

Feeding ecology, reproductive biology, and sexual dimorphism of *Boana raniceps* (Anura: Hylidae) in an area of Caatinga, northeastern Brazil

Ecología alimentaria, biología reproductiva y dimorfismo sexual de *Boana raniceps* (Anura: Hylidae) en un área de Caatinga, noreste de Brasil

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ABSTRACT

The number of studies on the ecology of the genus *Boana* is vast in Brazilian biomes. Among the different species of this genus, *B. raniceps* is considered a common and widely distributed species. Despite this, only a few studies have explored the ecology of this species in the Caatinga biome. In this study we present information on the diet composition, reproduction, and sexual dimorphism of *B. raniceps* in the Caatinga biome, northeastern Brazil, providing additional information about the natural history of the species. We observed that *B. raniceps* has a generalist diet, consuming a great diversity of prey categories, but with a numerical and volumetric prevalence of Coleoptera. Interestingly, there was an ontogenetic and sexual variation in the diet, with the Relative Importance Index (RII) for each prey category differed between males, females, and juveniles. Females were found bearing mature eggs in both the rainy and dry seasons. The number of eggs carried by each female ranged from 153 to 3904. There was sexual dimorphism in body size, with females larger than males. However, size was not a limiting factor in fecundity. Here, we present new information on the natural history of *B. raniceps* and reinforce the need for further studies with widely distributed and known species. This is the first study to demonstrate ontogenetic and sexual variation in the diet of anurans of the genus *Boana*.

Keywords: Caatinga, Diet composition, Natural history, Reproductive biology, Sexual dimorphism.

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RESUMEN

El número de estudios sobre la ecología del género *Boana* es enorme en todos los biomas brasileños. Sin embargo, los estudios sobre la dieta, la reproducción y el dimorfismo sexual de *B. raniceps* son escasos en el bioma de Caatinga. En este estudio presentamos información sobre la composición de la dieta, la reproducción y el dimorfismo sexual de *B. raniceps* en el bioma de Caatinga, noreste de Brasil, proporcionando información adicional sobre la historia natural de esta especie. Observamos que *B. raniceps* tiene una dieta generalista, que consume una gran diversidad de categorías de presas, pero con prevalencia numérica y volumétrica de Coleoptera. Curiosamente, hubo una variación ontogénica y sexual en la dieta, pues el Índice de Importancia Relativa (RII) para cada categoría difiere entre machos, hembras y juveniles. Se encontraron hembras con huevos maduros tanto en la estación lluviosa como en la seca. El número de huevos transportados por cada hembra osciló entre 153 y 3904. Hubo dimorfismo sexual en el tamaño, siendo las hembras más grandes que los machos. Sin embargo, el tamaño no fue un factor limitante de la fecundidad. Aquí, presentamos nueva información sobre la historia natural de *B. raniceps* y reforzamos la necesidad de realizar más estudios incluso con especies ampliamente distribuidas y conocidas. Este es el primer estudio que demuestra la variación ontogénica y sexual en la dieta de los anuros del género *Boana*.

Palabras clave: Biología reproductiva, Caatinga, Composición de la dieta, Dimorfismo sexual, Historia natural.

INTRODUCTION

Many studies on the natural history of species of *Boana* addressed aspects of their diet, sexual dimorphism, and reproductive biology in different Brazilian biomes, like in the Atlantic Forest (Giasson and Haddad 2007, Reinke and Deiques 2010, Lisboa *et al.* 2011, Lima *et al.* 2013, de Bastiani *et al.* 2016, Leite-Filho *et al.* 2017, Pacheco *et al.* 2017, Faraulo *et al.* 2019, Moser *et al.* 2019, Tupy *et al.* 2021, Moser *et al.* 2022), in Amazon (Telles *et al.* 2013, Bonnefond *et al.* 2020), in the Caatinga (Leite-Filho *et al.* 2015, Oliveira *et al.* 2018), in the Cerrado (Guimarães and Bastos 2003, Araújo *et al.* 2007, Muniz *et al.* 2008, Guerra *et al.* 2018), in the Pantanal (Prado and Haddad 2005, Prado *et al.* 2005, Sabagh *et al.* 2010, Bonnefond *et al.* 2020), and in ecotonal areas (Nascimento *et al.* 2015, Freitas *et al.* 2022). The list of studies on the ecology and natural history of species of the genus *Boana* is extensive, however, due to the high richness of species in Brazil ($n = 65$ spp.; Segalla *et al.* 2021), knowledge about the ecology of several species and for some regions is still scarce.

