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ECOSYSTEMS

Acoustic partitioning explains the coexistence between two *Physalaemus* species (Anura, Leptodactylidae) in the Atlantic Forest in Eastern Bahia State, Brazil

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Abstract: In this study we investigate the niche interaction between the frogs *Physalameus cuvieri* and *Physalaemus kroyeri* that occur in syntopy in water bodies of the Atlantic Forest located in the eastern Bahia State, Brazil. We investigated the niche width and overlap in the calling activity time, microhabitat use, diet composition, advertisement call, and body size. Both species preferred the same substrate and calling substrate categories, and showed low niche width values and high spatial niche overlap values. The pseudocommunity analysis revealed the absence of competition in space use. Ants and termites were the most important items in the diet of both species with the pseudocommunity analysis indicating an absence of competition in the diet. The two species demonstrate a greater similarity in body proportions and a high overlap in the calling activity time. However, they showed divergence in acoustic parameters, especially in the dominant frequency and call duration. Our results reinforce the role of advertisement call as a relevant attribute for anuran coexistence and highlight the importance of analyzing the various axes of the multidimensional niche for the most reliable description of the existence and magnitude of niche partitioning.

Key words: Advertisement call, diet, microhabitat use, niche partitioning.

INTRODUCTION

The main objective of investigating interaction levels between species in an assemblage is to identify the drivers, causes, and effects that interaction exerts on diversity, hence providing the basis for understanding the mechanisms that regulate the coexistence between species (Losos 1996, Holt 2001). In general, this research has focused on identifying the niche partitioning (structure) in the use of resources that involve a set of species from an assemblage (Arzabe et al. 1998, Rossa-Feres & Jim 2001, Leite-Filho et al. 2017). However, the presence or magnitude of the phenomenon may be more evident between the pairs of phylogenetically close species (França et al. 2004, Cajade et al. 2010, Jiménez & Bolaños 2012), allowing for the development of several hypothesis tests on the effects of competition or evolutionary history on promoting the microevolutionary processes that play a relevant role in maintaining diversity (Webb et al. 2002, Losos 2008).

Winemiller et al. (2015) highlighted that the spatial, trophic, life history, defense, and metabolic niche dimensions are the most relevant for measuring the interaction levels among species in an assemblage. In anurans, the spatial, trophic, and acoustic dimensions are considered as the most important for explaining the coexistence, and partition in the use of the habitat, microhabitat, prey composition or acoustic space has been often evidenced (Hödl 1977, Lima & Magnusson 1998, Parmelee 1999, Sinsch et al. 2012). Nevertheless, the richness and composition of species from an assemblage (Cardoso et al. 1989, Santos & Rossa-Feres 2007), the complexity of the habitat (resource availability) (Bernarde & Anjos 1999, Caldas et al. 2019), and the level of phylogenetic proximity between species (Protázio et al. 2015a, Caldas et al. 2019) can strongly affect the magnitude of resource partition among species.

In general, species with a close phylogenetic proximity are expected to have a high overlap in resource use because they have the same ecological and behavioral requirements due to their evolutionary linkage (Wiens et al. 2010). On the other hand, in saturated environments (high richness) and scarce resources, the pairs of phylogenetically close species may also show partitioning in some niche dimensions, thereby evidencing a niche complementarity (Santos & Rossa-Feres 2007, Sinsch et al. 2012, Protázio et al. 2019). Thus, niche complementarity can reduce the negative effects of interaction because it decreases the overlap levels and increases the chances of coexistence (Schoener 1974). Despite this, knowledge in terms of the way anurans share resources in assemblages has not yet been fully elucidated, which highlights the need for further investigations involving the different dimensions of the ecological niche for a more accurate interpretation of the mechanisms driving the phenomenon.

Physalaemus cuvieri and *P. kroyeri* (Figure 1) are two small frogs belonging to the Leptodactylidae family and Leiuperinae subfamily (Frost 2022). *Physalaemus cuvieri* has a wide distribution, present throughout the center and eastern Brazil and the eastern region of Paraguay, Argentina, and northern Uruguay (Lourenço et al. 2015, Frost 2022). On the other hand, *P. kroyeri* has a more restricted distribution, being endemic to Brazil, and can be found in the north of the State of Minas Gerais and in the states of Bahia, Paraíba, Piauí, and Pernambuco (Lourenço et al. 2015, Frost 2022). Both species belongs to the *P. cuvieri* species group, having as synapomorphy the persistence of ventrolateral gaps in the larval stage (Nascimento et al. 2005, Vittorazzi et al. 2014, Lourenço et al. 2015). In the adult phase, the two species show great behavioral, morphological, and ecological similarities using ponds, swamps, or lakes in open areas for breeding, with reproductive mode type 11 (Bokermann 1966, Haddad & Prado 2005).

