

Diet of two sympatric species of the *Leptodactylus fuscus* group: *Leptodactylus longirostris* (Boulenger, 1882) and *Leptodactylus mystaceus* (Spix, 1824) in the Brazilian Amazon rainforest

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ABSTRACT

Leptodactylus longirostris and *L. mystaceus* are sympatric species of frogs occurring in the Amazon basin in forest areas. In this study, diet composition, niche overlap and niche breadth were described for the two of species from the north domain of the Brazilian Amazon forest. A total of 68 individuals of *L. longirostris* and 43 individuals of *L. mystaceus* were analyzed. The most important prey for *L. longirostris* was Hymenoptera (Formicidae) and for *L. mystaceus* was Coleoptera. The niche breadth of *L. mystaceus* was wider than the another species. The value of the niche breadth ($B \leq 0.50$) of both sympatric frogs suggests a specialization on ants (Formicidae) and beetles (Coleoptera).

Key Words: Species coexistence; Food items; Leptodactylidae; Feeding overlap.

RESUMEN

Dieta de dos especies simpátricas del grupo *Leptodactylus fuscus*: *Leptodactylus longirostris* (Boulenger, 1882) y *Leptodactylus mystaceus* (Spix, 1824) en la selva amazónica brasileña. *Leptodactylus longirostris* y *L. mystaceus* son especies simpátricas de ranas que se encuentran en la cuenca del Amazonas en áreas forestales. En este estudio, se describió la composición de la dieta, la superposición de nichos y la amplitud de nichos para las dos especies del dominio norte de la selva amazónica brasileña. Se analizaron un total de 68 individuos de *L. longirostris* y 43 individuos de *L. mystaceus*. La presa más importante para *L. longirostris* fue Hymenoptera (Formicidae) y para *L. mystaceus* fue Coleoptera. La amplitud del nicho de *L. mystaceus* era más amplia que la de la otra especie. El valor de la amplitud del nicho ($B \leq 0.50$) de ambas ranas simpátricas sugiere una especialización en hormigas (Formicidae) y coleópteros (Coleoptera).

Palabras claves: Coexistencia de especies; Items-Presa; Leptodactylidae; Superposición de alimentación.

Introduction

Anurans occupy an important position in trophic chains from both terrestrial and aquatic environments, being important consumers of arthropods at adult stages (Duellman and Trueb, 1994). According to Toft (1980) neotropical anurans can be classi-

fied in a continuum between specialist predators, that feed on a specific prey, or generalists, that feed on arthropods in general. The trophic guilds and functional traits related to food niche dimension identified in the studies of Toft (1980) and subse-

quent studies demonstrate that the trophic axis of ecological niche has an important role structuring anuran community (Lima and Magnusson, 1998; Vignoli and Luiselli, 2012; Cloyed and Eason, 2017).

Within anuran communities, the occurrence of ecologically similar species is important to understanding patterns of competition and partition of resource in trophic niche dimension (Leibold and McPeck, 2006; Vogt *et al.*, 2017). Congeneric species exhibits very similar ecological demands and so may be expected to show intense competition for limiting resources (Holt, 1977). Resource partitioning can reduce competition and promotes the coexistence of congeneric species that, presumably, occupy similar niches. In Neotropical region, due to their high diversity, anuran communities often contain sympatric congeneric species that share similar microhabitats.

The genus *Leptodactylus* Fitzinger, 1826 are one of the most diverse genera in Neotropical region, widely distributed in South America (Frost, 2020). Particularly, *L. fuscus* species group has the great number of species (De Sá *et al.*, 2014), in which the coinciding range of distribution of the different species may lead to sympatric occurrences. Over the upper Amazon Basin region, *Leptodactylus longirostris* and *Leptodactylus fuscus* occurs in sympatry over a portion of their ranges.

