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Niche partitioning between two *Physalaemus* species (Anura, Leptodactylidae) in semiarid Caatinga in Northeast Brazil

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Abstract. We investigated the niche relationship between the frogs *Physalaemus albifrons* and *Physalaemus cicada* in temporary ponds in the semiarid Caatinga. We analysed niche breadth and its overlap based on spatial (microhabitat), trophic (diet composition), temporal (calling period), acoustic (advertisement call), and morphological aspects to evaluate the relationship between the species. Both species called in January, March, October and November; and calling activity was positively correlated with air temperature. We found differences in substrate type, with *P. albifrons* remaining partially submerged and *P. cicada* mainly using holes and also in the distance from the edge of the ponds, with *P. cicada* occurring further from the edge than *P. albifrons*. However, calling males of both species used the water surface as a calling microhabitat. Despite of that, pseudocommunity analysis indicated the absence of competition in the use of these microhabitats. Ants were the most important item in the diet of *P. albifrons,* while collembolans were the most important item for *P. cicada*. The analysis showed the absence of a random pattern in the use of food resources, indicating competition. *Physalaemus albifrons* had the largest snout-vent length and a longer head, while *P. cicada* had the smallest snout-vent length and a wider head. Canonical correlation analysis demonstrated an association between the prey measurements and the head size of the frogs. Advertisement calls were different between the species, with the call of *P. albifrons* being composed of a single note and *P. cicada* producing a long chirp consisting of several notes. Despite the spatial partition, which is considered to be the primary regulator of the relationship between species in anuran assemblages, our results indicated that food and acoustic partitions are more important in the temporary ponds studied, allowing the coexistence of the two species.

Key words: Anurans, temporal niche, spatial niche, food niche, acoustic niche.

Introduction

Niche partitioning is an ecological phenomenon that results from the interaction between species and is considered the most important mechanism for coexistence in natural assemblages (Gordon 2000). Species that coexist over an evolutionary period may have low levels of resource use overlap, reducing competition and the possibility of extinction (Losos 1995, Webb et al. 2002). At the same time, high overlap in one dimension of an ecological niche does not necessarily result in extinction. Species with a high overlap in one dimension of the niche can reduce negative interactions by decreasing overlap in another dimension, thus increasing the possibility of coexistence – a phenomenon known as niche complementarity (Schoener 1974, Silva et al. 2008).

In animal assemblages, five niche dimensions are fundamental to measure levels of interaction (habitat, life history, trophic, defense and metabolic), and the way in which species use these resources determines coexistence (Winemiller et al. 2015). Considering frog assemblages, the spatial niche appears to be the most important and considered the primary regulating effect on relationships among individuals (Höld 1977, Toft 1985, Eterovick et al. 2010). The use of microhabitats can therefore allow an efficient exploitation of the habitat and permit access to different resources (Cardoso et al. 1989, Duré & Kehr 2004, Abrunhosa et al. 2014). On the other hand, the temporal and food niches are considered to be of secondary importance, because different species often have a high overlap in their reproductive periods and the food items they consume (Duré & Kehr 2004, Lima et al. 2010).

For closely related anuran species, differences in the use of space and acoustic parameters are considered essentials for coexistence (Höld 1977, Bourne & York 2001, Eterovick et al. 2010, Jimenéz & Bolaños 2012). Since related species may have similar feeding strategies, body shapes and reproductive periods due to their shared evolutionary history (Toft 1985, Gottsberger & Gruber 2004), differences in the use of calling microhabitats can help reduce niche overlap and ensure the use of specific breeding sites (Duellman & Pyles 1983, Rossa-Feres & Jim 2001). Additionally, differences in advertisement call attributes can allow sound propagation and enable recognition of the acoustic signal by females, increasing the chances of reproductive success (Ryan 1988, Wells 1988).

Physalaemus albifrons (Spix, 1824) and *Physalaemus cicada* Bokermann, 1966 belong to the Leptodactylidae family and are found in areas of semiarid Caatinga in northeast Brazil. The two species have very similar ecological characteristics; males call while partially submerged, reproduce in temporary ponds and use a foam nest (Bokermann 1966). Recent studies have indicated an uncertain phylogenetic relationship between the two species. Cytogenetic aspects and morphology of the larvae attest to the possibility of phylogenetic proximity between *P. albifrons* and *P. cicada*, with both species placed within the *P. cuvieri* group, contradicting the hypothesis that *P. albifrons* and *P. cicada* form part of distinct species groups (Candioti et al. 2011, Vittorazzi et al. 2014). On the other hand, molecular studies have argued for the exclusion of *P. cicada* from the *P. cuvieri* group, phylogenetically distancing *P. cicada* from all the species of this group, including *P. albifrons* (Lourenço et al. 2015), and highlighting the need for new studies of different aspects of the biology of *Physalaemus* to clarify these issues.

Ecological descriptions of closely related species often report significant overlap in one niche dimension, which can be associated with biological constraints inherent in the phylogenetic relationships among species (Heyer & Bellin 1973, Zimmerman & Simberloff 1996) and environmental aspects that influence resource availability (Lister 1981, Menin et al. 2005). Thus, studies that investigate variation in the ecological traits of closely related species may support discussions about the evolutionary relationship between these species and the presence of microevolutionary processes (Ryan 1986, Richardson 2001). In this study, we investigated the niche relationship between *P. albifrons* and *P. cicada* inhabiting temporary ponds in the Caatinga by analysing their diet, microhabitat use, morphology and advertisement call. Based on the hypothesis of niche partitioning in some dimension of the ecological niche, we aim to answer the following questions: (i) How does *P. albifrons* and *P. cicada* use the resources in a habitat where the two species live in syntopy? (ii) What instance of the different dimensions of the niche made possible the coexistence of the two species?

Materials and Methods

Study area

This study was carried out in three temporary ponds located in the municipality of Cabaceiras, in the state of Paraíba, Brazil. Cabaceiras is in the Caatinga biome and located in the south of the ecoregion known as the Cariri Paraibano. This ecoregion is characterised by the most common type of Caatinga, which is dense and deciduous arboreal-shrubby vegetation (Velloso et al. 2002, Giulietti et al. 2007). The region is characterised by water scarcity caused by irregular rainfall, soil with a low water holding capacity, and the presence of plateaus that intersect with wet fronts (Sampaio 2010). Cabaceiras has the lowest precipitation rate in Brazil with an average of 350 mm rainfall per year, usually between October and April, and the frequent occurrence of severe and prolonged droughts (Velloso et al. 2002, Giulietti et al. 2007). The climate in the region is classified as hot semiarid (BSh) according to the Köppen classification (Velloso et al. 2002).