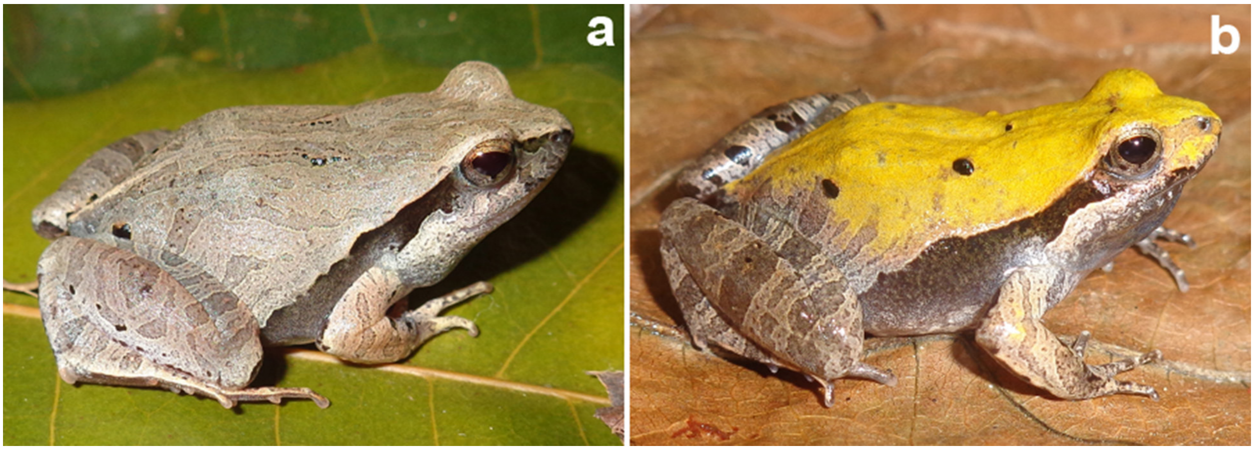

Figure 1. ***Physalaemus cuvieri*** **(a) and** ***Physalaemus kroyeri*** **(b) from Cruz das Almas municipality.**

The two species were found in syntopy in areas of Atlantic Forest in eastern Bahia State, showing a high overlap in the reproductive period, and also vocalizing synchronously in the same water bodies. Thus, they are excellent models for investigating how pairs of phylogenetically close species share resources involving different dimensions of the ecological niche. In this study, we investigated the niche relationship between syntopic populations of *P. cuvieri* and *P. kroyeri* in an area of the Atlantic Forest by analyzing the microhabitat use, prey composition, body size, advertisement call parameters, and calling activity time. Based on the hypothesis of niche partitioning involving some dimensions of the ecological niche, we aim to answer the following questions: (i) How do syntopic populations of *P. cuvieri* and *P. kroyeri* utilize resources in environments with high spatial (habitat) and temporal (reproductive period) overlap? (ii) Which dimensions of the multidimensional niche make coexistence between the two species possible?

MATERIALS AND METHODS

Study area

The study was conducted in Cruz das Almas municipality located in the eastern Bahia State, Northeast Brazil (Figure 2). Cruz das Almas is inserted in the Atlantic Forest Biome, in the region known as "Recôncavo Baiano," characterized by its original vegetation of Seasonal Semideciduous Forest (Brazão & Araújo 1981). However, this vegetation was strongly reduced to small isolated fragments of secondary vegetation or large open areas for pasture and plantation. According to the Köppen

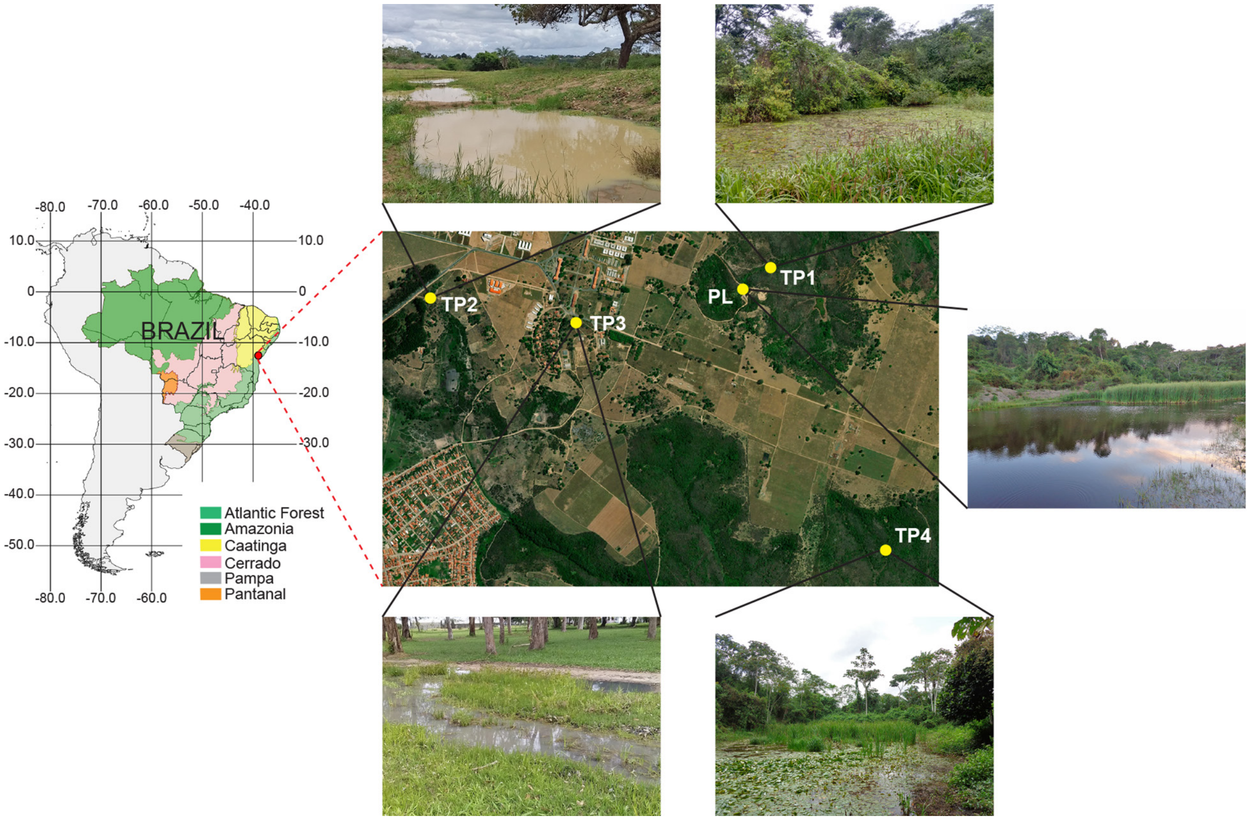

Figure 2. Localization map of Cruz das Almas municipality showing the five-body water studied. PL – Permanent Lagoon; TP1 – Temporary Pond 1; TP2 – Temporary Pond 2; TP3 – Temporary Pond 3; TP4 – Temporary Pond 4.

classification, the climate is tropical monsoon (Am), with annual precipitation of 1,131.2 mm and an average temperature of 23.9 °C (Silva et al. 2016).

