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Dinner Time in the Atlantic Forest: Trophic Niche Partitioning of Two Sympatric *Boana* Species in the Southern Bahia State, Brazil

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Abstract. Understanding the ecological traits of species, such as dietary habits, is important for elucidating their natural history and ecological interactions. Thus, we investigated the trophic ecology and niche partitioning of two treefrog species (*Boana atlantica* and *B. semilineata*) in an Atlantic Forest fragment in southern Bahia, northeastern Brazil. In this study, we obtained the diet of 39 *B. atlantica* and 25 *B. semilineata* through stomach flushing. We recorded 72 prey items in these two hylids organized into 11 categories. The most consumed prey were plant material and Araneae. Although the niche breadth of *B. atlantica* was higher than that of *B. semilineata*, these hylids had a substantial trophic niche overlap (Pianka's niche overlap index = 0.89). Our findings provide novel insights into the feeding ecology of these endemic Atlantic Forest treefrogs, enhancing our understanding of their ecological roles and trophic resource partitioning in this biodiversity hotspot.

Keywords: Amphibians, Diet composition, Feeding habit, Hylidae.

INTRODUCTION

To coexist in an environment, a species needs specific resources and conditions that define its ecological niche (Hutchinson, 1957). Processes associated with foraging habitat selection, prey availability, and intraspecific and interspecific competition are crucial to understand the species' trophic niche (Moser et al., 2017). Beyond ecological interactions, this information is important for comprehending the natural history of the species, population fluctuations, and the effects of environmental change on populations and communities (Anderson et al., 1999; Santos et al., 2004; Richter-Boix et al., 2007).

Anurans play an important role in maintaining environmental stability, participating in different food networks (Poulin et al., 2001; Egeter et al., 2015; Ceron et al., 2019), and contributing to the energy flow and nutrient cycling (Colón-Gaud et al., 2009; Huckembeck et al., 2014). In general, most anuran species are opportunistic and generalist predators consuming a great diversity of invertebrate prey (Solé and Rödder, 2009). However, amphibians' diets are influenced by various factors, such as prey availability, competition, foraging strategies, ontogeny, morphology, and environmental characteristics (Wells, 2010; Luría-Manzano and Ramírez-Bautista, 2019; Blanco-Torres et al., 2020; Moroti et al., 2021), making it important to study their trophic ecology. A recent review of Brazilian anuran dietary studies shows that, despite increasing research, only about 19% of species have published diet data, with many endemic and threatened taxa still lacking dietary information, particularly outside the Atlantic Forest ecoregion (Moser et al., 2025).

Anuran communities may be structured according to spatial, temporal, and trophic niches, where ecological factors such as competition and historical factors like phylogeny influence these niche dimensions (Leite-Filho et al., 2017; Caldas et al., 2019). Some studies investigated the trophic niche overlap of congeneric anurans (e.g., Oliveira et al., 2015; Moser et al., 2017; Araújo et al., 2023), including *Boana* species (Protázio et al., 2017; Moser et al., 2018). It is generally accepted that, in accordance with Gause's (1932) competitive exclusion principle, species must segregate along at least some niche axes, including trophic niche partitioning, to enable their successful coexistence in sympatry (Kneitel, 2019). Thus, understanding the partitioning of food resources is essential to comprehend species coexistence.

Boana atlantica (Caramaschi and Velosa, 1996) and *Boana semilineata* (Spix, 1824) are two endemic treefrogs from the Atlantic Forest that occur in sympatry from Alagoas to Bahia (Frost, 2025). *Boana semilineata* is known to have a generalist diet consisting primarily of coleopterans, acari, orthopterans, and plant fragments (Protázio et al., 2017). While some aspects of *B. atlantica*'s natural history are known, including its reproductive biology (Camurugi and Juncá, 2013) and advertisement call (Napoli and Cruz, 2005), its trophic ecology remains understudied. Thus, we aimed to (i) describe the diet of two treefrog species that occur in sympatry in a permanent pond within an Atlantic Forest fragment in southern Bahia, Brazil; (ii) test the trophic niche overlap between these hylids; and (iii) evaluate how body mass, body size, and mouth breadth influence prey volume in these anurans. We expected dietary differentiation between the two sympatric hylid species, resulting in low to moderate trophic niche overlap, and a positive relationship between anuran morphology and prey volume.

