong to the diet of anurans (*e.g.*, (Parmelee, 1999; Pacheco *et al.*, 2017). This fact may be related to the fact that Coleoptera is a well-diversified group of organisms and is abundant in natural environments (Texeira *et al.*, 2009); in addition, their chitinous exoskeleton slows the digestion of these prey, remaining in the anuran stomach for a longer time (Mahan and Johnson, 2007). On the other hand, orthopterans are more common in tree strata (Tupy *et al.*, 2021), where they usually forage, becoming easy prey for generalist predators. Larvae are also a salient prey item for *B. raniceps* and, in general, frogs of the *Boana* genus; for instance, *B. albopunctata, B. albomarginata*, and *B. pombali* (Pacheco *et al.*, 2017; Tupy *et al.*, 2021). Larvae ingestion by anurans is fitness advantageous because they are prey with low mobility and straightforward digestibility (Batista *et al.*, 2011; Pacheco *et al.*, 2017). Additionally, they are items of high energy value and are abundant in humid environments. Consequently, ingesting larvae benefits anurans and may be associated with their prolonged reproductive activity (Caldas *et al.*, 2016; Batista *et al.*, 2011). Therefore, the low cost of acquisition and the high energy return during the reproductive period might explain *B. raniceps'* preference for larvae.

Plant material was the item with the highest frequency of occurrence in the diet of *B. raniceps*. Although the ingestion of this item is usually considered accidental in the diet of anurans (Solé and Pelz, 2007; Sabagh *et al.*, 2010; Protázio *et al.*, 2018), including for *B. raniceps* (Sabagh *et al.*, 2010; Leite Filho, 2015), the high amount of this material indicates intentional consumption by the species in the areas studied here. Uncommon herbivory has already been reported for some anuran species, such as *Xenohyla truncata* and *Euphlyctis hexadactyla* (Silva *et al.*, 1989; Das, 1996; Silva and Britto-Pereira, 2006; de-Oliveira-Nogueira *et al.*, 2023), with plants being a significant part of their diet. On the other hand, *Boana* species, such as *B. albomarginata* and *B. pombali*, consumed plant material during the dry period, possibly as a water source (Tupy *et al.*, 2021). In addition, the presence of this item can aid in the digestion of arthropod exoskeletons, contribute to eliminating intestinal parasites, and serve as an additional source of nutrients (Anderson *et al.*, 1999). Nonetheless, we sampled the individuals during the rainy season, and the high frequency of plant material, especially among males, may indicate its purposeful consumption and a leaning for this food in high-altitude *B. raniceps* populations. In this sense, required seasonal studies addressing the anuran diet in these mountains should clarify the importance of plant pieces for this treefrog diet.