Among the different species of this genus, *Boana raniceps* (Cope, 1862) is one of the most widely distributed treefrog species in South America, occurring in Argentina, Boliv-

ia, Brazil, French Guiana, Paraguay, and Venezuela (Uetanabaro *et al.* 2008), inhabiting several natural habitats, which include forests, lagoons, puddles, and rivers in addition to even degraded and urban habitats (Frost 2023). Several studies regarding biological aspects of *B. raniceps* are available for the Amazon (Bonnefond *et al.* 2020), Caatinga (Arzabe 1999, Leite-Filho *et al.* 2015, Oliveira *et al.* 2018), Cerrado (Guerra *et al.* 2018), Atlantic Forest (Leite-Filho *et al.* 2017) and Pantanal (Prado and Haddad 2005, Prado *et al.* 2005, Sabagh *et al.* 2010, Bonnefond *et al.* 2020). However, most of these do not focus on the ecology of the species and much information about its natural history remains unknown.

Studies that seek to investigate the ecology of a population are necessary to understand how they share the available resources in their microhabitats, making it possible to better understand the biology of the species and their interactions with the environment (Caldas *et al.* 2016). Thus, it is of great importance to know the ecological characteristics of these populations, aiming at the conservation of their species and the environments where they live (Colli *et al.* 2003). Despite the importance of conducting studies in different habitats to understand the ecology of widely distributed species, studies on the natural history of *Boa-*

na raniceps in Caatinga biome are restricted to records of food items, use of microhabitats, and observations of the vocalization period (Arzabe 1999, Leite-Filho *et al.* 2015, Oliveira *et al.* 2018). For example, there is no information about sexual dimorphism and various reproductive aspects.

In this study, we characterize specifically: the diet composition, relative importance of diet items between sex and age classes, influence of snout-vent-length on the number of eggs in females, and on the volume of testicles in males, number of mature eggs in females, pattern of reproductive activity, and the occurrence of sexual dimorphism of a population of *Boana raniceps* in the Caatinga biome, northeastern Brazil.

MATERIALS AND METHODS

Study area

Fieldwork was carried out in the Mauriti municipality (7°23'21" S and 38°46'28" W, 374 m alt.), in the southern State of Ceará, northeastern Brazil. The study area is located in the biome Caatinga, this biome is considered one of the richest semi-arid regions in the world (Albuquerque *et al.* 2012), with more than 800 000 km², is composed of a mosaic of dry forests and shrubby vegetation (savanna-steppe), in most of its extension, is characterized by a hot and semi-arid climate, with average annual rainfall ranging between 250 and 900 mm concentrated in a single period of the year (three to six months) and average annual temperatures are relatively high, 26°C to 29°C (Vieira *et al.* 2007).

Species sampling

The specimens of *Boana raniceps* were captured during visual surveys with a team of three people for ten days trips distributed in November 2013 (dry season) and in February 2014 (rainy season). Individuals were collected manually through active visual search (Crump and Scott Jr. 1994), in which the researcher moves around carefully searching for individuals in all possible locations. In addition, the Search in Reproduction Environments method was used, where researchers make observations and collections in possible spawning and mating environments (Scott Jr. and Woodward 1994). All collections were performed during the night between 17:00h and 00:00h hours, which comprises the highest peak of vocalization activity, thus totaling a sampling effort of 270 hours. Indi-

viduals were euthanized with a lethal injection of lidocaine 2 %, then fixed with 10 % formalin and preserved with 70 % ethanol (Callefo 2002). Specimens were collected by the permanent license for capture/collection/transport of ICMBio SISBIO n° 29613-1. All collected specimens were deposited in the Coleção Herpetológica of Universidade Regional do Cariri-URCA.

