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Diet composition and coexistence of *Boana geographica* and *Boana raniceps* (Anura: Hylidae) from Central Amazonia, Brazil

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Abstract. Investigating feeding patterns among species is essential to understanding and preserving populations, especially in habitats like the Amazon. This study analyzed the patterns of food resource use of two coexisting species of Hylidae, *Boana geographica* and *B. raniceps*, in Central Amazonia, Brazil. High trophic niche overlap (0.74) and differences in the most important food items were observed between the two species. For *B. geographica*, anuran tadpoles were the prey with the greatest volume (63.73%) and frequency (30%). For *B. raniceps*, the items with the highest volume were Orthoptera (53.14%) and Araneae (30.39%), and the most frequent item was Coleoptera (18.75%). The most important food items for *B. geographica* were tadpoles (Ix = 39.41) and for *B. raniceps* were Orthoptera (Ix = 25.05) and Coleoptera (Ix = 16.85). For both species, no correlation was found between predator size and mouth width in relation to the size and volume of the prey. *Boana raniceps* was considered a passive, generalist forager with a sit-and-wait feeding strategy like most Hylidae. On the other hand, *B. geographica* may be regarded as an active generalist forager due to the high consumption of tadpoles. Despite the high overlap in their diet composition, the differences in prey categories with greater dietary importance likely seem to enable these species' coexistence.

Keywords: Amphibian, sympatric species, trophic ecology, niche overlap.

Introduction

Research on trophic ecology and feeding behavior in ectothermic vertebrates reveal a complex set of interrelated characteristics involving the type and number of prey consumed, the energetic cost of foraging, and the metabolic characteristics of predators (Taigen & Pough 1983, Maneyro et al. 2004, Jefferson et al. 2014). In this sense, the diet of anurans is determined by factors such as availability of prey (Pacheco et al. 2017), changes in habitat (Piatt & Souza 2011), body size (Lima 1998), age (Bayrakcı & Çiçek 2022), foraging strategies (Toft 1981), and evolutionary factors (Wells 2007).

Hylidae are generally recognized as generalist predators (Ferreira et al. 2012, Barbosa et al. 2014), also presenting opportunistic foraging strategies (Araujo-Vieira et al. 2018), which are beneficial when habitat changes occur in relation to species specialized in feeding on certain prey species (Anderson et al. 1999). However, prey characteristics such as size, abundance, nutritional value, and habitat availability may influence predation (Ferreira et al. 2012).

The diet and use pattern of anuran food resources can provide information on trophic ecology considering the coexistence between the species of a given community (Duré et al. 2009, Le et al. 2018, Moser et al. 2019) since coexisting species of Hylidae may exhibit a similar diet (Lima et al. 2010), suggesting the availability of prey rather than competition (Jiménez & Bolaños 2012). In addition, the structure of the environment as a hydroperiod and vegetation composition can alter the dynamics of resource partitioning between coexisting species of anurans (Menin et al. 2005), as well as the differential use of microhabitats (Van Sluys & Rocha 1998). Anthropogenic environmental disturbances also affect the amphibian trophic niche (López et al. 2015).

Boana geographica (Spix, 1824) and *B. raniceps* (Cope, 1862) are tree frogs with wide geographic distribution, including the Brazilian Amazon (Frost 2022). They occur in sympatry in Central Amazonia, occupying the same microhabitat (Menin et al. 2019). Several studies have evaluated the trophic balance of Hylidae sharing resources (Van Sluys & Rocha 1998, Menin et al. 2005, Lima et al. 2010, Jiménez & Bolaños 2012, Moser et al. 2019). Nevertheless, information about the coexistence of the species above is scarce. In this study, we describe and compare the food resource use, niche breadth, and overlap of *B. geographica* and *B. raniceps* in the rural area of Itacoatiara, Central Amazonia, Brazil.

Material and Methods

Study Area

The study area, named Litiara, is located in the rural area of the municipality of Itacoatiara, AM, Brazil (03°08'19.9"S; 058°27'32.5"W) at km 17 of the AM-010 highway. The place has several artificial ponds for fish breeding surrounded by undergrowth and arboreal. The climate is hot and humid, with temperatures between 21.1 °C and 36 °C (Peel et al. 2007). The rainy season is between November and May (Marques Filho et al. 1981).

Collection of specimens and biometrics

Specimens were collected at night (19:00 to 22:00 h) between December 2013 and May 2014 using active sampling (Heyer et al. 1994). After capture, the specimens were immediately anesthetized and euthanized with 5% lidocaine hydrochloride and fixed in 10% formalin to preserve the stomach contents. The frogs were sacrificed for use in other reproductive and anatomical studies. The collection of frogs was authorized by the Chico Mendes Institute for Biodiversity Conservation (ICMBio proc. #37557-1).