MATERIAL AND METHODS

Study area

This study was conducted in a permanent pond inside the Michelin Ecological Reserve (-13.82348° S, -39.17286° W, WGS84) in Bahia State, northeastern Brazil (Fig. 1). It encompasses a total area of 3.096 ha within the Atlantic Forest Biome, considered a Dense Ombrophilous Lowland Forest (Veloso et al., 1991), and characterized by the presence of Atlantic Forest fragments at various stages of regeneration (Flesher, 2014). It has an average precipitation of 2000 mm and daily temperatures between 18 ˚C and 30 ˚C, with rainfall throughout the year (Flesher, 2014). The area of the pond was ca. 450 m², with a maximum depth of 1.5 m, located in a forest fragment embedded within a rubber tree plantation area. Besides trees, the vegetation around the pond edge is composed of shrubs and herbaceous species.

Sampling design

We conducted fieldwork to search for specimens of *B. atlantica* and *B. semilineata* at a permanent pond during the night period (18 to 23 h) between March and May 2011, using auditory and visual searches (Heyer et al., 1994). Individuals were identified based on their advertisement calls, dorsal coloration patterns, and morphological traits (see Caramaschi and Velosa, 1996, for the diagnosis of *B. atlantica*, and Izecksohn and Carvalho, 2001, for the diagnosis of *B. semilineata*). We collected and transported the observed individuals in plastic bags to the lab in the Center for Biodiversity Studies of the Michelin Ecological Reserve. To avoid pseudoreplication, specimens were captured and released only at the end of each field campaign, ensuring that no individual was resampled within the same campaign. In the lab, the specimens were weighed on electronic scales and had their snout-vent length (SVL) and mouth breadth (MB) measured with a digital caliper with 0.01 mm precision. Subsequently, they were stomach flushed following the protocol proposed by Solé et al. (2005) and released into the pond, from which they had been collected.

Data analyses

In the laboratory, the stomach contents were separated, and the prey items were identified to the lowest possible taxonomic level (usually order) using the specialized literature (Rafael et al., 2024). Then, we calculated the frequency of occurrence (FO% = number of stomachs containing item i / total number of stomachs × 100), and the numeric abundance (N%

= number of individuals of item i / total individuals of all items × 100). Since we did not calculate the volume of each prey item consumed, we used an adapted formula (IRI = (FO% + N%) / 2) for the index of relative importance originally proposed by Pinkas et al. (1971).

Additionally, to measure the total volume of prey consumed by the *Boana* specimens, we placed each individual's stomach contents in an oven set to 60ºC to dry and stabilize the mass. We used a GEHAKA AG-200 scale (accuracy of 0.1 mg) to weigh the stomach contents. Collinearity among morphological predictors was evaluated using variance inflation factors (VIF). As all VIF values were below 2, no collinearity issues were detected, and all variables were retained for analysis (James et al., 2013). We then fitted generalized linear models (GLMs) to evaluate whether prey volume was influenced by body mass, snout–vent length (SVL), and mouth breadth (MB) in the two *Boana* species. We initially fitted a full model including all predictors simultaneously (Volume ~ Mass + SVL + MB), assuming a Gamma error distribution with a log-link function. Model adequacy was assessed through residual diagnostics appropriate for GLMs. In addition, we evaluated alternative models with reduced sets of predictors and compared model performance using Akaike's Information Criterion (AIC). Models with ΔAICc lower than 2 were interpreted as having the most substantial support (Burnham and Anderson, 2002).