Due to the irregularity of the rainfall regime in Cabaceiras, the temporary ponds have an intense flooding and drying cycle (hydroperiod) and were completely dry in August and September 2010, common phenomenon in the region. In periods of flood, the ponds are widely used by local people as a water source for cattle and goat breeding – cultures traditionally used for milk production. Holes left on the banks by the footsteps of cattle and goats are common, as well as by fallen bushes and branches knocked over during feeding; these sites are frequently used as microhabitats by frogs.

Sampling

We sampled three temporary ponds located on the bed of a temporary stream known as the Junco stream (07°29'S, 36°20'W; elevation 462 m). The ponds were visited monthly between May 2010 and August 2011 and were sampled on three consecutives nights, resulting in 48 nights of study. Fieldwork was conducted between 18:00 h and 00:00 h. Seasonal occurrence and the microhabitats used by the frogs were determined by a visual and acoustic search performed when walking along the perimeter of the temporary ponds one time per night. When possible, the individuals located were collected and when we were unable to collect it, we observed where he went and conducted searches at a different location to avoid pseudoreplication. Individual collected were killed with an intraperitoneal injection of lidocaine, fixed in 10% formalin, preserved in 70% alcohol and housed in the Herpetological Collection of the Universidade Federal da Paraíba.

The following information was registered for the individuals: (i) type of substrate used; (ii) distance to pond edge; (iii) water depth (for individuals that floated on water); (iv) air temperature (breast height); (v) substrate temperature. The air and substrate temperatures were measured in the field soon after the collection of the specimens, using a DeltaTrak® thermometer with 0.2ºC precision. The distance to pond edge and water depth were recorded using a measuring tape (precision 1.3 mm).

Spatial niche

To establish the spatial niche, the microhabitat was characterised based on the following descriptors: (i) type of substrate; (ii) air temperature; (iii) soil temperature; (iv) water temperature; (v) distance to pond edge (internal and external); (vi) water depth. The differences in air, soil and water temperature, distance to pond edge and water depth for the two species were evaluated using the Mann-Whitney U test. Six substrate types were considered: exposed soil; soil between vegetation; partially submerged in water; partially submerged in water between vegetation; on rocks; and in holes. The inverse of the Simpson Diversity Index (Simpson 1949) was used to calculate the niche breadth of the substrate type (*B*):

$$B = \frac{1}{\sum_{i=1}^{n} p_i{}^2},$$

where *p* is the proportion of the substrate category *i*, and *n* is the total number of categories. This calculation generates values that range from 1 to 6, where 1 corresponds to the exclusive use of only one substrate type (specialists) and 6 corresponds to the use of all substrate types (generalists). We calculated the overlap of the substrate type based on the equation suggested by Pianka (1973):

$$\phi_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}},$$

where *p* represents the proportion of substrate category *i*, *n* is the number of categories, and *j* and *k* represent the species being compared. The overlap index ranges from 0 to 1, where 0 represents the absence of overlap and 1 represents complete overlap.

Pseudocommunity analysis was used to evaluate the presence of non-random patterns in the substrate type using the Ecosim Niche Overlap Module (Gotelli & Entsminger 2005). For this analysis, we created a data matrix of the substrate type and reformulated based on 1000 randomisations to simulate the random patterns that could be expected in the absence of structure. The partition of the substrate type was verified by comparing the observed niche overlap and the mean simulated overlap, where niche overlap values smaller than those expected by chance (simulated); suggested that competition was regulating the use of the resource (Gotelli & Graves 1996). In the Ecosim Niche Overlap Module we used the "Pianka Niche Overlap Index", "randomisation algorithm 2" and "randomisation algorithm 3" options.

The individuals were grouped into ten different categories based on distance from the edge of the pond, considering the internal and external edges described by Rossa-Feres & Jim (2001). For both internal and external edges, individuals were grouped into one of the following categories: (i) individuals up to 50 cm from the edge; (ii) individuals between 51 and 100 cm from the edge; (iii) individuals between 101 and 150 cm from the edge; (iv) individuals between 151 and 200 cm from the edge; (v) individuals observed in a microhabitat more than 200 cm from the edge. The Simpson Diversity Index (Simpson, 1949) was used to calculate the breadth of the distance to the edge niche. Niche breadth values varied from 1 to 10, where 1 corresponds to the exclusive use of only one category (specialists) and 10 to the use of all the categories (generalists).

For water depth, individuals were grouped into eight categories: (i) up to 3 cm; (ii) 4–7.9 cm; (iii) 8–11.9 cm; (iv) 12–15.9 cm; (v) 16–19.9 cm; (vi) 20–23.9 cm; (vii) 24–27 cm; (viii) above 27.1 cm. The

Simpson Diversity Index (Simpson 1949) was also used to calculate the niche breadth based on water depth. Niche breadth values varied from 1 to 8, where 1 corresponds to the exclusive use of a category (specialists) and 8 to the use of all the categories (generalists). We calculated the overlap in the distance to the edge and water depth using the equation suggested by Pianka (1973), with the same formula described for microhabitat type, and used the null model to investigate the presence of non-random patterns in the resource use, following the same criteria described above. We also analyzed the spacial niche overlap by considering all the descriptors together.

In addition, we used the Kernel density function to calculate the estimated niche overlap between the two species with the distance to the edge and water depth. The Kernel density estimator is a non-parametric estimator based on Kernel distribution and integral functions and can be used for continuous data when the distribution of traits is unknown (Mouillot et al., 2005). Although data of a continuous nature can be converted into data with discrete nature, this method can promote the loss of information due to the condensation of data (Mouillot et al., 2005; Geange et al., 2011). Thus, the construction of artificial categories to use in the Pianka overlap model may conceal the actual overlap between species and skew our results.