Frogs were identified according to Lima et al. (2012), Ilha & Dixo (2010), and Frost (2022). Voucher specimens were deposited in the Paulo Bürhnheim Zoological Collection of the Federal University of Amazonas – Section Amphibians (CZPB-AA): *B. raniceps* (CZPB-AA 623–625) and *B. geographica* (CZPB-AA 644, 648, 655) (Menin et al. 2019).

The snout-vent length (SVL) and mouth width (MW) of the previously fixed individuals of both species were measured using a caliper analogical (0.05 mm). Anurans were dissected carefully to expose the digestive tract and analyze the stomach content. The prey found in the stomach of each anuran were counted and identified to the lowest possible taxonomic level under a stereomicroscope (Gallo et al. 2002). The width and length of each prey items contents were measured using an analogical caliper (0.05 mm) to subsequently calculate its approximate volume, estimated using the formula: $V = 4/3\ \pi.(C/3).\ (W/2)^2$, where C = length and W = width of the prey (Dunham 1983). Besides that, the importance index (Ix) (Powell et al. 1990) was calculated for each category of prey, represented by the sum of the proportions of the number, volume, and frequency of occurrence of each prey divided by three. In addition, for each species, the niche breadth was calculated by the standardized Index of Levins: $Ba = [(\Sigma\ _jP^2_{ij})^{-1}-1](n-1)^{-1}$ (Hurbert 1978). To assess whether trophic niche overlap occurred between the species, the Morisita-Horn overlap index (O) was used with Lizaro Morisita Calc.1.0. This index ranges from 0 to 1, where 0 indicates no overlap, and 1 indicates total overlap.

Statistical analyses

The snout-vent length, mouth width, and prey volume of both Hylid species were compared using the *t*-test. Relationships between snout-vent length and mouth width of the anurans and the length and volume of the prey were analyzed using simple linear regression and *F*-test. The values used in linear regression were log-transformed. The regressions were submitted to analysis of covariance (ANCOVA) to compare the slopes and interceptions of the lines between the two species (Zar 2010).

Results

We analyzed 220 stomachs (141 of *Boana geographica* and 79 of *Boana raniceps*). The mean SVL of *B. geographica* (34.74 ± 6.21 mm) did not differ significantly from *B. raniceps* (38.34 ± 12.05 mm; $t = 1.70$, $DF = 1$, $p = 0.0939$). The species also did not differ in relation to the width of the mouth (*B. geographica*: 12.68 ± 3.30 mm, *B. raniceps*: 13.02 ± 3.94 mm; $t = 0.42$, $DF = 1$, $p = 0.6735$) and to prey volume (*B. geographica*: 127.67 ± 178.76 mm^3, *B. raniceps*: 132.25 ± 248.78 mm^3; $t = 0.10$, $DF = 1$, $p = 0.9179$). The proportion of empty stomachs was higher for *B. geographica*, with 83 individuals (58.9%), and *B. raniceps*, with 26 (32.9%). Plant remains were found in 20 stomachs (14.2%) of *B. geographica* and 13 (16.5%) of *B. raniceps*.

Boana geographica consumed nine different types of prey and *B. raniceps* – 12; eight food items (Araneae, Blattodea, Coleoptera, Diptera, Hemiptera, Lepidoptera, Orthoptera, and Diplopoda) were shared by both species (Table 1). Tadpoles were consumed exclusively by *B. geographica*, whereas Hymenoptera, Odonata, Isoptera, and Homoptera were exclusive to *B. raniceps* (Table 1). Considering the importance index (Ix), tadpoles (Ix = 39.41), Hemiptera (Ix = 13.73), Coleoptera (Ix = 12.78), and Diplopoda (Ix = 12.18) were more important in the diet of *B. geographica*. In contrast, for *B. raniceps* Orthoptera (Ix = 25.05), Coleoptera (Ix = 16.85), Araneae (Ix = 12.91), and Blattodea (Ix = 11.43) were the most important items (Table 1).

The relationship between SVL and volume and length of prey consumed by *B. geographica* was not significant ($F = 19.92$, $DF = 1$, $p = 0.16$), with a low coefficient of determination ($R^2 = 0.04$). The relation between SVL and length of prey followed the same pattern, with no significance ($F = 2.09$, $DF = 1$, $p = 0.15$) and a low coefficient of determination ($R^2 = 0.04$). Similarly, the relationship between the mouth width of the frogs and the volume and length of the prey items of *B. geographica* did not show an adjustment for the variables. The mouth width and volume of prey showed no significance ($F = 1.06$, $DF = 1$, $p = 0.30$), with a low coefficient of determination ($R^2 = 0.02$), as well as mouth width and length of prey obtained no significance ($F = 0.38$, $DF = 1$, $p = 0.54$), with a low coefficient of determination ($R^2 = 0.0081$).