We estimated the numerical trophic niche breadth (*Bnum*) of the two *Boana* species using the standardized Levins' index (Levins, 1968), which ranges from 0, indicating dietary specialization, to 1, indicating a generalist diet. Then, we used Pianka's niche overlap index (Pianka, 1973) to calculate the trophic niche overlap (*Ojk*) between *B. atlantica* and *B. semilineata*. We used a bipartite network graph as an exploratory tool to visualize prey diversity between the two hylid species, with interaction strength represented by the index of relative importance of each prey item for both *Boana* species. Statistical analyses were done using the R packages *bipartite* (Dormann et al., 2009), *ggraph* (Pedersen et al., 2022), *ggplot2* (Wickham, 2016), *igraph* (Csardi and Nepusz, 2006), *spaa* (Zhang, 2016), *tibble* (Müller and Wickham, 2023), *vegan* (Oksanen et al., 2019), and *usdm* (Naimi et al., 2014).

RESULTS

We found 64 anuran specimens (39 *B. atlantica* and 25 *B. semilineata*), including 48 with stomach contents (30 *B. atlantica* and 18 *B. semilineata*). We found 72 prey items grouped into 11 categories, with plant material (N = 23) and Araneae (N = 20) as the most consumed prey. Plant fragments were found in the stomach contents of 23 individuals, while Araneae appeared in 17.

We observed that *B. atlantica* consumed 10 prey categories (*Bnum* = 5.31), with plant material (IRI = 27.1) and Araneae (IRI = 27.0) being the most abundant and frequently encountered prey types. In contrast, Acari, Blattaria, Hemiptera, and Hymenoptera were consumed less frequently (IRI = 2.09), with only one individual recorded for each (Table 1). Additionally, we found no support for the influence of anuran weight (T = 0.559, P = 0.580), size (T = -0.584, P = 0.564), and mouth breadth (T = -0.460, P = 0.649) on the volume of the stomach contents.

Likewise, plant material (IRI = 46.5) and Araneae (IRI = 25.5) were the most prominent prey items in the diet of *B. semilineata*. This species consumed only six prey categories and had a narrower numerical trophic niche breadth (*Bnum* = 3.37). Hymenoptera, Lepidoptera, and Odonata were consumed less frequently, with only one individual recorded for each (Table 1).

We also observed that the volume of the stomach contents was not influenced by the anurans' weight (T = 1.194, P = 0.250), size (T = -1.160, P = 0.263), and mouth breadth (T = 0.978, P = 0.342). Model comparison based on AIC indicated that the null model best fit the data for both species. Models including morphological predictors (SVL, mouth breadth, or body mass), alone or combined, did not improve performance (ΔAIC > 2), indicating no effect of morphology on prey volume.

We observed that the two *Boana* species consumed different numbers of prey categories. *Boana semilineata* exhibited a more specialist dietary strategy (*Bnum* = 0.24), whereas *Boana atlantica* showed an intermediate to generalist strategy (*Bnum* = 0.43), indicating a broader trophic niche breadth. In addition, the two species exhibited a high trophic niche overlap (*Ojk* = 0.89), with five prey categories shared by both species (Fig. 2).

DISCUSSION

We observed that the *Boana* species studied had a generalist and opportunistic diet, which is a common pattern for most Neotropical anurans (Toft, 1981; Wells, 2010), including the genus *Boana* (e.g., Araújo et al., 2007; Moser et al., 2018; Rodrigues et al., 2023, Machado et al., 2024). The presence of prey with high mobility in the diet composition of these hylids, such as Araneae, Odonata, Orthoptera, and Diptera, may indicate a sit-and-wait strategy (Parmelee, 1999**;** Protázio et al., 2017). This foraging strategy pattern seems to be predominant for Hylidae species (e.g., Mahan and Johnson, 2007; Castro et al., 2016; Silva et al., 2021), including the genus *Boana* (e.g., Protázio et al., 2017; Sant'anna et al., 2022; Rodrigues et al., 2023).