Feeding ecology

For the analysis of diet composition, the stomach of each specimen was removed and the content analyzed under a stereomicroscope to identify prey items to the most inclusive taxonomic level possible. We recorded length and width (0.01 mm) of intact items with digital calipers and estimated prey volume (V) using the ellipsoid formula: $V = 4/3 \cdot \pi(L/2) \cdot (W/2)^2$, where V = volume, L = length, and W = width. To determine the relative contribution of each prey category, we calculated the Relative Importance Index (RII) (Powell *et al.* 1990) for pooled individuals and separately for adults of each sex and for juveniles, using the formula: $RII = (F\% + N\% + V\%) / 3$, where $F\%$, $N\%$, and $V\%$ are the percentages of frequency, number, and volume of prey, respectively. Then, we performed a Canonical Correspondence Analysis (CCA) and a Chi-squared test (X^2), with RII values, to test for differences in diet composition between sex and age classes.

Reproductive biology

Sex was determined by dissection and direct examination of the gonads, considering the males analyzed as reproductively mature when they had convoluted epididymides. We considered females reproductive when they had matured ovarian eggs, visually confirmed by the presence of yellow pigmentation. The eggs were counted manually with the help of a petri dish and graph paper (counted how many eggs filled a square of the paper and multiplied by the total of filled squares). We describe the pattern of reproductive activity of the species based on the mature individuals males and females found throughout the sampling period (both seasons). To characterize the relationship between body size and fecundity, we performed a Pearson correlation between both testicular volume and number of eggs with the individual's snout-vent length (SVL).

Sexual dimorphism

Prior to fixation, we measured the individual mass with spring scales (Pesola®) and made morphometric measurements with a digital caliper (0.01 mm precision).