Table 1. Number (N), volume (V) in mm³, frequency of occurrence (F), and importance index (Ix) of prey consumed by *Boana geographica* and *B. raniceps* in Amazonia, Brazil.

Preys	*Boana geographica* (N=38)							*Boana raniceps* (N=40)						
	N	(%)	V	(%)	F	(%)	Ix	N	(%)	V	(%)	F	(%)	Ix
Arthropoda														
Araneae	2	4.08	0.34	0.01	1	2.50	2.20	5	7.94	1,698.86	20.39	5	10.42	12.91
Insecta														
Blattodea	2	4.08	115.56	1.89	2	5.00	3.66	8	12.70	756.68	9.08	6	12.50	11.43
Coleoptera	8	16.33	430.69	7.03	6	15.00	12.78	17	26.98	401.34	4.82	9	18.75	16.85
Diptera	1	2.04	376.07	6.14	1	2.50	3.56	4	6.35	102.98	1.24	2	4.17	3.92
Hemiptera	11	22.45	228.97	3.75	6	15.00	13.73	9	14.29	94.28	1.13	6	12.50	9.31
Homoptera	-	-	-	-	-	-	-	1	0.05	4.02	0.05	1	2.08	0.73
Hymenoptera	-	-	-	-	-	-	-	5	7.94	419.28	5.03	5	10.42	7.80
Isoptera	-	-	-	-	-	-	-	1	1.59	11.55	0.14	1	2.08	1.27
Lepidoptera	1	2.04	4.15	0.07	1	2.50	1.54	4	6.35	265.66	3.19	4	8.33	5.96
Ordonata	-	-	-	-	-	-	-	1	1.59	60.21	0.72	1	2.08	1.46
Orthoptera	5	10.20	450.70	7.35	5	12.50	10.02	6	9.52	4,427.24	53.14	6	12.50	25.05
Myriapoda														
Diplopoda	7	14.29	597.69	9.75	5	12.50	12.18	4.0	3.17	89.54	1.07	2	4.17	2.81
Vertebrata														
Anura (tadpoles)	12	24.49	3,905.47	63.73	12	30.00	39.41	-	-	-	-	-	-	-
Total	49		6,109.28					65		8,331.64				

The relationship between SVL and the volume of prey of *B. raniceps* was significant ($F = 21.3844$, $DF = 1$, $p < 0.0001$), but the coefficient of determination was low ($R^2 = 0.26$). The relationship between SVL and length of prey was also significant ($F = 22.8586$, $DF = 1$, $p < 0.0001$), with a low coefficient of determination $R^2 = 0.27$. The relationship between the mouth width of *B. raniceps* and the volume and length of prey did not show an adjustment, but it was significant ($F = 10.7567$, $DF = 1$, $p < 0.0021$), and it had a low coefficient of determination ($R^2 = 0.15$). The relationship between mouth width and length of prey was significant ($F = 9.8197$, $DF = 1$, $p < 0.0030$), although the coefficient of determination was low ($R^2 = 0.14$).

The relationship between frog size and prey volume did not differ significantly between species ($F = 2.69$, $DF = 1$, $p = 0.1054$). Likewise, the relationship between the width of the mouth and prey volume did not differ significantly ($F = 1.63$, $DF = 1$, $p = 0.2054$). The breadth niche for *B. geographica* was 0.57, and for *B. raniceps* – 0.58. The trophic niche overlap between species was 0.74.

Discussion

The empty stomachs found in *Boana geographica* and *Boana raniceps* and the small number of food items may be related to the feeding period of these animals since individuals with empty stomachs may have been collected early in the evening before prey capture. Those with a full stomach had more time to hunt, as suggested for specimens of the *Dendropsophus* genus (Menin et al. 2005). For *Boana cinerascens* (Spix, 1824) was found that 35% of stomachs contained no food items (Telles et al. 2013), as well as *Boana albopunctata* (Spix, 1824) with 30% empty stomach (Pacheco et al. 2017). Furthermore, the study was carried out during the rainy season of the Amazon region, a period that the species use to reproduce, which may also have contributed to the capture of individuals with empty stomachs since, during this period, the specimens reduce their feeding activity (Solé & Pelz 2007, Mendonça et al. 2020). In addition, some individuals' stomachs were recorded as containing remnants of decomposing plant material. However, consumption of plant material has been reported for *B. raniceps* (Sabagh et al. 2010) and *B. cinerascens* (Telles et al. 2013) as accidental ingestion during prey capture. Investigating two hylid species during the dry season in the northeast of Brazil, Tupy et al. (2021) suggested that ingestion of plant material may provide an alternative to hydration. In this study, the species were studied during the rainy season, and it was not possible to determine whether the indigestion of plant material for both hylids was accidental or purposeful.