Field activities were conducted from April 2015 to March 2019, totaling 20 sampling days. We sampled five different water bodies, where we observed individuals of *P. cuvieri* and *P. kroyeri* in simultaneous activity performed in the same space, evidencing a high temporal overlap:

i) Temporary pond 1 (12°39’29’’S; 39°04’48’’W) – It is located in a region known as “Mata da Cascalheira”, a secondary forest habitat surrounded by cultivated areas and pasture. The ponds originate right after the rains from the formation of a temporary stream;

ii) Temporary pond 2 (12°39’35.5’’S; 39°05’37.7’’W) – It is formed at the edge of an experimental plantation of eucalyptus (*Eucaliptus* sp.). The puddle is located on the campus of the Federal University of Recôncavo da Bahia in a peri-urban environment, and is formed soon after the first rains. It lasts for about two weeks, after which it dries out completely;

iii) Temporary pond 3 (12°39’43.5’’S; 39°05’113.6’’W) – It is formed on the side of a road. The pond is also located in the field of the Federal University of Recôncavo da Bahia in a peri-urban environment. This pond forms right after the first rains and lasts for about two weeks, after which it dries up completely;

iv) Temporary pond 4 (12°40’24.5’’S; 39°04’15.6’’W) – It is located inside a forest fragment known as “Riacho do Machado”. The pond lies just below a hillside region having a predominance of medium-sized trees and shrubs;

v) Permanente lagoon (12°39’36.8’’S; 39°04’41.8’’W) – It is located in the region known as “Mata da Cascalheira”. It is a body of water that is approximately 3 meters deep, with a predominance of reeds and macrophytes. The marginal vegetation comprises shrubs.

During field activities, other species engaged in the vocalization activity concomitant with those of *P. cuvieri* and *P. kroyeri*. Despite this, only *Leptodactylus macrosternum* was observed vocalizing in the same calling microhabitat used by *P. cuvieri* and *P. kroyeri*, but with a smaller number of individuals than the two *Physalaemus*. In addition, a single individual of the congener *P. albifrons* was also identified vocalizing together with *P. cuvieri* and *P. kroyeri*. However, because of the low sampling, *P. albifrons* was not included in our study.

Data collection

Field activities started at approximately 18:00 h and ended at 00:00 h, and were conducted by a minimum of three researchers. We used active and acoustic search to locate the individuals. All the collected specimens were euthanized with 2% lidocaine injection. They were then fixed with 10% formalin and stored in the Herpetological Collection of the Federal University of Recôncavo da Bahia (CHUFRB) (authorization SISBIO 46558-1 and 46558-2, and Ethics Committee on Animal Use of the Federal University of Recôncavo da Bahia – CEUA-UFRB 23007.007559/2016-71). In addition, we also analyzed the specimens of *P. cuvieri* and *P. kroyeri* housed at CHUFRB collected from the same study sites.

All individuals of *P. cuvieri* and *P. kroyeri* visualized had the used substrate (partially submerged, soil between vegetation, exposed soil, hole or emergent vegetation), the acoustic behavior (calling or silente), and the recording time registered for defining the spatial and temporal preference. We used the frequency data in each substrate category for calculating the spatial niche range using the inverse of Simpson’s (1949) diversity index:

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

From this index, values ranging from 1 (specialist) to the total number of substrate categories identified (generalist) are generated. The niche overlap in substrate type was also calculated with Pianka's (1973) equation:

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

The overlap values range from 0 (no overlap) to 1 (complete overlap). Subsequently, a pseudocommunity analysis was performed for checking the presence of non-random patterns in the substrate type between the two species. The pseudocommunity analysis is based on a null model and creates expected patterns in the absence of competition. Thus, the average observed overlap was compared with the simulated average for checking the presence of non-random patterns (Gotelli & Graves 1996). The pseudocommunity analysis was performed in EcoSim 7.0 (Gotelli & Entsminger 2007), using the type 2 randomization algorithm (RA2) with 1000 randomizations. Because reproductive males of anurans may show specificity for calling microhabitat, we also studied the relationship between calling males of *P. cuvieri* and *P. kroyeri*. We evaluated whether males exhibited partitioning in the calling substrate type to reduce the competition levels and allow for reproductive success, using the same parameters described above.

For the diet analysis, stomachs and intestines were removed by incision in the ventral region of the individuals (Parmelee 1999). Additionally, we also used stomach flushing for diet analysis, by following the protocol described by Solé et al. (2005). The food items were then analyzed in a Petri dish and observed under an Olympus SZ51 stereomicroscope. All items were identified to the taxonomic level of order, except ants, considered a separate prey category of Hymenoptera. All prey found in the gastrointestinal tracts were counted per individual to determine the numerical frequency (*NF%*). The prey that was intact had their length and width measured with digital calipers (accurate up to 0.01 mm) to establish the volumetric frequency (*VF%*), estimated using the ellipsoid formula:

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

Subsequently, the frequency of occurrence of prey category (*OF%*) was defined from the ratio between the total number of gastrointestinal tracts with prey category *i* divided by the total number of gastrointestinal tracts analyzed. Then, the relevant items in the diet of *P. cuvieri* and *P. kroyeri* were determined by calculating the importance index of each prey category using the formula:

$$I = \frac{NF\% + VF\% + OF\%}{3}$$

Finally, we calculated the niche width in the diet, food niche overlap, and performed a pseudocommunity analysis to check the presence of competition in the trophic niche using the same parameters described for the substrate type.