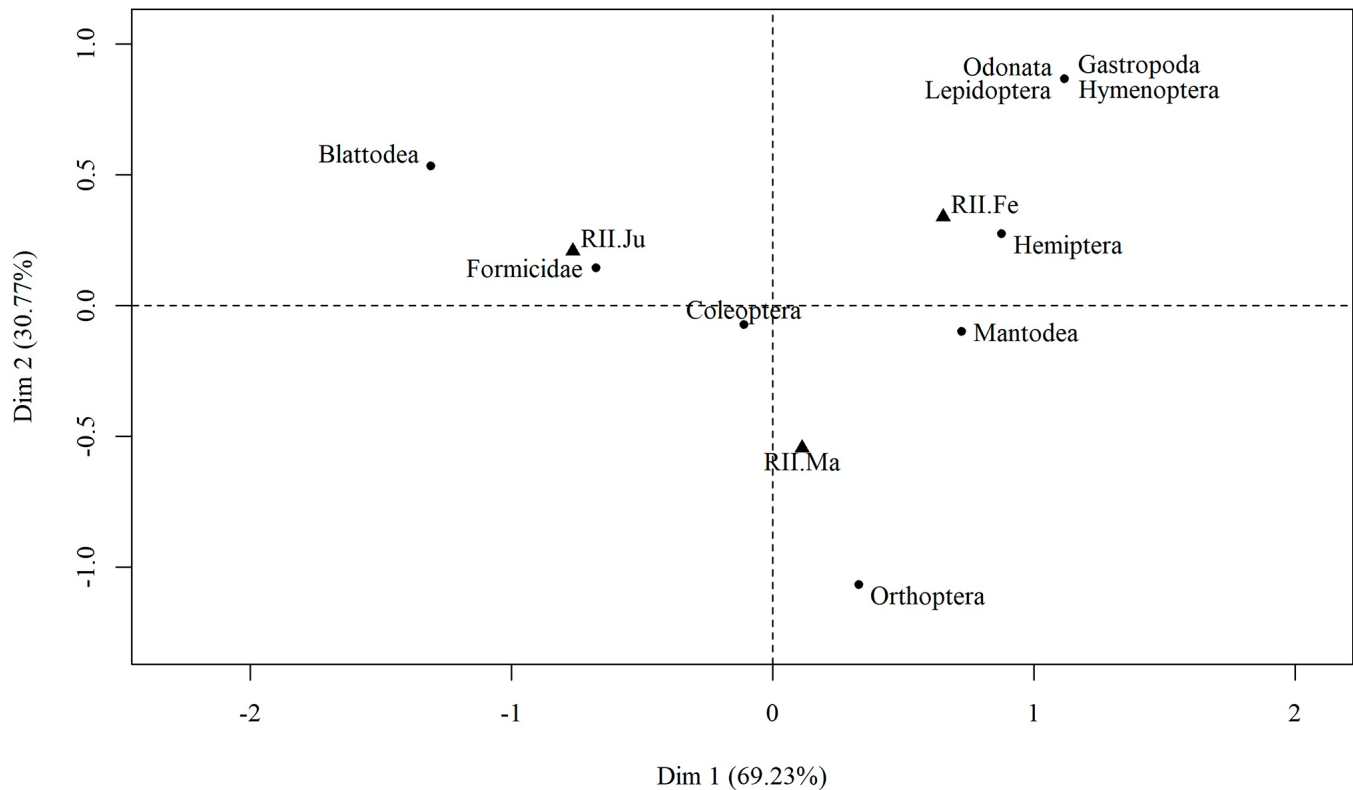


Figure 1. Canonical Correspondence Analysis with Relative Importance Index (RII) for each prey category in diet of males (RII Ma), females (RII Fe) and juveniles (RII ju) of *Boana raniceps* in an area of Caatinga, northeastern Brazil.

The following morphological variables were taken (Duellman 1970, Heyer *et al.* 1990, Freitas *et al.* 2008): snout-vent length (SVL), head width (HW), head length (HL), head height (HH), jaw length (JL), forearm length (FL), arm length (AL), hand length (HAL), thigh length (TL), tibia length (TIL), and foot length (FOL). The Mann-Whitney test was used to analyze the presence of sexual size dimorphism in the morphological variables.

Statistical analyses

For statistical analyses, all data were tested for normality and homoscedasticity with Shapiro-Wilk and Levene tests, respectively. When the assumptions for parametric variables were not met, we applied nonparametric tests (Sokal and Rolf 1995). We performed all analyzes in the software R (R Core Team 2020), using the “vegan” package (Oksanen *et al.* 2019).

RESULTS

Feeding ecology

We analyzed 34 specimens of *Boana raniceps*, being 18 males, 11 females, and five juveniles. Of these, 29 (85.29

%) presented content on their stomach. We found 85 prey items, distributed in ten prey categories (Table 1). Coleoptera (69.41 %) was more important numerically, followed by Formicidae (9.41 %) and Mantodea (7.05 %). Coleoptera is also more important in frequency (52.08 %), had the highest Relative Importance Index (RII) (49.79 %) and volumetrically it was the second most important category (27.9). Formicidae and Mantodea were the second most important prey items in frequency (12.5 % each). Regarding RII, Hemiptera and Orthoptera had the highest values after Coleoptera, with 16.28 % and 8.53 %, respectively (Table 1). Surprisingly, we report gradual order or sequence changes in the relative importance of diet items between sex and age classes. Relative Importance Index for each prey category differed between males, females, and juveniles ($\chi^2 = 147.79$, $df = 18$, $P < 0.001$). Coleoptera was the prey category that contributed most to the diet of adults and juveniles, followed by Hemiptera which contributed with 22.37 % in females’ diet and Orthoptera (18.31 %) in males’ diet. Blattodea was reported only in juveniles, contributing with 19.53 %. The total variance explained by the first two axis of the Canonical Correla-

Table 1. Diet of *Boana raniceps* in an area of Caatinga, northeastern Brazil. F = absolute frequency; F% = relative frequency; N = Number of prey items; N% = relative number of prey items; V = Volume; V% = relative volume; and RII = Relative Importance Index.