The Kernel overlap estimator computes the overlap coefficient Δ and generates values ranging from 0 (no overlap) to 1 (full overlap). In addition, we performed 1000 randomizations with bootstrap, extracted the expected overlap mean for each bootstrap sample, and then compared with the estimated overlap in the Kernel density using the Wilcoxon rank sum test. The Kernel density estimation was performed in software R, with the package overlap (Meredith & Ridout, 2018).

We also investigated the relationship between calling males of *P. albifrons* and *P. cicada* in the ponds. For this analysis we used the type of calling substrate, air and water temperature, distance to the edge and water depth. As males of both species exclusively vocalised while partially submerged, we considered the existence of two categories of calling substrate in an attempt to make our analysis less conservative and evaluate possible preferences on a fine scale. Our expectation is that males may present differences in a microhabitat descriptor, which guarantees reproductive success and coexistence in the same pond. The Mann-Whitney U test was used to verify the differences in the descriptors of the calling microhabitat between males. We also calculated the breadth and overlap in the type of calling susbstrate, distance to the edge and water depth, and used a null model to verify the presence of non-random patterns in calling microhabitat use, using the same procedures as described above.

Diet

Food items were identified through direct observation of the stomach content using a stereomicroscope. Prey categories were identified to taxonomic level of order, except plant material and ants (Formicidae) which were considered here as a separate prey category to non-ant Hymenoptera. We also considered the monophyletic order of Hemiptera, composed of Heteroptera (bugs), Auchenorrhyncha (cicadas) and Sternorrhyncha (aphids) (Triplehorn & Johnson 2004). We recorded the length and width of intact items with a Mitutoyo® digital caliper (precision of 0.01 mm) and estimated the volume of each prey (*V*) using an ellipsoid formula (Dunham, 1983):

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right),$$

where *w* is the width of the prey and *l* is the length of prey. For volumetric analysis, we used only prey items that were intact to avoid volumetric under- or overestimation. We also calculated the number and volume percentage of each prey category. The breadth of the food niche (*B*) was calculated using the inverse of the Simpson Diversity Index (Simpson 1949), with the same formula that was used for microhabitat. The food niche breadth calculated from the inverse Simpson Diversity Index generated values from 1 to the total number of prey categories identified. We also calculated the percentage of occurrence of prey categories, based on the ratio between the total number of stomachs containing the category of prey *i*, divided by the total number of stomachs.

To determine the relative contribution of each prey category, we calculated the Relative Importance Index (IRI) for the grouped stomachs using the equation:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the occurrence percentage, $N\%$ is the numeric percentage and $V\%$ represents the volumetric percentage of the prey category *i*. Dietary overlap was calculated using the Relative Importance Index and the equation suggested by Pianka (1973), with the same formula as described in the selection of susbstrate. In this analysis, we considered the prey in the availability in the environment by dividing the volume of each prey category by the total volume of prey available in the environment. To do this, we used information obtained in Protázio et al. (2015), which investigated electivities in the diet of 15 species of frogs in the same area as the present study, including *P. albifrons* and *P. cicada*. Afterward, a null model was used to investigate the presence of non-random patterns in the use of food resources, following the same criteria as described for microhabitat use.

We also investigated the relationship between the morphology of the head of *P. albifrons* and *P. cicada* and the prey size. For this, we performed a canonical correlation analysis using the maximum length and width of prey in relation to the length and width of the frog's head. The aim of this analysis was to determine whether changes in food niche are associated with morphological differences among frogs. Canonical correlation analysis was performed with the BioEstat 5.0 program (Ayres et al. 2007).

Morphometry

Eleven morphometric variables were measured using a Mitutoyo® digital caliper (precision of 0.01 mm) and a Leica® EZ4 stereomicroscope: snout vent length (SVL); head length (HL); head width (HW); eye-nostril distance (END); internarial distance (IND); inter-eye distance (IED); thigh length (THL); tibia length (TL); foot length (FL); tympanum diameter (TD); eye diameter (ED). Morphometric terminology was based on Napoli & Pimenta (2009).

All morphometric variables were logarithmically transformed (Log10) to obtain normality (Zar 1999). The effect size generated by isometric variation was reduced by linear regression residuals through the creation of a body size variable, representing the total partition of the variation in the size and shape of each individual (Somers 1986). Body size values were obtained from the equation $p^{-0.5}$, where *p* is the number of variables measured (Jolicoeur 1963), multiplied by the sum of all the observations. The body size variable was subsequently used to perform simple regressions against the other morphometric variables and the residuals generated were retained. These residuals were used to create a new covariance matrix of the adjusted variables from the Principal Component Analysis (Hammer 2009). Simple Regressions and Principal Component Analyses were carried out with the BioEstat 5.0 (Ayres et al. 2007) and PAST 2.12 (Hammer et al. 2001) programs, respectively.

Acoustic

The advertisement calls of *P. albifrons* and *P. cicada* were registered one time for each calling male with a professional Marantz PMD660 recorder coupled to a Sennheiser ME66 unidirectional microphone, with a frequency rate of 44100 Hz and 16 bits of resolution. All the advertisement calls were recorded at a distance of approximately one meter from the vocalising male and analysed for a period of one minute. Acoustic records were deposited in the acoustic collection of the Herpetology Laboratory of the Universidade Federal da Paraíba. The terminology used in acoustic analysis followed the suggestions of Duellman & Trueb (1994). The calls were digitised and analysed for spectral and temporal aspects using the Raven Pro 1.3 program. The spectral parameters were obtained using the Discrete Fourier Transformation algorithm and a filter band of 248 Hz. The temporal parameters were measured through direct analysis of the oscillograms. The following acoustic variables were measured: dominant frequency (Hz); fundamental frequency (Hz); number of notes per call; note length (ms); call duration (ms); call repetition rate (min); distance between calls (ms); number of pulses per note.

Mann-Whitney U test was used to verify differences in acoustic variables of the advertisement call. Additionally, the mean, standard deviation and minimum and maximum variation of each acoustic variable were also calculated. Many acoustic variables can be correlated (Morais et al., 2015), indicating collinearity and biasing our results. Thus, we used a PCA to select the most relevant acoustic variables from logarithmized data. Mann-Whitney U test was performed with the BioEstat 5.0 (Ayres et al. 2007). The significance level was 0.05 for all statistical tests.