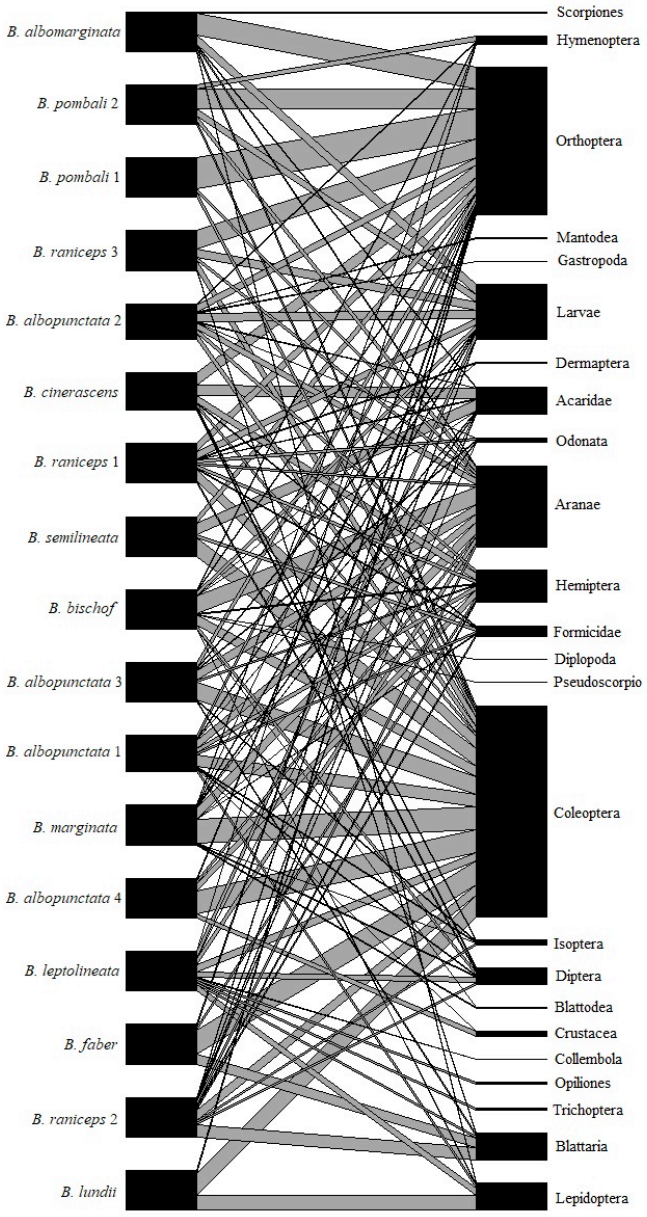

Figure 3. Bipartite network diagram representing the predator-prey interactions among different species of the genus *Boana* in Brazil. The bar width of the predators (left side column, with Boana species names) represents niche breadth, and the bar width of the prey (right side column, with arthropod order names) is the level of importance for the diet of the *Boana* species.

The composition of prey consumed by *B. raniceps* did not vary significantly concerning the mountain where individuals were collected. Despite the geographic distance between the studied mountains, we believe that there were no differences in the composition of the diet between the three populations studied due to the similarity among their environments since the three mountains are inserted in the same plant physiognomies and have similar environmental resources (Moro *et al.*, 2015), indicating that structurally similar habitats harbor a range of comparable food resources. Although seasonal variation influences the anuran diet, due to the availability and replacement of prey in the environment at different times of the year (Guimarães *et al.*, 2011), we sampled *B. raniceps* individuals only in the rainy season and were unable to investigate seasonal variation in prey consumption.

Although males consumed prey volumetrically slightly larger than females (Table 2), there was no predator body size effect on the food item volume, as already observed for other species of the genus (López *et al.*, 2009; Rosa *et al.*, 2011). This fact may be related to the absence of sexual dimorphism in species size, as well as the compensation of energy expenditure between males (calling activity) and females (egg production) during the reproductive period (Rosa *et al.*, 2011). In addition, predator size had little contribution to prey selection, showing a less selective and more opportunistic behavior for *B. raniceps*. It is worth noting that recent studies indicate that characteristics such as locomotion mode and body shape influence prey selection better than predator size (Blanco-Torres *et al.*, 2020).

Concerning anuran-prey ecological networks, we observed that the species of the genus *Boana* tend not to be nested. Thus, there are few specialist species, and they interact little with the generalists (Ceron *et al.*, 2019). The effect of this generalist feeding habit results in low specialist values, providing a more diversified diet (Blüthgen *et al.*, 2006; Ceron *et al.*, 2019). Furthermore, due to the non-specificity of interactions, there is no selective prey choice, reducing the modularity of ecological networks (Dudczak *et al.*, 2021). Prey-predator interactions in anuran communities may vary depending on ecoregions and seasonality (Ceron *et al.*, 2022). Therefore, despite being congeners, these species are well distributed in Brazil, likely influencing the high diversity of prey items consumed and, consequently, low specificity and non-formation of modules.

5. Conclusion

Boana raniceps is a widely distributed species found in low and high areas in northeastern Brazil. This species showed high diversity and greater trophic niche width in contrast to other species of the genus, and its diet composition was not different among the three sampled mountain ranges. *B. raniceps* has an arthropod-rich diet featuring generalist and opportunistic predator traits. Except for plant material, Coleoptera and Orthoptera were the most frequent categories among the items ingested by the species, which may be associated with the abundance and diversity of prey in the environment (Texeira *et al.*, 2009; Tupy *et al.*, 2021). Although not the main focus of this work, we compared the diversity of prey consumed by other *Boana* species, revealing showed similar eating habits (i.e., generalist predators of a wide prey diversity), in which the observed variations may reflect the availability of prey in the sampled locations. Overall, the present study constitutes a complete review of the prey items consumed by the genus *Boana* in Brazil, describing the general pattern of anuran-prey networks in these hylids.

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7. Conflict of interest

The authors declare that there are no conflicts of interest.

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Hábitos alimentarios de *Boana raniceps* (Cope, 1862) en tres montañas del semiárido brasileño