In this study, *B. geographica* and *B. raniceps* presented 13 prey items in their diet: arthropods and tadpoles. Parmelee (1999) recorded six food items (Orthoptera, Diptera, Lepidoptera, Coleoptera, Araneae, and Acari) for a community of hylids in the Peruvian Amazon. In Central Amazonia, seven food categories were recorded for *B. cinerascens* (Acari, Diptera, Hemiptera, Hymenoptera, Isoptera, Coleoptera, and Orthoptera) (Telles et al. 2013); in our single study, Acari was not consumed.

Among the food items found in the stomachs of *B. raniceps*, the order Orthoptera and individuals of the Araneae family were the most volumetrically representative and had a high dietary importance. This same order has been recorded for *B. albopunctata* in Minas Gerais (Pacheco et al. 2017) and an item of greater volume for *B. albopunctata* in Brasília (Araújo et al. 2007), and for *B. cinerascens* in Manaus, AM (Telles et al. 2013).

Coleoptera was also the most frequent prey in the diet of *B. raniceps* (Sabagh et al. 2010) and *B. albopunctata* (Araújo et al. 2007, Guimarães et al. 2011). Coleoptera are considered one of the most abundant groups in studies on the diet of anurans and may occur in different periods of the year (Neves et al. 2014, Tupy et al. 2021). However, it is not possible to infer whether this was the most abundant prey in the environment since the available food resources were not analyzed in this study.

Tadpoles were the most important food item consumed by *B. geographica*, which was investigated for their diet for the first time in this study. In general, anurans and tadpoles constitute a small part of the diet of some species, such as *Leptodactylus latrans* (Steffen, 1815) and *L. labyrinthicus* (Spix, 1824) (França et al. 2004, Solé et al. 2009) and *Pseudis tocantins* Caramaschi and Cruz, 1998 (Neves et al. 2014). In this study, *B. geographica*, despite being a tree species (Lima et al. 2012), actively foraging in aquatic environments, and tadpoles are an important part of their diet. The occupation of the micro-habitat can also explain this behavior because, during the collection, it was observed that these individuals occupied the bush and shrubs that bordered the fish ponds; however, further analysis and observation of this behavior is needed to make more inferences.

The unusual food item for both species was Diplopoda; this item is usually found in the diet of Bufonidae and Leptodactylidae terrestrial frog species (Almeida et al. 2019, Solé et al. 2019). We can observe in the environment that in times of intense rain, Diplopoda climb the bushes to escape the water accumulated in the soil, probably because *B. geographica* and *B. raniceps* had access to this food item.

The niche breadth was similar for both species, and niche overlap was high, with eight prey items consumed by both species. Sabagh et al. (2010) also found a high overlap in the diet of *B. raniceps* and *S. acuminatus*. They recorded 11 different prey categories, of which seven were common among both species (Araneae, Hymenoptera (Formicidae), Diptera (Brachycera), Coleoptera, Blattaria, Orthoptera, and Hemiptera). Lima et al. (2010) also found a high overlap in trophic niches of *Phyllomedusa burmeisteri* Boulenger, 1882 and *Pithecopusrohdei* (Mertens, 1926) in a cacao plantation in southern Bahia. However, the high overlap of niches in this study does not necessarily indicate the competition among hylids since the most important food items were different for both species.

For both species, no adjustment was found between body size and mouth in relation to the biometric variables of the prey. The anurans consumed prey of varied sizes and volumes regardless of mouth width and size. This trend was also observed for *B. albopunctata,* which feed on the prey of different sizes (Araújo et al. 2007), and in *Aparasphenodon brunoi* Miranda Ribeiro, 1920 (Teixeira et al. 2002). However, for *B. albopunctata* (Pacheco et al. 2017) and *Boana pulchella*

(Duméril & Bibron 1841) (Rosa et al. 2011), and other Hylidae species, a relationship was observed between body size and size/volume of prey. There is no pattern for the Hylidae anurans, probably associated with the characteristic opportunistic and non-selective feeding habits of this family.

Based on the diet observed for both species of anurans, in this study, *B. raniceps* was considered a passive, generalist forager with a sit-and-wait feeding strategy like most Hylidae (López et al. 2009, Guimarães et al. 2011, Jiménez & Bolaño 2012). Despite the similar diet between the studied species, *B. geographica* may be considered an active generalist forager due to the high consumption of tadpoles. This finding indicates a search for higher volume food in the bodies of water. Consequently, the data indicate a similar diet but with different prey of greater dietary importance, enabling species' coexistence in the same micro-habitat.

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