Results

The two species varied in abundance, with *P. cicada* (125 individuals) being more abundant than *P. albifrons* (30 individuals) (Table 1). The highest abundance of *P. albifrons* occurred in January and the highest abundance of *P. cicada* occurred in December. The abundance of *P. cicada* was negatively correlated with water depth (rs = -0.32; p = 0.04) and soil temperature (rs = -0.37; p = 0.02), but there were no correlations with the abundance of *P. albifrons*. The analysis of calling males showed that both species vocalised synchronously in October, November, January and March, and had preference for calling in the first hour of the night, between 18:00 and 21:00. In both species the calling activity was correlated with air temperature (*P. albifrons*: rs = 0.31; p = 0.04; *P. cicada*: rs = 0.41; p = 0.01).

The most frequent substrate type of *P. albifrons* was partially submerged in water, followed by exposed soil and partially submerged in water between vegetation, while *P. cicada* was more abundant in holes followed by exposed soil and partially submerged in water (Table 2). We found differences between the two species in their distance to the pond edge (U = 626.5; p = 0.001), with *P. cicada* (n = 105; 96.9 ± 135.7 cm) occurring further from the edge than *P. albifrons* (n = 21; 43.4 ± 85.9 cm). Niche breadth analysis indicated that *P. cicada* was more generalist than *P. albifrons* and analysis based on the null model indicated an absence of competition between the two species in all descriptors of microhabitat (Table 2). The analysis with all the descriptors of the spacial niche together, also indicated absence of competition (observed mean = 0.91; simulated mean = 0.27; p = 1.0). Kernel density analysis also indicated high overlap values for pond edge distance and water depth and absence of difference between observed and random overlap values (Table 2, Fig. 1).

Table 1. Abundance of individuals between May 2010 and August 2011 in temporary ponds of Cabaceiras, Brazil. Values in parentheses represent abundance of males conducting calling activity.

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Physalaemus albifrons	1	–	–	–	7	4(4)	1(1)	–	13(6)	–	2(2)	–	1	–	1	–
Physalaemus cicada	1	–	1	–	17	19(17)	19(12)	34	21(10)	6	1(1)	1	–	–	5	–

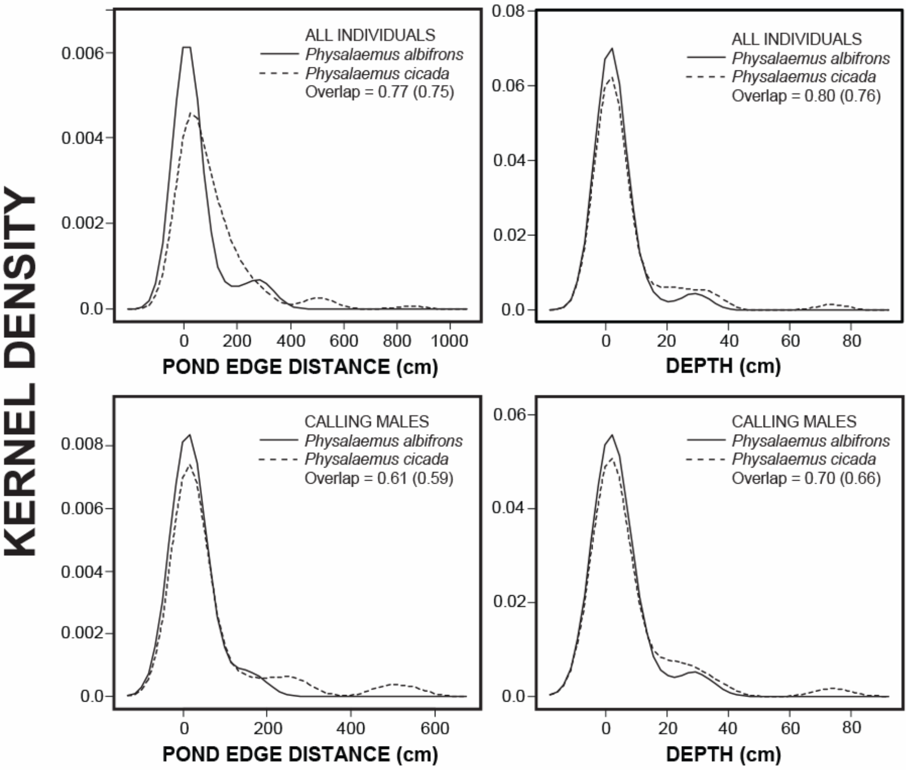

Figure 1. Plot of the Kernel density estimation showing the distribution of the *Physalaemus albifrons* and *P. cicada* from pond edge distance (cm) and depth (cm). Niche overlap values represent observed and simulated mean with bootstrap.

Table 2. Frequency, niche breadth and niche overlap of *Physalaemus albifrons* and *P. cicada* in temporary ponds in Cabaceiras, PB, Brazil. Sample sizes are in bold. For niche overlap, values represent observed and simulated mean. *p* represents observed ≤ expected.

Microhabitat	*Physalaemus albifrons*	*Physalaemus cicada*
Substrate	**30**	**125**
Exposed soil	5 (16.7)	27 (21.6)
Soil between vegetation	3 (10.0)	11 (8.8)
Partially submerged in water	14 (46.7)	28 (22.4)
Partially submerged in water between vegetation	5 (16.7)	27 (21.6)
Rock	–	1 (0.8)
Hole	3 (10.0)	31 (24.8)
Niche breadth	3.41	4.70
Pianka niche overlap R2 *p = 0.73*	0.80 (0.69)	
Pianka niche overlap R3 *p = 0.94*	0.80 (0.64)	
Depth (cm)	**18**	**54**
0 – 3	16 (89.9)	42 (77.8)
4 – 7	–	2 (3.7)
8 – 11	–	1 (1.9)
12 – 15	1 (5.6)	1 (1.9)
16 – 19	–	1 (1.9)
20 – 23	–	2 (3.7)
24 – 27	–	1 (1.9)
Above 27	1 (5.6)	4 (7.4)
Niche breadth	1.26	1.63
Pianka niche overlap R2 *p = 1.00*	0.99 (0.46)	
Pianka niche overlap R3 *p = 0.99*	0.99 (0.18)	
Kernel density *p = 0.50*	0.80 (0.76)	
Pond edge distance (cm)	**21**	**105**
External		
0 – 50	–	8 (7.6)
51 – 100	–	13 (12.4)
101 – 150	–	16 (15.2)
151 – 200	–	6 (5.7)
above 200	2 (9.5)	7 (6.7)
Internal		
0 – 50	17 (80.9)	45 (42.9)
51 – 100	1 (4.8)	2 (1.9)
101 – 150	–	1 (1.0)
151 – 200	1 (4.8)	1 (1.0)
above 200	–	6 (5.7)
Niche breadth	1.49	4.17
Pianka niche overlap R2 *p = 1.00*	0.89 (0.49)	
Pianka niche overlap R3 *p = 0.93*	0.89 (0.25)	
Kernel density *p = 0.70*	0.77 (0.75)	