In total, 11 morphometric variables were measured using digital calipers (precision of 0.01 mm) and a stereomicroscope, following Napoli & Pimenta (2009): snout-vent length (SVL); head length (HL); head width (HW); eye-nostril distance (END); internarial distance (ID); intereye distance (IED); thigh length (THL); tibia length (TL); foot length (FL); tympanum diameter (TD); and eye diameter (ED). All morphometric variables were logarithmically transformed (Log10) to obtain normality. The effect size generated by isometric variation was reduced by the linear regression residuals by the creation of a "body size" variable, which represented 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 measured variables (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 generated residuals were retained. These residuals were used to create a new covariance matrix of the adjusted variables from the Principal Component Analysis. Simple regressions and Principal Component Analyses were conducted with the Past 4.01 software (Hammer et al. 2009).

The advertisement call of *P. cuvieri* and *P. kroyeri* were recorded with a Tascam DR-05X recorder coupled to a Yoga HT-320 unidirectional microphone at approximately 1 m of distance from the calling males, with a sampling rate of 44100 Hz and 16 bits of resolution. For each male recorded, a track of one-minute was analyzed in the program Raven Pro 1.5 (Lab of Ornithology, Cornell University), and produced spectrograms using the Discrete Fourier Transformation, with 256 samples, overlap 50%, Hann window type and window width 256. In the acoustic analysis, spectral parameters were obtained from the spectrograms, whereas temporal parameters were obtained from the oscillograms. We measured five acoustic parameters, following the definitions of Köhler et al. (2017): call duration (s), distance between call (s), call repetition rate (call/second), fundamental frequency (Hz), and dominant frequency (Hz). We followed the acoustic nomenclature of Hepp & Pombal (2020), who considered the advertisement call of the two species to be a continuous whine-like emission, nonpulsed, and having the presence of harmonics with downward frequency modulation at the beginning of the call and up-downward at the half or end.

Subsequently, we used the Kernel density function to calculate the distribution estimate of the advertisement call parameters between the two species. The Kernel density estimator is a nonparametric estimator used for continuous data with unknown distribution (Geange et al. 2011). In addition, we performed a permutation test of equality using 1000 randomizations with bootstrap. We also used the Kernel density function to calculate the estimated temporal distribution of the calling males, using the time of the acoustic report as descriptor. Additionally, Mann-Whitney U test was used to verify diferences in acoustic parameters of the advertisement call. The Kernel density estimation was performed in R software (R Core Team 2019), using the sm.density.compare function of the "sm" package (Bowman & Azzalini 2019), whereas the Mann-Whitney U test was performed in Past 4.01 software (Hammer et al. 2009).

RESULTS

Physalaemus cuvieri used four categories of substrate, whereas *P. kroyeri* used five substrate categories. Both species showed a preference for partially submerged substrate (Figure 3). The values and niche width of substrate type were low and similar between the two species (*P. cuvieri*: 1.49; *P. kroyeri*: 1.51). Calling males of both species showed a preference for vocalizing while staying partially submerged, indicating specialization on the calling substrate (*P. cuvieri*: 1.04; *P. kroyeri*: 1.00). Both species showed a high overlap in substrate (0.99) and calling substrate

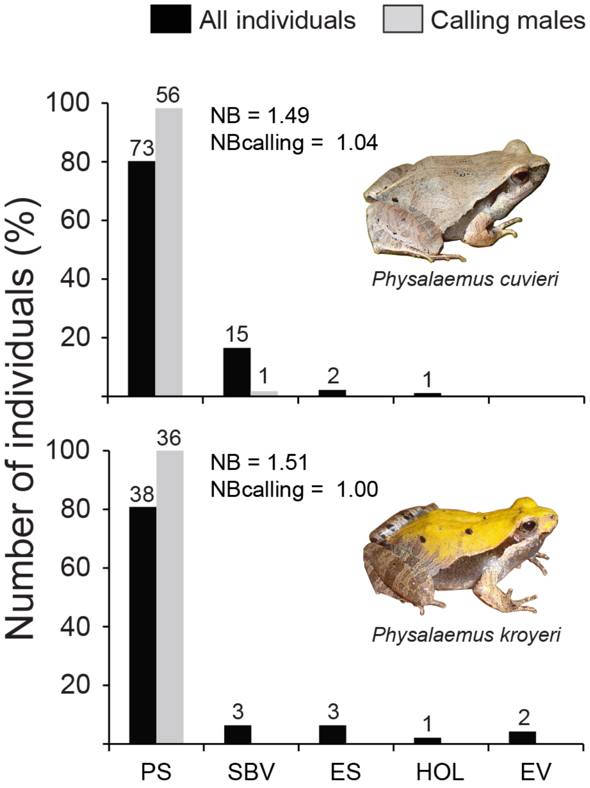

Figure 3. Substrate and calling substrate of *Physalaemus cuvieri* and *Physalaemus kroyeri*. PS: Partially submerged; SBV: Soil between vegetation; ES: Exposed soil; HOL: Hole; EV: Emergent vegetation. The value above bars represents the number of individuals. NB: niche breadth; NBcalling: niche breadth of the calling substrate.

(1.0). For the substrate, the pseudocommunity analysis revealed an observed mean of 0.99 and a simulated mean of 0.69, with the chance of the observed mean being lower than the expected mean not significant (*p* = 0.99), thereby indicating no competition. For the calling substrate, the pseudocommunity analysis revealed an observed mean of 1.0 and a simulated mean of 0.65, with the chance of the observed mean being less than expected also not significant (*p* = 0.99).