Resumen: Estudiar la ecología trófica de los animales es una herramienta importante para comprender su historia de vida, su relación con el medio ambiente y con otras especies, así como su papel en los ecosistemas. En este sentido, describimos los hábitos alimentarios de *Boana raniceps* en tres cordilleras de gran altitud del noreste de Brasil e investigamos las diferencias entre los sexos en la dieta y la relación entre el tamaño y el volumen de presas consumidas. Adicionalmente, investigamos las interacciones presa-predador en el género *Boana* utilizando un enfoque de red ecológica. Analizamos 62 ejemplares de *B. raniceps* recolectados en tres montañas en el estado de Ceará, noreste de Brasil, y consultamos datos disponibles en la literatura para obtener información sobre la dieta de otras especies de *Boana*. Identificamos 82 presas distribuidas en 11 categorías. En general, no hubo diferencias en la composición de la dieta de *B. raniceps* entre las tres montañas. Aunque los machos y las hembras comparten la mayoría de las presas consumidas, tienden a consumir presas volumétricamente diferentes. El tamaño de los individuos no influyó en el volumen de presas consumidas. Además, las interacciones presa-predador en el género *Boana* tienden a presentar baja modularidad, especialización complementaria y anidamiento. Por lo tanto, las especies del género *Boana* siguen el patrón general de dieta de la mayoría de las especies de ranas brasileñas (hábitos generalistas y oportunistas), siendo probablemente influenciadas por la disponibilidad de presas en el hábitat. En general, el presente estudio contribuye con una revisión completa de los elementos de presa consumidos por el género *Boana* en Brasil, describiendo el patrón general de las redes de anuros-presas en estos hílidos.

Palabras Clave: Ecología trófica; dieta; Hylidae; Rana arbórea del Chaco.

Hábitos alimentares de *Boana raniceps* (Cope, 1862) em três montanhas do semiárido brasileiro

Resumo: O estudo da ecologia trófica dos animais é uma ferramenta importante para compreender sua história de vida, sua relação com o ambiente e com outras espécies, bem como seu papel nos ecossistemas. Nesse sentido, descrevemos os hábitos alimentares de *Boana raniceps* em três cadeias de montanhas de alta altitude do Nordeste do Brasil, investigando as diferenças entre os sexos na dieta e a relação entre o tamanho e o volume das presas consumidas. Além disso, investigamos as interações presa-predador no gênero *Boana* utilizando uma abordagem de rede ecológica. Analisamos 62 exemplares de *B. raniceps* coletados em três montanhas no estado do Ceará, no Nordeste do Brasil, e consultamos dados disponíveis na literatura para obter informações sobre a dieta de outras espécies de *Boana*. Identificamos 82 presas distribuídas em 11 categorias. No geral, não há diferenças na composição da dieta de *B. raniceps* entre as três montanhas. Embora machos e fêmeas compartilhem a maioria dos itens de presa consumidos, eles tendem a consumir presas com diferenças volumétricas. O tamanho dos indivíduos não influencia o volume de presas consumidas. Além disso, as interações presa-predador no gênero *Boana* tendem a apresentar baixa modularidade, especialização complementar e aninhamento. Portanto, as espécies do gênero *Boana* seguem o padrão geral da dieta da maioria das espécies de rãs brasileiras (hábitos generalistas e oportunistas), sendo provavelmente influenciadas pela disponibilidade de presas no habitat. No geral, o presente estudo contribui com uma revisão completa dos itens de presa consumidos pelo gênero *Boana* no Brasil, descrevendo o padrão geral das redes anuro-presa nessas hylidas.

Palavras-chave: Ecologia trófica; dieta; Hylidae; Rã-da-chaco.

Nayla Letícia Assunção Rodrigues Graduated in Biological Sciences from the Federal de Educação, Ciência e Tecnologia do Piauí - IFPI Campus Pedro II, Piauí, Brazil. She is currently a Master's student in the Graduate Program in Ecology and Biodiversity Conservation - PPGECB at the Universidade Estadual de Santa Cruz - UESC, Bahia, Brazil, and a member of the Grupo de Pesquisa em Biodiversidade e Biotecnologia do Centro-Norte Piauiense - BIOTECPI, IFPI Campus Pedro II.

ORCID: 0000-0002-6847-1269

Kássio Castro Araújo He is a Biologist with a M.Sc. and Ph.D. in Ecology and Natural Resources from the Universidade Federal do Ceará, Fortaleza, Brazil. Actually, he is a post-doctoral researcher at Federal de Educação, Ciência e Tecnologia do Piauí - IFPI Campus Pedro II, Piauí, Brazil. He is interested in herpetology, ecology, and animal behavior.

ORCID: 0000-0003-4091-8521

Robson Waldemar Ávila He has a Ph.D. in Biology from the Universidade Estadual de São Paulo - UNESP, São Paulo, Brazil. He is a Professor at Universidade Federal do Ceará - UFC, Ceará, Brazil, with research in herpetology and helminths associated with amphibians and reptiles.

ORCID: 0000-0003-3641-8321

Etielle Barroso de Andrade He is a Professor at Instituto Federal de Educação, Ciência e Tecnologia do Piauí - IFPI Campus Pedro II, Piauí, Brazil. He has a Ph.D. in Biodiversity and Biotechnology from the Postgraduate Program in Biodiversity and Biotechnology Network of the Legal Amazon from Universidade Federal do Maranhão (Bionorte/UFMA), Maranhão, Brazil. He is a Biologist interested in general aspects of natural history, taxonomy, and conservation of herpetofauna, with emphasis on anurans.

ORCID: 0000-0002-5030-1675