The analysis of calling showed that males of both species vocalized exclusively within the pond, partially submerged in water and partially submerged in water between vegetation (Table 3). We did not find differences in air temperature, water temperature, distance to the edge or water depth among species. Males of *P. cicada* exhibited the largest niche breadth in the type of calling substrate (1.99) and distance to the edge (1.54), while *P. albifrons* males exhibited the largest niche breadth in water depth (1.64). However, the two species exhibited higher values of overlap than was expected by chance for all calling microhabitat descriptors, indicating that competition does not regulate the use of this resource (Table 3). The same result was found in the analysis with all descriptors of the spatial niche together (observed mean = 0.99; simulated mean = 0.56; p = 1.0). Kernel density analysis also indicated high overlap values for pond edge distance and water depth and absence of difference between observed and random overlap (Table 2, Fig. 1).

A total of 75 stomachs were analysed (15 from *P. albifrons* and 60 from *P. cicada*), and 1,653 consumed items were identified and counted. The diet of *P. albifrons* was composed of ten prey categories, with plant material (46.09), termites (47.56) and ants (21.95) representing the largest numeric proportion, and plant material (87.30), lepidopterans (27.23) and unidentified items (27.23) representing the largest volumetric proportion. Plant material (92.86) and ants (75.00) represented the largest occurrence frequency. The Relative Importance Index calculated without the presence of plant material, identified ants (34.74) and termites (30.83) as the most important items in the diet of *P. albifrons* (Table 4). A total of 16 prey categories were found in the diet of *P. cicada*, with collembolans (90.13), beetles (2.67) and plant material

Table 3. Frequency, niche breadth and niche overlap in calling activity of males of *Physalaemus albifrons* and *P. cicada* in temporary ponds in Cabaceiras, PB, Brazil. Sample sizes are in bold. Niche overlap values represent observed and simulated mean. *p* represents observed ≤ expected.

Microhabitat	*Physalaemus albifrons*	*Physalaemus cicada*
Substrate	**13**	**39**
Partially submerged in water	8 (61.5)	21 (53.8)
Partially submerged in water between vegetation	5 (38.5)	18 (46.2)
Niche breadth	1.90	1.99
Pianka niche overlap R2 *p = 0.82*	0.99 (0.83)	
Pianka niche overlap R3 *p = 0.50*	0.99 (0.97)	
Depth (cm)	**13**	**37**
0 – 3	10 (76.9)	29 (78.4)
4 – 7	1 (7.7)	–
8 – 11	–	–
12 – 15	1 (7.7)	1 (2.7)
16 – 19	–	1 (2.7)
20 – 23	–	2 (5.4)
24 – 27	–	1 (2.7)
Above 27	1 (7.7)	3 (8.1)
Niche breadth	1.64	1.60
Pianka niche overlap R2 *p = 1.00*	0.99 (0.47)	
Pianka niche overlap R3 *p = 0.94*	0.99 (0.20)	
Kernel density *p = 0.60*	0.70 (0.66)	
Pond edge distance (cm)	**13**	**39**
Internal		
0 – 50	11 (84.6)	31 (79.5)
51 – 100	1 (7.7)	1 (2.6)
101 – 150	0	1 (2.6)
151 – 200	1 (7.7)	1 (2.6)
above 200	0	5 (12.8)
Niche breadth	1.37	1.54
Pianka niche overlap R2 *p = 0.99*	0.98 (0.61)	
Pianka niche overlap R3 *p = 0.81*	0.98 (0.28)	
Kernel density *p = 0.92*	0.61 (0.59)	

Table 4. Diet and Importance Index of *Physalaemus albifrons* and *P. cicada* in temporary ponds in Cabaceiras, PB, Brazil. *N* = number of prey; *N%* = numerical percentage; *V* = volume of prey; *V%* = volumetric percentage; *F* = frequency of occurrence; *F%* = percentage of occurrence; *I* = Importance Index.

Prey categories	*Physalaemus albifrons*							*Physalaemus cicada*						
	N	*N%*	*V*	*V%*	F	*F%*	*I*	*N*	*N%*	*V*	*V%*	*F*	*F%*	*I*
Acari	–	–	–	–	–	–	–	7.00	0.45	0.14	0.09	4.00	8.00	2.85
Aranae	1.00	1.22	0.39	0.75	1.00	25.00	13.11	1.00	0.06	–	–	1.00	2.00	1.03
Un identified	4.00	4.88	14.16	27.23	2.00	50.00	27.37	23.00	1.46	0.06	0.04	18.00	36.00	12.50
Coleoptera	2.00	2.44	4.10	7.88	2.00	50.00	20.11	42.00	2.67	40.51	26.70	26.00	52.00	27.12
Collembola	–	–	–	–	–	–	–	1416.0	90.13	20.23	13.33	7.00	14.00	39.16
Lepidoptera	1.00	1.22	14.16	27.23	1.00	25.00	13.11	1.00	0.06	–	–	1.00	2.00	1.03
Isoptera	39.00	47.56	10.36	19.92	1.00	25.00	30.83	13.00	0.83	7.34	4.84	3.00	6.00	3.89
Formicidae	18.00	21.95	3.78	7.27	3.00	75.00	34.74	20.00	1.27	14.42	9.50	11.00	22.00	10.93
Orthoptera	–	–	–	–	–	–	–	2.00	0.13	6.99	4.61	2.00	4.00	2.91
Hymenoptera non ant	–	–	–	–	–	–	–	2.00	0.13	0.08	0.05	1.00	2.00	0.73
Insect larvae	15.00	19.29	5.05	9.71	2.00	50.00	26.00	8.00	0.51	0.01	0.01	5.00	10.00	3.51
Diptera	1.00	1.22	–	–	1.00	25.00	13.11	13.00	0.83	8.69	5.73	7.00	14.00	6.85
Lepidoptera larvae	1.00	1.22	–	–	1.00	25.00	13.11	3.00	0.19	45.35	29.89	3.00	6.00	12.03
Hemiptera	–	–	–	–	–	–	–	18.00	1.15	6.43	4.24	9.00	18.00	7.79
Pseudoscorpiones	–	–	–	–	–	–	–	2.00	0.13	1.47	0.97	2.00	4.00	1.70
Plant material	53.00	46.09	173.2	87.30	13.00	92.86	75.42	42.00	2.60	18.17	10.70	19.00	31.67	14.99
Numeric breadth				4.39							1.23			
Volumetric breadth				4.53							5.07			
N				15							60			