Leptodactylus longirostris Boulenger, 1882 is a small to moderate sized frog, snout-vent-length (female 33.3–45.6 mm; male 33.1–44.2 mm, De Sá *et al.*, 2014). This species occurs in the Guiana Shield region and in the Brazilian states of Amazonas, Pará, Roraima and Amapá. It is commonly found occupying open and forested areas (Crombie and Heyer, 1983; De Sá *et al.*, 2014; Dias-Souza *et al.*, 2018). *Leptodactylus mystaceus* (Spix, 1824) has a moderate size (female 44.5–56.1 mm; male 42.4–52.2 mm, De Sá *et al.*, 2014), widely distributed in the Amazon basin throughout Brazil (Affonso *et al.*, 2016). In Guiana Shield region of Amapá state, *L. mystaceus* and *L. longirostris* were found occurring in sympatry in savanna and open forest areas (Lima *et al.*, 2017; Silva e Silva and Costa-Campos, 2018).

Both species share some biological traits, but currently there is no information about diet composition for *L. longirostris* and *L. mystaceus* occurring in sympatry across open forest environments in Eastern Amazon. Understanding trophic interactions is essential for the development of successful conservation strategies at local scale (Young *et al.*, 2001; Wells, 2007). In Neotropics, effects associated

with landscape fragmentation cause alteration in trophic interactions, which may contribute to population declines. Herein, the diet composition of two sympatric species *L. longirostris* and *L. mystaceus* in the north domain of the Brazilian Amazon, Guiana Shield region were analyzed to improve its conservation status of these species and provide management tools in these environments. Four questions are made: 1) which prey types was consumed by each species? 2) what was the level of niche overlap and niche breadth between the two frog species? 3) there were relationships between the body size and jaw width with the prey volume? 4) did the diet of *L. longirostris* and *L. mystaceus* is similar to other species of the genus?

Materials and methods

Study area – Sampling was carried out in the Parque Natural Municipal do Cancão, Serra do Navio Municipality (0°54'9.9" N, 52°0'19.9" W), Amapá State, Brazil (Fig. 1). This area comprises 370.26 hectares within the Amazon forest, including vegetation of *terra firme* rainforests, streams, open areas, and treefall gaps (Silva e Silva and Costa-Campos, 2018). It is situated in the monsoon climate (climate symbol “Am”) with precipitation values ≥ 60 mm in the driest month, according to the Köppen-Geiger (Peel *et al.*, 2007).

Sampling – Individuals of *L. longirostris* and *L. mystaceus*, were deposited in the Herpetological Collection at the Universidade Federal do Amapá (CECC), in the city of Macapá, Amapá State, Brazil. Individuals

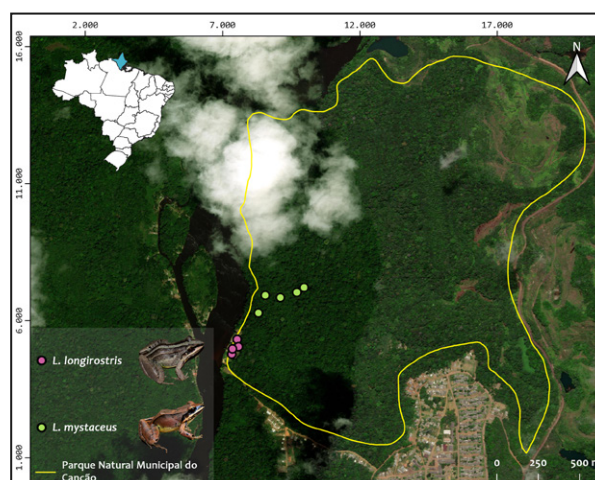


Figure 1. Map of the Parque Natural Municipal do Cancão, Serra do Navio municipality, Amapá State, Brazil, indicating the points where *Leptodactylus longirostris* and *Leptodactylus mystaceus* were collected.

were collected by hand using the visual and auditory search method (Heyer *et al.*, 1994) from October 2017 to March 2018.

Laboratory protocols – Each individual was euthanized with lidocaine overdose, fixed in 10% formalin, and conserved them in 70% alcohol solution, according to the collection license provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio #48102-2). Individuals was dissected for the removal of stomach contents (stomach and intestine considered as a single sample) through a ventral incision and analyzed with the aid of a stereoscopic microscope ZEISS model Stemi 2000-C. The stomach flushing technique (Solé *et al.*, 2005) was not used because the examined anurans were also used for another study, which required euthanasia to obtain samples. The identification of the prey consumed was conducted out at the taxonomic level of order according to the identification key of Rafael *et al.* (2012).