In the diet of *P. cuvieri*, eight prey categories were found. The most important items were ants (58.12) and termites (40.20) (Table I), whereas in the diet of *P. kroyeri*, seven prey categories were found with the most important items being termites (51.25) and ants (46.50). Numerical and volumetric niche width values were similar, with *P. cuvieri* (numeric breadth: 1.75) having numerical niche width values slightly higher than *P. kroyeri* (numeric breadth: 1.27). The overlap analysis revealed an average observed overlap of 0.92 and a simulated overlap of 0.51. The pseudocommunity analysis showed no competition in the food niche (*p* = 1.0). Because of the poor adjustment in the dispersion of the analyzed number of items per stomach (*P. cuvieri*: 4.77 ± 5.79; *P. kroyeri*: 7.22 ± 13.3), we refined our analysis by removing the effects of individuals that displayed as outliers (one *P. cuvieri* and three *P. kroyeri*). The new adjusted analysis promoted a better adjustment of the data for number of items per stomach (*P. cuvieri*: 3.25 ± 1.96; *P. kroyeri*: 2.35 ± 2.16) and revealed that the numerical and volumetric niche width values remained similar to the values of the previous analysis (*P. cuvieri*: numeric breadth = 1.68, volumetric breadth = 1.00; *P. kroyeri*: numeric breadth = 1.28, volumetric breadth = 1.0). Ants and termites were the most important preys in the diet of both species (*P. cuvieri*: 60.08, 33.33; *P. kroyeri*: 86.39, 3.19, respectively).

Physalaemus cuvieri (28.8 mm) showed a greater snout-vent length than *P. kroyeri* (22.9 mm) (Table II). The Principal Component Analysis revealed that the first and second components (PC) explained 59.11% of the variation in the data set. PC1 was positively influenced by the internarial distance and intereye distance and was negatively affected by tympanum diameter and foot length. However, PC2 was positively affected by tympanum diameter and intereye distance and negatively influenced by eye-nostril distance and eye diameter. Nevertheless, the observation of loadings and scatter plot revealed that *P. cuvieri* and *P. kroyeri* occupy the same morphometric space, evidencing a strong similarity in body proportions (Figure 4).

Table I. **Diets of *Physalaemus cuvieri* and *Physalaemus kroyeri* in Cruz das Almas municipality, Bahia State. N = numerical frequency, V = volumetric frequency, F = occurrence frequency, I = importance index.**

Categories	***Physalaemus cuvieri* (*n* = 38; empty: 25)**							***Physalaemus kroyeri* (*n* = 35; empty: 12)**						
	N	**N%**	**V**	**V%**	**F**	**F%**	**I**	**N**	**N%**	**V**	**V%**	**F**	**F%**	**I**
Acari	9	14.5	0.59	17.5	5	38.5	23.48	3	1.81	0.18	0.15	2	8.7	3.55
Araneae	–	–	–	–	–	–	–	1	0.60	–	–	1	4.3	2.48
Blattaria	1	1.6	–	–	1	7.7	4.65	–	–	–	–	–	–	–
Coleoptera	1	1.6	–	–	1	7.7	4.65	2	1.20	–	–	1	4.3	2.78
Isoptera	26	41.9	–	–	5	38.5	40.20	85	51.20	103.9	85.14	4	17.4	51.25
Mantodea	1	1.6	–	–	1	7.7	4.65	–	–	–	–	–	–	–
Orthoptera	3	4.8	–	–	2	15.4	10.11	–	–	–	–	–	–	–
Formicidae	14	22.6	2.79	82.5	9	69.2	58.12	70	42.17	17.99	14.73	19	82.6	46.50
Insect larvae	–	–	–	–	–	–	–	2	1.20	–	–	2	8.7	4.95
Unindentified	7	11.3	–	–	3	23.1	17.18	3	1.81	–	–	3	13.0	7.43
Numeric breadth	1.75							1.27						
Volumetric breadth	1.00							1.01						
Niche overlap *p* = 1.0	0.92 (0.51)													

The advertisement call of both species was formed by a single note (Figure 5). *Physalaemus cuvieri* showed a shorter advertisement call (0.297 ± 0.029 s) and shorter intercall interval (2.085 ± 2.067 s) than *P. kroyeri* (0.761 ± 0.076 s and 9.018 ± 4.814 s, respectively) (Table III). The advertisement calls had many harmonics and displayed a general downward frequency modulation at the beginning of the call. In *P. cuvieri*, most of the call energy was in the first harmonic, while in *P. kroyeri* most of the call energy was concentrated between the fourth and seventh harmonics. Subharmonics were present in the initial third of the advertisement call of *P. cuvieri*. The dominant frequency of *P. cuvieri* was lower (755.98 ± 68.36 Hz) than that of *P. kroyeri* (2,748 ± 228.23 Hz), and the fundamental frequency of *P. kroyeri* (539.6 ± 37.66 Hz) was lower than that of *P. cuvieri* (755.98 ± 68.36 Hz). The Kernel density analysis and the Mann-Whitney U test revealed differences in all parameters of the advertisement call, notably in call duration and dominant frequency, thus indicating partitioning in the acoustic niche (Table III, Figure 6). Contrarily, the analysis of the calling activity time of the males indicated a high overlap and lack of partition in the temporal niche.

DISCUSSION

In this study, *P. cuvieri* and *P. kroyeri* showed a high temporal, spatial, and feeding overlap, but a low acoustic overlap, thereby indicating

Table II. **Morphometric variables (mm) and Principal Component Analysis (PCA) of 11 morphometric variables of *Physalaemus cuvieri* and *Physalaemus kroyeri* from Cruz das Almas municipality, Bahia State, Brazil. Values above parentheses represent mean ± standard deviation. Values in the parentheses represent the minimum and maximum. In PCA, the variables are adjusted.**