Table 5. Morphometry variables (mm) and results Principal Component Analysis (PCA) of 11 morphometry variables of *Physalaemus albifrons* and *P. cicada* from Cabaceiras, PB, Brazil. Values above parentheses represent mean ± standard deviation. Values in parentheses represent the minimum and maximum. In PCA, the variables are adjusted.

Variables	*Physalaemus albifrons* *n* = 19	*Physalaemus cicada* *n* = 105	Component I	Component II	Component III
Snout-vent length	26.3 ± 1.87 (22.5 - 29.3)	19.8 ± 3.29 (11.4 - 27.4)	0.1374	-0.1481	0.4571
Head length	7.7 ± 0.56 (6.7 - 8.7)	5.8 ± 0.69 (4.0 - 8.3)	0.2437	-0.0379	0.0078
Head width	9.2 ± 0.85 (7.5 - 11.3)	5.9 ± 0.89 (3.4 - 8.3)	0.0289	0.2090	0.0474
Eye-nostril distance	2.0 ± 0.21 (1.5 - 2.5)	1.7 ± 0.26 (1.1 - 2.5)	0.5458	-0.3319	-0.3223
Internarial distance	2.2 ± 0.18 (1.8 - 2.5)	1.6 ± 0.19 (1.0 - 2.0)	0.1681	0.1232	-0.5474
Inter-eye distance	4.7 ± 0.38 (3.5 - 5.2)	3.4 ± 0.44 (2.1 - 4.4)	0.1723	-0.0473	-0.1310
Thigh length	12.1 ± 0.78 (10.4 - 13.2)	8.0 ± 1.25 (4.9 - 10.7)	0.0377	0.1038	0.2904
Tibia length	11.3 ± 0.65 (10.1 -12.4)	8.1 ± 1.14 (4.8 - 10.2)	0.1223	-0.0598	0.2884
Foot length	17.5 ± 1.32 (14.8 - 19.5)	12.0 ± 1.82 (6.7 - 14.9)	0.0301	0.0166	0.3791
Tympanum diameter	1.3 ± 0.24 (0.8 - 1.8)	0.7 ± 0.22 (0.3 - 1.3)	-0.6997	-0.5258	-0.1877
Eye diameter	3.7 ± 0.37 (3.1 - 4.4)	2.2 ± 0.23 (1.5 - 2.8)	-0.2411	0.7171	-0.1471
Eigenvalue	–	–	0.0574	0.0368	0.0182
% variation explained	–	–	37.73	24.21	11.97

(2.67) being the items with the largest numerical proportions, and lepidopteran larvae (28.89), beetles (26.70) and collembolans (13.33) as those with the highest volumetric proportions. Beetles (52.00), plant material (31.67) and unidentified items (36.00) represented the largest occurrence frequency. The Relative Importance Index calculated without the presence of plant material identified collembolans (39.16) and beetles (27.12) as the most important items for *P. cicada.*

The analysis of niche breadth found that *P. cicada* had the largest volumetric niche breadth (5.07) and *P. albifrons* the highest numeric (4.39) and food niche breadth (4.46). Pseudocommunity analysis generated a mean observed overlap of 0.10 and a mean simulated overlap of 0.59, demostrating that the chances of the observed mean being equal to or less than the mean expected by chance was significant ($p <$ 0.0001), indicating that competition regulates food use. However, in spite of differences in sample size between species, we considered that the species with smallest sample (30 individuals) were enough to support our conclusions, being even higher that other similar studies published elsewhere (Parmelee, 1999, Menin et al. 2005, Leite-Filho et al. 2017).

Physalaemus albifrons (26.3 mm) presented a larger snout-vent length than *P. cicada* (19.8 mm) (Table 5). Principal Component Analysis revealed that the first and second components explained 63.5% of the total variance in the dataset (Table 5). The scatter plot generated from the first two components revealed morphological differentiation between the two species (Fig. 2). The first component was positively influenced by eye-nostril distance, head length and internarial distance, and negatively affected by tympanum diameter and eye diameter. The second component was positively influenced by eye diameter, head width and internarial distance, and negatively affected by tympanum diameter, eye-nostril distance and snout-vent length. The loadings and scatter plot revealed that *P. albifrons* have the wider head than *P. cicada.* The correlation between head size and length and width of prey revealed a significant effect on the first canonical correlation of both species (*P. albifrons*: $p < 0.00$; *P. cicada*: $p = 0.05$), showing an association between head size and prey size. However, the correlation was higher for *P. albifrons* than *P. cicada* (Table 6).

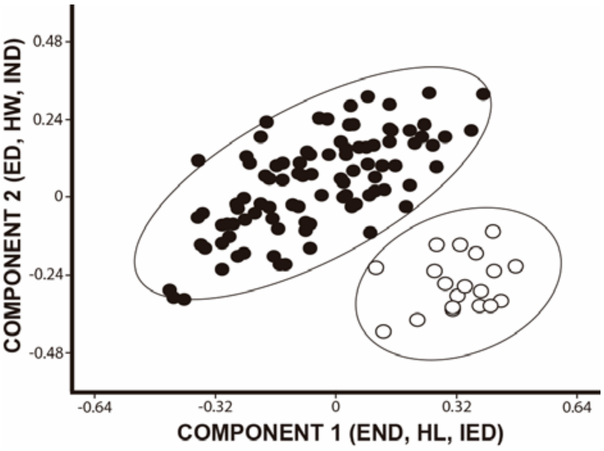

Figure 2. Mean of axes I and II from the Principal Components Analysis based on adjusted data for *Physalaemus albifrons* (white dots) and *P. cicada* (black dots) from Cabaceiras, PB, Brazil.