Although some species, such as *Xenohyla truncata* and *Phrynoderma hexadactylum*, may exhibit an uncommon frugivory or herbivory pattern (Das, 1996; Oliveira-Nogueira et al., 2023), most studies suggest that anurans consume plant material incidentally while preying on invertebrates (Sabagh et al., 2010; Castro et al., 2016, Araújo et al., 2023). However, we observed that the most consumed prey item by both *Boana* species was plant fragments. The consumption of plant material can aid in the elimination of intestinal parasites and provide an additional supply of water and nutrients, provided it is digestible (Anderson et al., 1999; Tupy et al., 2021). Additionally, Silva et al. (1989) demonstrated that during the dry season, when invertebrate populations diminished, *Xenohyla truncata* incorporated fruits and bromeliad seeds into its diet. While the ingestion of plant debris is frequently documented in *Boana* species (e.g., Moser et al., 2018; Tupy et al., 2021; Rodrigues et al., 2023), further research is necessary to elucidate the significance of plant fragments in the diet of these hylids.

Anuran–prey selection might be mediated by different traits, such as morphology, foraging strategy, prey mobility, and availability (Lima and Moreira, 1993; López et al., 2009; Blanco-Torres et al., 2020). However, the volume of stomach contents of *B. atlantica* and *B. semilineata* was not influenced by their weight, snout-vent length, and mouth breadth. Although some studies support the hypothesis that larger frogs tend to eat a larger prey volume (e.g., Rosa et al., 2011; Pacheco et al., 2017; Araújo et al., 2023), it is still an unclear issue because others do not support this relationship (e.g., Rodrigues et al., 2023; Ferreira et al., 2024). As a result, establishing a link between morphology and prey volume in anurans is difficult, particularly from an intraspecific perspective.

We observed that *B. atlantica* and *B. semilineata* had a high trophic niche overlap with opportunist characteristics. These species share five prey categories, including the prey items with the highest IRI such as plant material and spiders (see Fig. 2). Studies encompassing the anuran community (e.g., Protázio et al., 2015; Leite-Filho et al., 2017), as well as investigations focused just on two species (e.g., Sabagh et al., 2010; Araújo et al., 2023), indicate that generalist and opportunistic amphibians frequently share prey items within their diet. Likewise, coexisting *Boana* species have a substantial trophic niche overlap (Moser et al., 2018; Tupy et al., 2021; Sant'anna et al., 2022), which may be related to their opportunistic trophic strategy. Given limited resources, species must segregate into certain niche axes to coexist (MacArthur and Levins, 1967; Gotelli, 2009). However, it is impossible to determine whether or not these species compete for trophic resources in the study area because we did not perform a prey availability analysis there. Thus, further studies are required to determine the mechanisms and processes that may allow *B. atlantica* and *B. semilineata* to coexist.

Overall, the studied hylids consume whatever is available in their surroundings, exhibiting a generalist dietary pattern and, as a result, a high degree of overlap in prey items. However, we cannot state that these species are truly competing for trophic resources. Our findings contribute to the understanding of the trophic ecology of two endemic *Boana* species from the Atlantic Forest. It is important to highlight the general lack of research on anuran diets, despite diet representing a fundamental aspect of natural history for understanding predator-prey interactions, hypothesis testing, and the assessment of conservation status (Moser et al., 2025). Consequently, natural history studies play a crucial role in informing conservation planning for species and their environments.

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Table 1. Absolute values and proportions (%) of frequency of occurrence (FO), abundance (N), and index of relative importance (IRI) of each prey category consumed in the diet of *Boana atlantica* and *Boana semilineata*.