Analyses – The obtained items were measured as length and width. We estimated the prey volume using the ellipsoid formula $V = 4\pi/3 * L/2 * (W/2)^2$, where V = volume, L = prey length, and W = prey width (Colli and Zamboni, 1999). The obtained items were measured as length and width (with a caliper to the nearest 0.1 mm). The Index of relative importance (IRI) of each prey category, proposed by Pinkas *et al.* (1971), following the equation: $IRI = (F\% + N\% + V\%)/3$, where IRI = Index of relative importance; $F\%$ = frequency of occurrence; $N\%$ = numerical frequency; $V\%$ = volumetric frequency of each category of prey item were calculated.

To access the level of specificity of the diet, the trophic niche breadth was calculated using the Levins index (B) as described by Pianka (1986), following the equation: $(B = 1/\sum p_j^2)$, where B = niche breadth and p_j = proportion of item j in the diet. In this case, when the value of B is between 0 and 0.50 the species was considered as specialist, and values between 0.51 and 1.0 was named generalist species.

Trophic Niche Overlap Index of Pianka (O_{jk}) (Pianka, 1974) as follow,

$$O_{JK} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where O_{jk} is the niche overlap index between the species j and k ; p_{ij} and p_{ik} are the proportions of prey categories consumed by the species; j , k , n are the total number of resource categories consumed by

species j and k . Index ranged from 0 to 1, in which values equal to zero indicate absence of overlap, and values equal to 1 point out to a complete overlap between species' diets (Krebs, 1999). This analysis was performed using EcoSim Version 7.71 (Entsminger, 2014 free trial <http://www.garyentsminger.com/ecosim/index.htm>).

To analyze the sampling size and taxonomic richness of prey consumed by the two leptodactylids species rarefaction curves based on the number of specimens and food items were plotted using Estimates 9.1 (Gotelli and Colwell, 2001 free trial <http://purl.oclc.org/estimates>). Principal Component Analysis (PCA) and One-Way ANOVA analysis to test if diet composition varies between *L. longirostris* and *L. mystaceus* were performed. PCA analysis conducted in the R software version 4.0.3 (R Development Core Team, 2017) using the vegan package (Oksanen *et al.*, 2015).

Snout-vent length (SVL) and jaw width for each frog specimen using a digital caliper (accuracy precision 0.01 mm) were measured. To test if the SVL or jaw width affects prey volume consumed simple linear regression as independent variables was used using prey-items volume as dependent variables (Zar, 1999). The values of prey items were log-transformed (\log_{10}) to fit requirements of normality. The analyses were performed Bioestat 5.0 software (Ayres *et al.*, 2007), using $p < 0.05$ as the significance level.

Results

Leptodactylus longirostris diet

Nine prey categories from the stomach contents of 68 *L. longirostris* specimens were determined. From the total, 27 (39.7%) stomachs were empty or composed of unidentifiable preys on advanced stage of decomposition. The three most abundant categories in terms of volume and frequency were Formicidae, Coleoptera and Hemiptera (Table 1). Other prey categories with large volumetric contribution, that had a low frequency in the stomachs, were Lepidoptera (larvae), Blattaria and Araneae. The IRI results showed that the most important preys, in decreasing order, were Formicidae ($IRI = 77.05$), Coleoptera ($IRI = 71.10$) and Hemiptera ($IRI = 20.68$). Results of correlation tests indicated that both jaw width (JW) and SVL were not correlated with variation in largest ingested prey (SVL, $F = 1.328$, $p = 0.259$; JW, $F = 0.847$, $p = 0.630$).

Table 1. Numerical frequency (N%), frequency of occurrence (F%), volume (V%) and Index of relative importance (IRI) in the diet of *Leptodactylus longirostris* and *Leptodactylus mystaceus* from the Serra do Navio municipality, Amapá State, Brazil.