The advertisement call of *P. albifrons* was composed of a single multi-pulsed note and formed by a series of harmonics of the descending modulating frequency (Fig. 3). The mean duration was 372.6 ms (± 51.30 SD) and the mean dis-

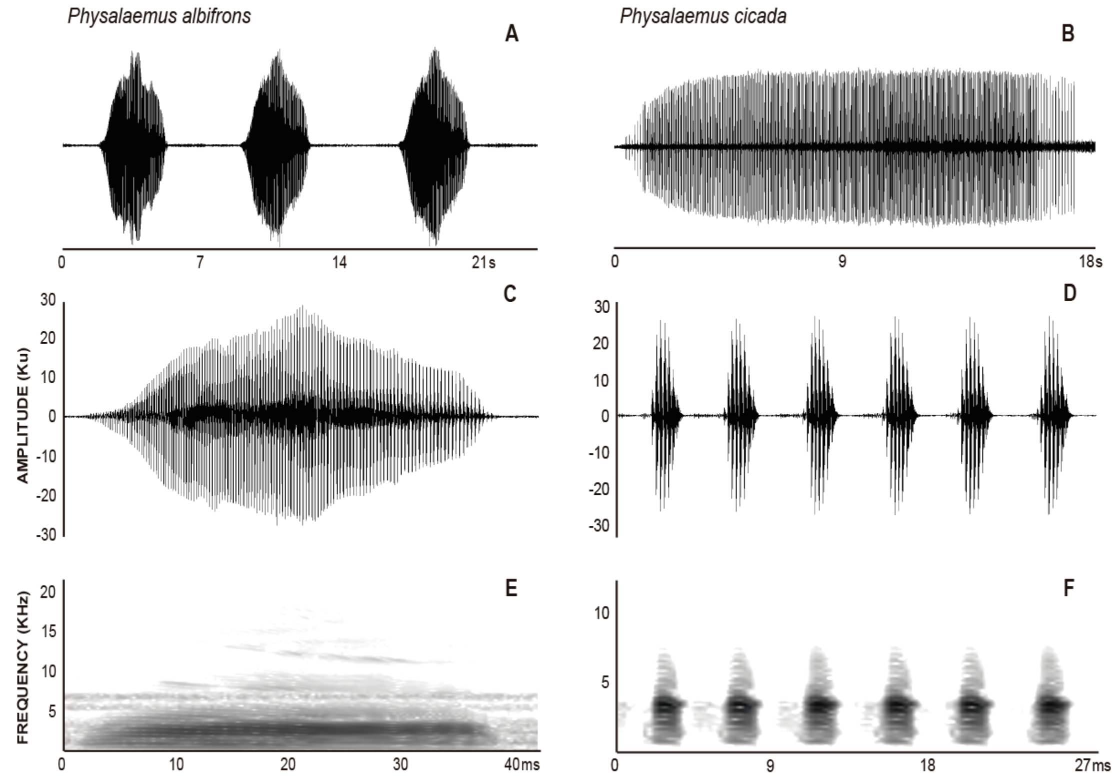

Figure 3. Advertisement call of *Physalaemus albifrons* and *P. cicada*. A and B – oscillogram; C and D – oscillogram with notes; E and F – spectrogram.

Table 6. Canonical correlation between prey size and head measurements of *Physalaemus albifrons* and *P. cicada* from Cabaceiras, PB, Brazil.

	Correlation Canonical	Eigenvalue	X^2	*GL*	*p*
		Physalaemus albifrons			
I	1.000	1.000	55.862	4	< 0.0001
II	0.921	0.849	2.836	1	0.0922
		Physalaemus cicada			
I	0.535	0.286	9.576	4	0.0482
II	0.195	0.038	0.994	1	0.3188

tance between calls was 706.0 ms (± 571.30 SD). However, during field activity we observed that the duration and distance between calls varied according to the abundance of calling males present in the chorus. The mean dominant frequency was 2918.4 Hz (± 155.6 SD), the mean fundamental frequency was 137.7 Hz (± 14.6 SD) and the average number of pulses per note was 134.6 (± 12.8 SD) (Table 7). In addition to the dominant frequency, two other frequency bands could be identified – one at around 8000 Hz and one at around 13000 Hz.

The call of *P. cicada* was a long trill composed of a series

Table 7. Acoustic parameters of *Physalaemus albifrons* and *P. cicada* from Cabaceiras, PB, Brazil and Mann-Whitney U test value. Values above parentheses represent mean ± standard deviation. Values in parentheses represent the minimum and maximum. * relevant variables in PCA.

Variables	*Physalaemus albifrons*	*Physalaemus cicada*	*Mann-Whitney U test*
	n = 4	*n* = 3	
Dominant frequency (Hz)	2840.9 ± 248.9 (2067.2 - 3100.8)	3429.6 ± 56.9 (3273.0 - 3617.6)	$p < 0.0001$*
Fundamental frequency (Hz)	167.6 ± 77.6 (110.4 - 433.4)	516.9 ± 45.1 (415.9 - 580.9)	$p < 0.0001$
Note/call	1.0 ± 0 (1.0 - 1.0)	371.6 ± 198.7 (30.0 - 915.0)	$p < 0.0001$*
Note duration (ms)	351.0 ± 71.9 (106.0 - 503.0)	20.8 ± 1.8 (13.0 - 27.0)	$p < 0.0001$
Call duration (ms)	351.0 ± 71.9 (106.0 - 503.0)	27321.0 ± 43034.5 (2198.0 -175730.0)	$p < 0.0001$
Call repetition rate (min)	48.57 ± 17.46 (12.0 - 77.0)	1.57 ± 0.8 (1.0 - 3.0)	$p < 0.0001$
Distance between calls (ms)	879.0 ± 663.6 (308.0 - 3796.0)	19067.3 ± 14648.0 (1003.0 - 48049.0)	$p < 0.0001$
Pulses/note	128.3 ± 20.2 (48.0 - 164.0)	8.0 ± 0.6 (5.0 - 10.0)	$p < 0.0001$