Category	F	F (%)	N	N (%)	V	V (%)	RII
INSECTA							
Coleoptera	25	52.1	59	69.4	1748.1	27.9	49.8
Blattodea	1	2.1	1	1.2	26.9	0.4	1.2
Odonata	1	2.1	1	1.2	324.3	5.2	2.8
Mantodea	6	12.5	6	7.1	263.0	4.2	8
Hemiptera	3	6.2	4	4.7	2377.0	37.9	16.3
Hymenoptera							
Non-Formicidae	1	2.1	1	1.2	35.7	0.6	1.3
Formicidae	6	12.5	8	9.4	13.8	0.2	7.4
Lepidoptera	1	2.1	1	1.2	243.5	3.9	2.4
Orthoptera	3	6.2	3	3.5	993.2	15.8	8.5
MOLLUSCA							
Gastropoda	1	2.1	1	1.2	244.6	3.9	2.4
Total	48	100	85	100	6270.3	100	100

tion Analysis was of 100 %. First axis explained 69.23 % and second axis 30.77 % of all data variation (Fig. 1).

Reproductive biology

Observations on the reproductive biology of *Boana raniceps* show that there was no correlation between female SVL and number of eggs ($t = 0.39945$, $P = 0.70$) and no correlation between male SVL and volume of testicles ($t = 0.53475$, $P = 0.60$); thus the body size was not a limiting factor in fecundity. Number of eggs in the oviducts of females varied from 153 to 3904 ($1,043.59 \pm 1,086$), with mature eggs in the dry (November) and rainy (February) seasons. Testicular volume varied from $3,021 \text{ mm}^3$ to $9,367 \text{ mm}^3$ ($5.50 \pm 2.01 \text{ mm}^3$).

Sexual dimorphism

Boana raniceps exhibited sexual size dimorphism in SVL ($w = 162$; $P < 0.05$), with females generally larger than males. Snout-vent-length ranged from 58.13 to 69.72 mm (mean = 65.25 ± 2.68 mm) in males and ranged from 62.06 to 78.57 mm (mean = 70.60 ± 5.44 mm) in females. No significant variations were observed for the other morphometric variables (Table 2).

DISCUSSION

Feeding ecology

Prey ingestion can be affected by several factors such as reproduction (Wells 2007), sex (Magalhães et al. 2016), body size and shape (Costa-Pereira et al. 2018, Tozetti and Martins 2019), and foraging behavior and phylogeny (Román-Palacios et al. 2019, Moroti et al. 2021). Tree-frogs in the family Hylidae are usually generalists and opportunists, with dietary specialization only in special conditions (Parmele 1999). Several species of the genus *Boana* are considered generalist predators, consuming a wide variety of food items (Pacheco et al. 2017, Protázio et al. 2018, de Oliveira et al. 2019, this study). For *B. raniceps*, Coleoptera and Orthoptera were the most important items in the Caatinga (Leite-Filho et al. 2015, this study); in the Pantanal, Blattaria and Coleoptera were the most important prey items (Sabagh et al. 2010); while in the Atlantic Forest, Araneae and Acari were the most important items (Leite-Filho et al. 2017). Thus, the species consumes different food items depending on the region. This fact may be due to the abundance and availability of prey in these regions. These results demonstrate the generalist and op-

Table 2. Mann–Whitney test results of sexual size dimorphism for each morphometric variable of *Boana raniceps*. Snout–vent length (SVL), head width (HW), head length (HL), head height (HH), forearm length (FL), arm length (AL), hand length (HAL), thigh length (TL), tibia length (TIL), foot length (FOL), and jaw length (JL). All values are given in mm.

Variables	Males (n = 11)	Females (n = 18)	w	P
SVL	65.2	70.6	162	< 0.01
HW	21.0	22.1	112	0.58
HL	22.3	23.2	87	0.61
HH	8.9	10.0	120	0.36
FL	10.4	12.4	118	0.41
AL	10.1	10.5	104	0.84
HAL	18.5	21.3	117	0.43
TL	36.1	37.6	111	0.61
TIL	37.5	40.5	109	0.67
FOL	45.3	48.9	94	0.84
JL	39.1	40.9	74	0.27

portunistic character of the species – which was already expected. What is striking is the ontogenetic and sexual variation in the diet – which represents the first record in the genus *Boana*.