	P. cuvieri **(n = 20)**	***P. kroyeri*** **(n = 36)**	**PC1**	**PC2**	**PC2**
Snout-vent length	28.8 ± 2.4 (20.7 - 32.2)	22.9 ± 2.7 (18.6 - 30.7)	0.008	-0.132	-0.074
Head length	8.7 ± 0.95 (7.0 - 10.5)	7.3 ± 0.68 (6.2 - 8.9)	-0.074	-0.269	-0.034
Head width	8.9 ± 0.55 (8.1 - 9.9)	7.6 ± 0.81 (6.1 - 9.1)	0.027	-0.114	-0.042
Eye-nostril distance	2.4 ± 0.26 (1.7 - 2.8)	2.1 ± 0.24 1.7 - 2.9	-0.117	-0.320	0.162
Internarial distance	1.9 ± 0.27 (1.5 - 2.4)	1.8 ± 0.31 (1.3 - 2.4)	0.775	0.254	0.466
Intereye distance	4.3 ± 0.42 (3.4 - 5.4)	3.5 ± 0.53 (2.3 - 4.5)	-0.002	-0.066	-0.124
Thigh length	12.9 ± 0.59 (11.8 - 13.6)	10.9 ± 0.97 (8.9 - 13.8)	-0.057	-0.089	-0.074
Tibia length	13.6 ± 0.58 (12.5 - 14.8)	11.3 ± 1.1 (9.5 - 14.2)	-0.128	-0.058	-0.188
Foot length	19.1 ± 1.12 (16.8 - 21.1)	15.4 ± 1.6 (12.7 - 18.6)	-0.540	0.708	0.321
Tympanum diameter	1.5 ± 0.22 (1.1 - 1.8)	1.4 ± 0.28 (0.93 - 2.2)	-0.121	-0.281	0.294
Eye diameter	3.2 ± 0.24 (2.7 - 3.8)	2.5 ± 0.34 (1.9 - 3.1)	0.230	0.368	-0.709
Eigenvalue	–	–	0.0057	0.0049	0.0025
% variation explained	–	–	36.24	22.87	13.29

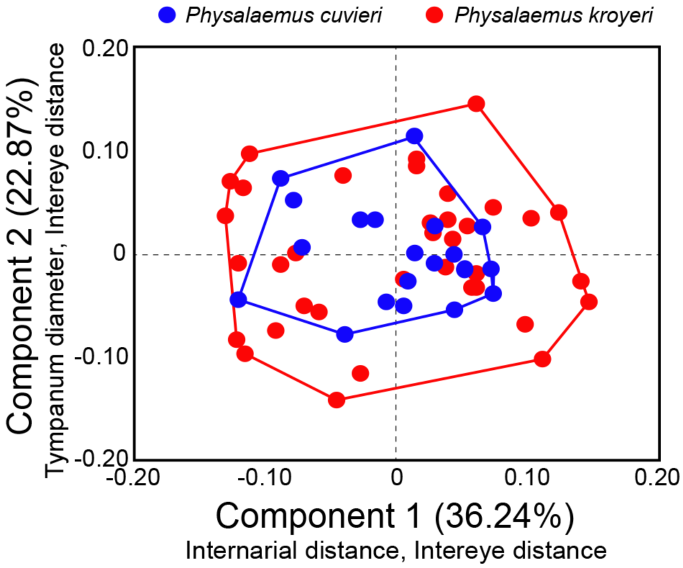

Figure 4. **Axes I and II of the Principal Components Analysis based on adjusted morphometric data for *Physalaemus cuvieri* and *P. kroyeri* from Cruz das Almas, Bahia State, Brazil.**