Prey category	<i>Leptodactylus longirostris</i>							<i>Leptodactylus mystaceus</i>						
	N	N (%)	F	F (%)	V	V (%)	IRI	N	N (%)	F	F (%)	V	V (%)	IRI
Araneae	4	5.06	3	7.14	16.58	2.26	12.96	3	21.43	3	25.00	57.30	2.04	16.16
Coleoptera	23	29.11	13	30.95	242.98	33.11	71.10	8	57.14	6	50.00	572.07	20.38	42.51
Hemiptera	10	12.66	3	7.14	19.39	2.64	20.68	---	---	---	---	---	---	---
Hymenoptera	2	2.53	2	4.76	11.63	1.58	7.82	---	---	---	---	---	---	---
Formicidae	27	34.18	13	30.95	262.35	35.75	77.05	---	---	---	---	---	---	---
Ponerineae	1	1.27	1	2.38	5.85	0.80	3.91	---	---	---	---	---	---	---
<i>Solenops</i> sp.	1	1.27	1	2.38	0.65	0.09	3.68	---	---	---	---	---	---	---
Lepidoptera larvae	2	2.53	2	4.76	84.00	11.45	11.11	---	---	---	---	---	---	---
Orthoptera	---	---	---	---	---	---	---	2	14.29	2	16.67	1954.29	69.63	33.53
Isoptera	4	5.06	2	4.76	15.78	2.15	10.54	---	---	---	---	---	---	---
Blattaria	1	1.27	1	2.38	71.48	9.74	6.89	---	---	---	---	---	---	---
Insecta larvae	4	5.06	1	2.30	3.19	0.43	7.59	---	---	---	---	---	---	---
Annelida	---	---	---	---	---	---	---	1	7.14	1	8.33	222.88	7.94	7.81

***Leptodactylus mystaceus* diet**

The stomach contents from 43 individuals, of which 11 (25.6%) stomachs were empty or contained only unidentifiable preys on advanced stage of decomposition were determined. Prey items into four taxonomic categories were classified. The most abundant prey categories were Coleoptera and Araneae. As for volume the categories with largest representation were Orthoptera and Coleoptera. The IRI revealed a great importance of Coleoptera and Orthoptera. We did not find a correlation between JW and SVL of predator and the volume of the largest prey ingested (SVL, $F = 0.299, p = 0.602$; JW, $F = 0.006, p = 0.936$).

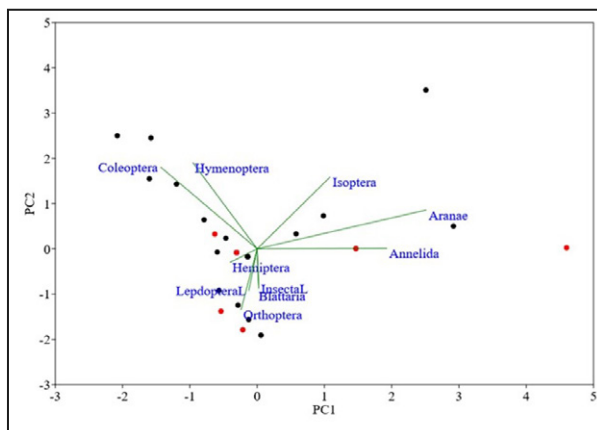


Figure 2. Principal components analysis to graphically represent the differences in the diet of *Leptodactylus longirostris* (black dots) and *Leptodactylus mystaceus* (red dots) from Brazilian Amazon rainforest.

Niche measures

Diet composition did not differentiate between both frogs species ($F = 9.168, df = 11, p = 0.359$; Fig. 2). Araneae and Coleoptera were common prey consumed by both species. Items consumed exclusively by *L. longirostris* were Blattaria, Hymenoptera (Formicidae), Hemiptera, Lepidoptera (larvae), Isoptera. While Orthoptera and Annelida were items consumed exclusively by *L. mystaceus*. Considering the abundance of prey items in each food category, *L. mystaceus* had a slightly larger niche (Levins standardized niche) $B_{st} = 0.5$ than *L. longirostris* $B_{st} = 0.39$. The trophic niche overlap of Pianka Index was 59% ($Ojk = 0.59$) considering the abundance of prey items in each prey category. The rarefaction curve of taxonomic prey richness did not reach the asymptote for *L. longirostris* and *L. mystaceus*, indicating prey richness is still underestimated (Fig. 3).