Morphological characteristics in amphibians and age class may be related to the selection of prey types (Polis 1984, Schoener 1986, da Rosa *et al.* 2011, Vignoli *et al.* 2017). One of the causes attributed to the ontogenetic differentiation in the diet is the morphological limitation of prey ingestion (Lima 1998, Moroti *et al.* 2021). In addition to these morphological differences, variations in the diet of adults and juveniles can also be attributed to differences in prey selectivity and foraging strategies, as well as the difference between the proportions of prey consumed by individuals of different sizes (Blackburn and Moreau 2006, Brasileiro *et al.* 2010). Thus, even widely distributed and known species should provide us with new findings.

Reproductive biology

Prolonged breeders have been recorded for several species of the genus *Boana*, such as *B. albopunctata* (Spix, 1824) (Muniz *et al.* 2008), *B. crepitans* (Wied-Neuwied, 1824) (Nascimento *et al.* 2015), *B. elegans* (Bastos and Haddad, 1995), *B. faber* (Wied-Neuwied, 1821) (Lima *et al.* 2013), and *B. pombali* (Caramaschi *et al.* 2004) (Faraulo *et al.* 2019). For *B. raniceps*, studies carried out in the Panta-

nal, for example, also showed prolonged reproductive patterns, from September to April (Prado and Haddad 2005, Prado *et al.* 2005). In the Caatinga, this same prolonged reproductive pattern was recorded between the months of November to June (Oliveira *et al.* 2018, this study). Despite the rainfall restrictions recorded in the Caatinga biome, where rainfall is restricted to a few months of the year, usually from January to May, *B. raniceps* maintained the pattern of prolonged reproduction recorded in other Brazilian biomes. Furthermore, the maximum clutch size in *B. raniceps* (3904 eggs) was similar to that found for the same species in other areas (3096 eggs; Prado and Haddad 2005) and much higher than that recorded for other species of the genus, such as *B. albomarginatus* (1706 eggs; Giasson and Haddad 2007), *B. cinerascens* (Spix, 1824) (298 eggs; Telles *et al.* 2013), *B. crepitans* (2561 eggs; Nascimento *et al.* 2015) and *B. goiana* (Lutz, 1968) (207 eggs; Dias *et al.* 2021). These data demonstrate a great reproductive investment and generalist character of the species.

Sexual dimorphism

Sexual size dimorphism, with larger females than males, is a general pattern found in anurans (Monnet and Cherry 2002) and is commonly reported in the literature (e.g., Özdemir *et al.* 2012, Cajade *et al.* 2013, Otero *et al.* 2017, Diaz *et al.* 2020). On the other hand, contrary to expecta-

tions (i.e., sexual selection, Woolbright 1983, Crump and Kaplan 1979, Prado et al. 2000), it's possible that female growth for this population of *Boana raniceps* is not related to the selective pressures involved in female fertility, since body size was not a limiting factor in the fecundity, as there was no correlation between SVL of females and number of eggs and no correlation between SVL of males and testis volume. Species that present larger females than males may be the result of other types of pressures, such as intra and interspecific interactions between males and females competing for the same ecological niche (which would corroborate in part by the sexual variation found in the diet, for example) or environmental restrictions (Shine 1989, Prado et al. 2005). In any case, further studies should be carried out to test these hypotheses.

In this study, we present additional information about ecology and natural history of *Boana raniceps*. We corroborate information about their generalist diet, prolonged reproduction with females carrying eggs during the wet and dry seasons, and sexual dimorphism of size, with females being larger than males. In addition, we describe for the first time an ontogenetic and sexual variation in the diet of anurans of the genus *Boana*.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

HTM, CFS, RWA concept and experimental design, HTM, CFS, RAB data gathering and analyses, HTM, CFS, RAB, RWA writing of paper. All authors have read and agree with the final version of the manuscript.

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