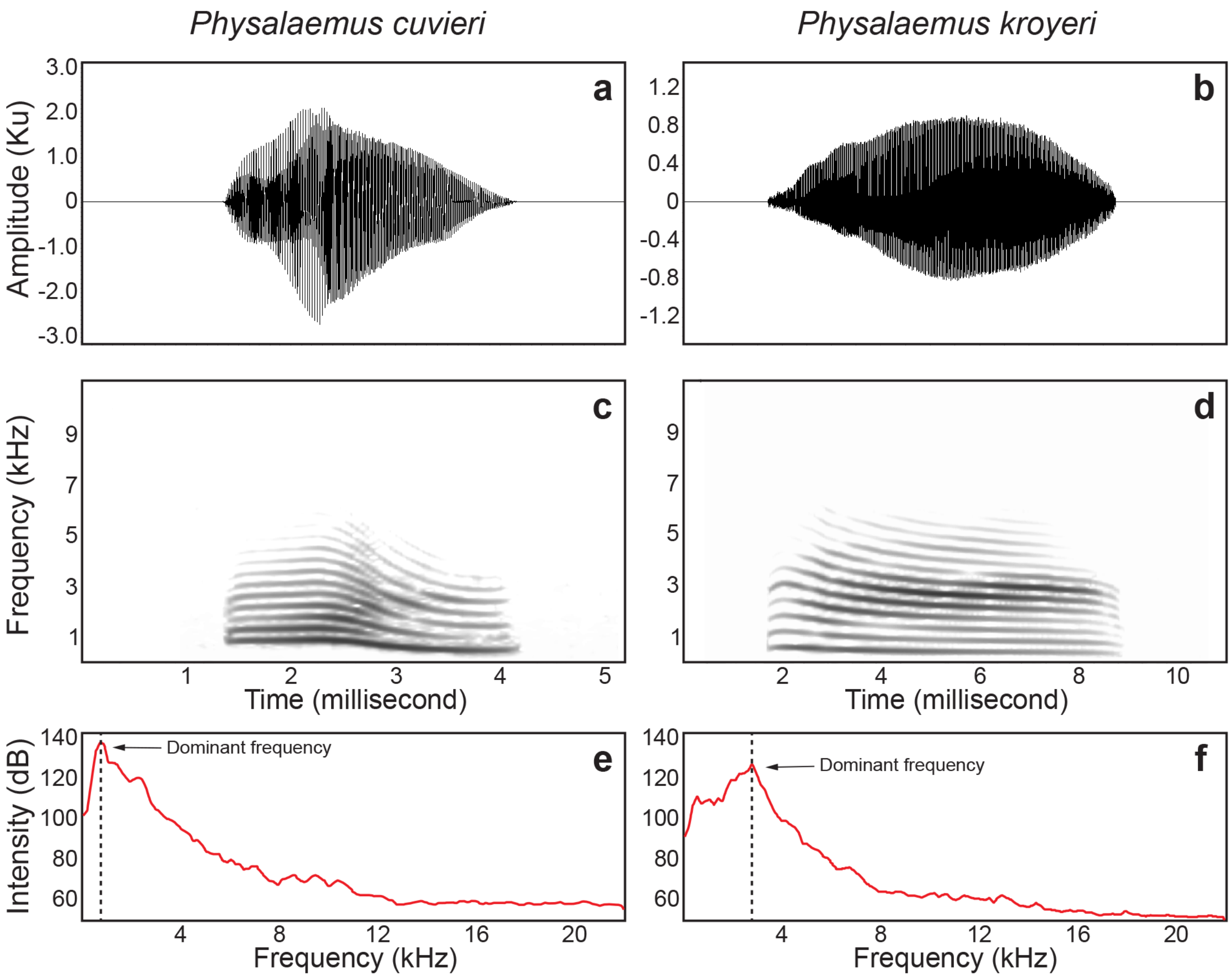

Figure 5. Advertisement call parameters of *Physalaemus cuvieri* and *Physalaemus kroyeri*. a–b: Oscillogram; c–d: Spectrogram; e–f: Power spectrum showing the dominant frequencies.

Table III. The advertisement calls of *Physalaemus cuvieri* and *Physalaemus kroyeri*.

	***Physalaemus cuvieri* (n = 8, *calls* = 80)**	***Physalaemus kroyeri* (n = 10, *calls* = 83)**	**Mann-Whitney U test**
Call duration (seconds)	0.297 ± 0.029 (0.251 - 0.330)	0.761 ± 0.076 (0.614 - 0.882)	*p* < 0.0001
Inter-call interval (seconds)	2.085 ± 2.067 (0.684 - 6.636)	9.018 ± 4.814 (4.719 - 17.32)	*p* < 0.0001
Fundamental frequency (Hz)	755.98 ± 68.36 (689.1 - 861.3)	539.96 ± 37.66 (538.0 - 572.0)	*p* < 0.0001
Dominant frequency (Hz)	755.98 ± 68.36 (689.1 - 861.3)	2748.56 ± 228.23 (2335.16 - 3273.00)	*p* < 0.0001
Call rate (call per minute)	32.62 ± 13.21 (10 - 46)	7.8 ± 2.97 (3 - 12)	*p* < 0.0001

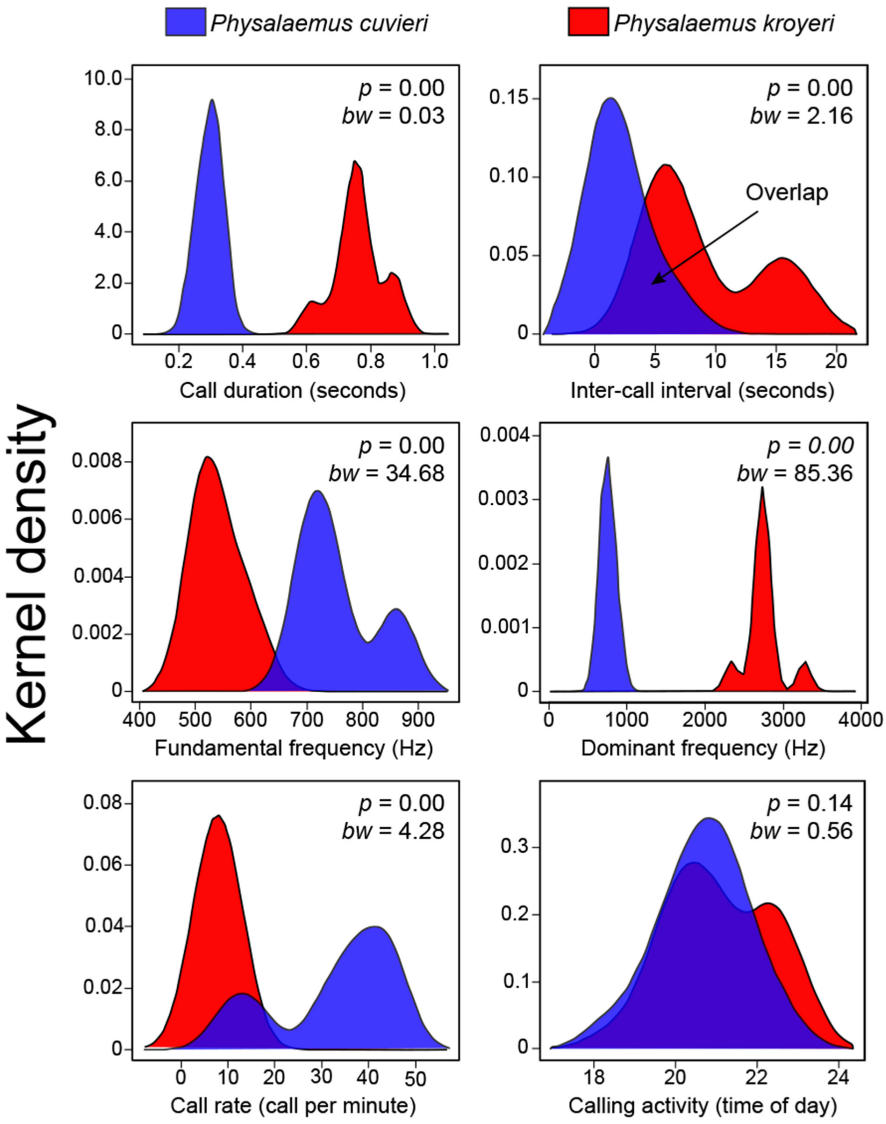

Figure 6. Plot of Kernel density estimate showing the acoustic space occupied for *Physalaemus cuvieri* and *Physalaemus kroyeri*. *p* is result of the permutation test of equality with 1000 randomization (bootstrap). Bandwidth (*bw*) is the mean of the optimal values for the normal distribution of the two groups.