	Boana atlantica					***Boana semilineata***				
	FO	**FO%**	**N**	**N%**	**IRI**	**FO**	**FO%**	**N**	**N%**	**IRI**
ARACHNIDA										
Acari	1	2.0	1	2.17	2.09	-	-	-	-	-
Araneae	14	28.0	12	26.1	27.0	6	27.3	5	23.8	25.5
HEXAPODA										
Blattaria	1	2.0	1	2.17	2.09	-	-	-	-	-
Coleoptera	6	12.0	6	13.0	12.5	-	-	-	-	-
Diptera	5	10.0	5	10.9	10.4	-	-	-	-	-
Hemiptera	1	2.0	1	2.17	2.09	-	-	-	-	-
Hymenoptera	1	2.0	1	2.17	2.09	1	4.55	1	4.76	4.65
Lepidoptera	2	4.0	2	4.35	4.17	1	4.55	1	4.76	4.65
Odonata	-	-	-	-	-	1	4.55	1	4.76	4.65
Orthoptera	6	12.0	4	8.70	10.3	3	13.6	3	14.2	14.0
OTHER ITEMS										
Plant material	13	26.0	13	28.3	27.1	10	45.5	10	47.6	46.5
TOTAL	50	100	46	100	100	22	100.0	21	100	100

Figure 1. Schematic map of the study site in the Michelin Ecological Reserve, Bahia State, northeastern Brazil.

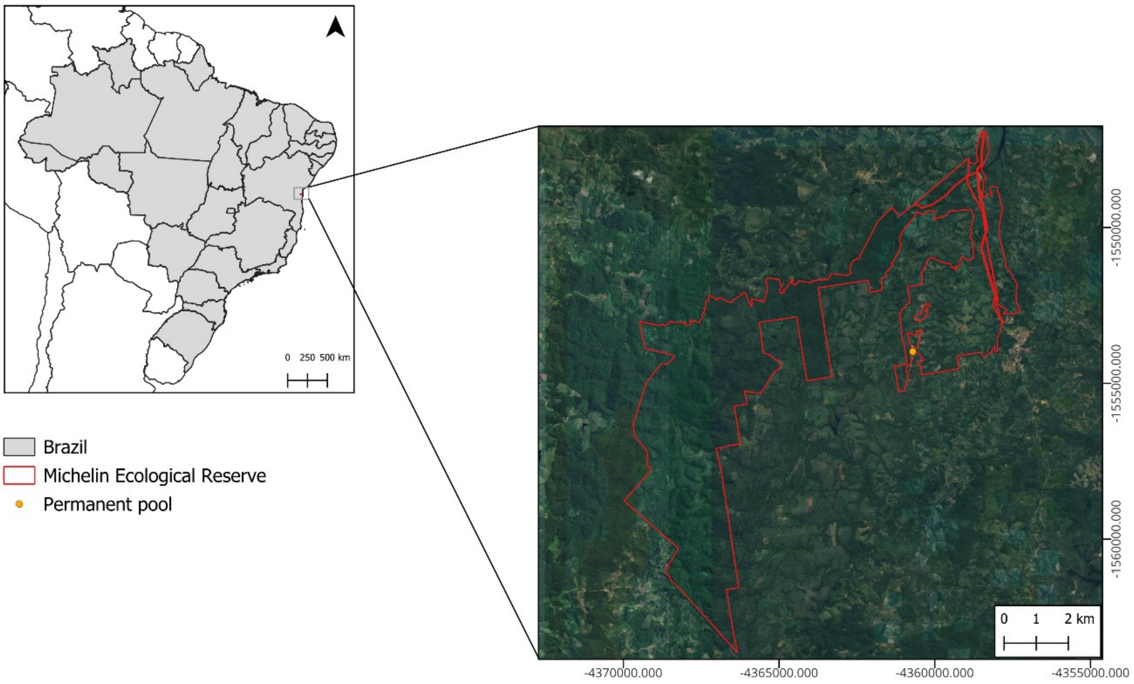

Figure 2. Schematic graph of the prey items consumed by the two *Boana* species studied in the Michelin Ecological Reserve, Bahia State, northeastern Brazil.