Discussion

Diet composition of *L. longirostris* and *L. mystaceus* were similar, indicating a trend through of *L. fuscus* species group to be conservative in feeding behavior (Silva and Rossa-Feres, 2010). The most important prey items were ants (Formicidae) for *L. longirostris* and beetles (Coleoptera) for *L. mystaceus*. Ants and beetles comprise two of the most diverse and abundant arthropod groups in terrestrial ecosystems of

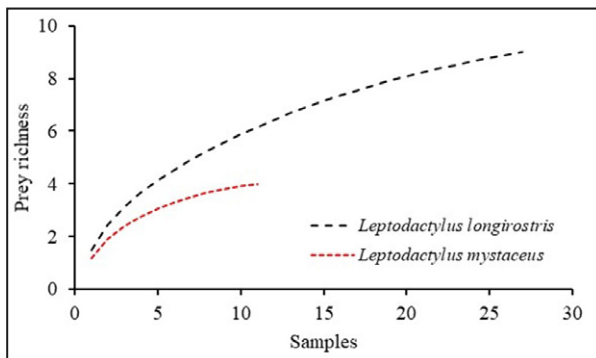


Figure 3. Rarefaction curves of the *Leptodactylus longirostris* and *Leptodactylus mystaceus* based on prey richness to the number of individuals sampled.

Neotropical region (Lofgren, 1986; Hölldobler and Wilson, 1990). Their abundance in leaf litter makes them prey of easy consumption present in the diet of many anurans from the genus *Leptodactylus* (Camera *et al.*, 2014; Baía *et al.*, 2020).

The great number of strongly chitinized preys such as ants and beetles, may be due to the opportunistic feeding behavior adopted by *Leptodactylus* species (Toft, 1981; Solé and Rödder, 2010; Santana *et al.*, 2019). However, this genus also preys on anurans (*L. macrosternum*, Sousa *et al.*, 2016; *L. podicipinus*, Ceron *et al.*, 2018; *L. chaquensis*, Cuestas-Carrillo *et al.*, 2019; *L. mystaceus*, Moreira-Brito *et al.*, 2020), small mammals (Castro *et al.*, 2011; Marques-Pinto *et al.*, 2019), as well as other sedentary invertebrate preys (e. g. larval forms of insects). It would be a reflect of the passive foraging mode of *Leptodactylus* species, which “sit and wait” for prey (Toft, 1980; 1981), eating more uncommon prey that comes in their way.

The niche breadth of *L. mystaceus* was broader than that of *L. longirostris*. One possible explanation may be that its has a diet more equitable with regards to prey distribution even this species consumed a lower number of preys. The niche breadth is narrowed as the abundance is increased toward a few prey categories within the set of prey (Pianka, 1974). This explain the niche breadth of *L. longirostris* is narrower due to the high consume of ants compared to other prey categories.

In addition, another possible explanation is that dietary niche breadth decreases as interspecific competition increase. Competition is caused by limiting ecological resources such as food, which drives to specialization that allows coexistence through segregation of resources explored between species, leading to a narrowing of niche breadth

(Gainsbury and Meiri, 2017). It would explain the presence of ants in the diet of *L. longirostris*, as ants are an uncommon food category found in the diet of *Leptodactylus* species (Toft, 1980; Rebouças and Solé, 2015).

The high niche overlap ($Ojk > 0.50$) recorded for *L. longirostris* and *L. mystaceus* reinforced that sympatric and congeneric amphibian species have similar diets (Baía *et al.*, 2020). This variation in diet richness found among these species may be influenced by prey size, mobility, palatability, availability and abundance in the environment (Menin *et al.*, 2005; Almeida *et al.*, 2019). The last may be explain the low number of prey items in the diet of *L. mystaceus*.

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