of multi-pulsed notes distributed at regular intervals (Fig. 3), with a mean of 371.6 (± 198.7 SD) notes per call. However, the initial and final notes showed a slight variation in amplitude and distance when compared to the more central notes. The mean duration of the notes was 20.8 ms (± 1.8 SD) and the mean call duration was 27321.0 ms (± 43034.5 SD), with the latter exhibiting highly variable durations. The mean distance between calls was 19067.3 ms (± 14648.0 SD); the lowest distance recorded was 1003.0 ms and the highest 48049.0 ms. The call had a harmonic structure with a dominant frequency range between 3273.0 Hz and 3617.6 Hz, with a mean of 3429.6 Hz (± 56.9 SD), and a fundamental frequency range between 415.9 Hz and 580.9 Hz, with a mean of 516.9 Hz (± 45.1 SD). The number of pulses per note ranged from 5 to 10, with a mean of 8.0 pulses (± 0.6 SD). Significant differences were identified in all acoustic variables, evidencing that the two species do not share the same acoustic space. However, additional analysis controlling the effect of colinearity between variables showed that component I of PCA explained 77.9% of the variation in the data set and the dominant frequency and number of notes per call were the most relevant variables in the separation between the two species (Table 7).

Discussion

Toads, frogs and tree frogs that coexist in the same environment typically display interactions that can involve several niche dimensions (Höld 1977, Rossa-Feres & Jim 2001, Bourn & York 2001). In tadpoles, the temporal partition appears to be the most important in relationships among species (Toft 1985). On the other hand, in adults, the spatial and acoustic partitions are considered the most relevant for the regulation of resource use and the main factors that guarantee coexistence (Toft 1985, Bernard & Anjos 1999, Cunha & Vieira 2004, Cajade et al. 2010). In the present study, *P. albifrons* and *P. cicada* showed high spatial and temporal overlap and partitioning of food and acoustic niches. Our results contradict the findings of the study by Kuzmin (1995), which argued that food partitioning is an unusual phenomenon in amphibians. In fact, it may be more common and significant than previously believed.

Despite the importance of food partitioning, analysis of all the individuals observed demonstrated a difference in the microhabitat niche breadth between species. The largest niche breadth in *P. cicada* was related with the substrate type due to land use, whereas the largest niche breadth in *P. albifrons* was related to water depth, which may be due to the frog's body size that enables it to occupy deeper layers in ponds. It is possible that the partition in the food niche observed between *P. albifrons* and *P. cicada* reflects the differences in microhabitat use, which can provide access to different prey spectra. Many studies that investigate the interaction between pairs of closely related species have reported the existence of a food niche partition (Duré & Kehr 2004, França et al. 2004, Macale et al. 2008). Mostly, this partition is often interpreted as being influenced by the space that the individuals occupy (Van Sluys & Rocha 1998, Duré & Kehr 2004, França et al. 2004). This perspective demonstrates the importance of the spatial niche for coexistence.

Although the smaller sample size of *P. albifrons* could biased our interpretations, analysis of prey composition of the two species demonstrated numerical and volumetric differentiation, which may be closely associated with the morphology of the species. *Physalaemus albifrons* demonstrated the largest breadth of the numeric, indicating highest consumption of few prey items, with their diet primarily composed of termites and ants. On the other hand, *P. cicada* demonstrated the largest volumetric niche breadth, indicating the consumption of larger prey, as evidenced by the frequency of large beetles. Variation in prey size was also observed between *Physalaemus gracilis* and *Physalaemus boligonigerus* in restinga habitats (Oliveira et al. 2015), and may be directly related to morphology. Animals with larger heads can consume prey of different sizes and usually display a larger volumetric niche breadth. Animals with small heads tend to eat smaller prey due to morphological constraints, and usually display a smaller niche breadth (Wells 2007, Sabagh et al. 2012). This relationship was observed by Rosa et al. (2011) in a study of the ontogenetic variation of *Boana pulchella*. These authors observed that an increase in the body size of individuals was related to an increase in the consumed prey size. Even though our results did not find a direct correlation between morphology and the volume of consumed items, the morphological differences observed between the two species suggest that morphology influences the size of prey consumed.

There is an evidence of a direct relationship in amphibians and reptiles between foraging strategy and dietary composition (Huey & Pianka 1981, Toft 1981, Vitt & Pianka 2005). Toft (1981) hypothesized that the diet of frogs that are active foragers may consist of more sessile, smaller and easier to manipulate prey, while sit and wait foragers may have a diet that consists of more mobile, soft-bodied and typically unwieldy prey. Despite this, the foraging behaviour can present a continuum of different types between foraging extremes or even reflect seasonal changes that are influenced by the abundance and prey behaviour (Toft 1980, Huey & Pianka 1981, Zug et al. 2001). We did not identify a clear relationship between foraging mode and the diet composition of *P. albifrons* and *P. cicada* suggesting that the two species present an intermediate foraging strategy. Although some families and species are recognised specialists in certain prey types (Toft 1985, 1995), amphibians are often considered to be opportunistic predators, in which diet composition depends on the prey availability in the environment (Almeida-Gomes et al. 2007, Sabagh et al. 2012). This interpretation helps to explain the diet composition of both species.

Physalaemus albifrons and *P. cicada* vocalised in the same period of the year, coinciding with increased rainfall, but demonstrated different acoustic attributes. This phenomenon has been reported by other researchers and enhances the importance of acoustic partitioning for the coexistence of closely related species (Fouquette 1960, Pombal 1997, Bourne & York 2001). In addition, the niche breadth of the different microhabitat descriptors exhibited similar values, with high overlap levels. For frogs, the use of reproductive habitats and microhabitats can be determined by phylogenetic constraints (Zimmerman & Simberloff 1996). Closely related species tend to use similar reproductive microhabitats, due to their evolutionary links (Eterovick et al. 2010). Both species exhibited reproductive mode 11 with the growth of exotrophic tadpoles in foam nests (Haddad & Prado 2005). In this way, the same physiological and behavioural requirements, determined by evolutionary history, are exhibited, which may explain the high levels of overlap observed in the field. Finally, our results suggest that the coexistence of *P. albifron*s and *P. cicada* is guaranteed by food and acoustic niche partitions, which may be associated with variations in body and head size.

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