that acoustic niche partitioning is relevant for the coexistence between the two leptodactylids. Many researchers have reported the existence of acoustic partitioning among anurans (Bourne & York 2001, Martins & Jim 2003, Santos & Rossa-Feres 2007, Silva et al. 2008, Protázio et al. 2015a, Bignotte-Giró et al. 2019), and it appears to be a much more common phenomenon than has been reported. However, previous studies that have shown the existence of acoustic partitioning among anurans have focused on the exclusive investigation of the interaction in the acoustic space, without considering the other niche dimensions (Duellman & Pyles 1983, Márquez et al. 1993, Pombal 2010, Lima et al. 2019), which may mask the real magnitude of the interaction and the dynamics of resource use across the different axes of the multidimensional niche.

On the other hand, it is possible that partitioning is reflected in other microhabitat descriptors, which help in reducing the overlap levels (Rossa-Feres & Jim 2001, Silva et al. 2008). Protázio et al. (2019) studied the niche interaction between two other *Physalaemus* species (*P. albifrons* and *Physalaemus cicada*) in the Caatinga of northeastern Brazil and identified differences in the distance to the pond edge and the in depth of the water column used by the two species. However, *P. albifrons* and *P. cicada* are not very similar in morphology, calls and behavior, which may explain the result found by the authors. A similar result was found in Argentina by Duré & Kehr (2004) who found that *Leptodactylus latinasus* prefer mud near ponds, whereas *Leptodactylus bufonius* preferred dry land, suggesting that partition identification may be associated with the scale of analysis and involve other descriptors of the spatial niche. In our study, only the advertisement call showed differences between the two species, reinforcing the role of the advertisement call as an important trait of niche interation.

In general, a negative relationship seems to exist between spatial niche overlap and acoustic niche overlap. Species with a high overlap in the acoustic space tend to show a low overlap in the spatial dimensions, whereas species with a high spatial overlap tend to show acoustic partitioning (Silva et al. 2008, Tárano 2010, Abrunhosa et al. 2014, Protázio et al. 2015a). This can drive to the interpretation of primary importance of space in the niche interaction (Cunha & Vieira 2004). However, our results reinforce the importance of the acoustic niche as a relevant ecological attribute in the interaction. We believe that in interactions involving closely related and sympatric species with acoustic communication, the acoustic dimension is more important than the spatial dimension. Because habitat and microhabitat use of anurans can be regulated by phylogenetic constraints (Zimmerman & Simberloff 1996), the high overlap in microhabitat use between the two *Physalaemus* species suggests a strong historical influence in the space use. *Physalaemus cuvieri* and *P. kroyeri* have type 11 reproductive mode with the development of exotrophic tadpole in foam nests (Haddad & Prado 2005). Hence, they must have the same behavioral and physiological requirements reflected in the preference for specific microhabitat (Ernst & Rödel 2006). This may explain the high values of overlap observed in substrate and calling substrate.

Anurans are often considered opportunistic predators, and their feeding may vary according to the availability of prey in the environment (Ceron et al. 2019). However, there is evidence of species that have preferential prey categories, which indicates different levels of specialization (Toft 1985). Yet, the feeding pattern observed in *P. cuvieri* and *P. kroyeri* suggests that both species exhibit an active foraging behavior, with direct search for food items (Parmelee 1999) that explains the striking coincidence of the presence of termites and ants as the most important items in the diet of both species. Other authors have also reported the presence of termites and ants as relevant items in the diet of other species of the genus *Physalaemus* in different biomes (e.g., *P. albifrons*, Protázio et al. 2019; *Physalaemus biligonigerus*, Oliveira et al. 2015; *Physalaemus centralis*, Marques-Pinto et al. 2019; *P. cicada*, Santana & Juncá 2007, Leite-Filho et al. 2015; *P. cuvieri*, Santos et al. 2004, Leivas et al. 2018, Caldas et al. 2019; *Physalaemus gracilis*, Moser et al. 2017; *Physalaemus lisei*, Moser et al. 2017), driving to the existence of a strong historical influence in the diet of the clade's species (Protázio et al. 2015b, Leivas et al. 2018).

However, there are previous research that showed the opposite, and evidenced the existence of food partition between pairs of species of the genus *Physalaemus*, as well as preference for prey categories other than termites and ants (Oliveira et al. 2015, Protázio et al. 2019). These findings suggests that behavioral (foraging behavior) and ecological factors (competition, predation risk, and prey availability) also strongly influence the interaction of different species of the clade in the food niche (Perry & Pianka 1997). Thus, the pattern in the food niche interaction observed between *P. cuvieri* and *P. kroyeri* from Cruz das Almas municipality may be peculiar to the study site, resulting from historical processes that operated in the community over a spatiotemporal scale (evolution, chances, dispersal limit, biotic, and abiotic filters) (Hillerislambers et al. 2012).

The evidence of acoustic partitioning observed between the two species strengthens the importance of advertisement call as a relevant attribute in the niche relationship and appears to be sufficient for ensuring the coexistence of the two *Physalaemus*. The differentiation in the advertisement call between the pairs of anuran species is recognized as relevant to avoid hybridization and ensure reproductive isolation (Fouquette 1960). Because the advertisement call presents a strong phylogenetic signal (Ryan & Rand 1999, Erdtmann & Amézquita 2009), the divergence in acoustic traits between the pairs of closely related and sympatric species can be interpreted as a shift of reproductive character (Blair 1974, Gerhardt 1994a). Thus, variations in the parameters of advertisement call appear to reflect an evolutionary adjustment of the signal as an attempt to avoid or reduce acoustic interference from neighboring heterospecific males (Chek et al. 2003).

Acoustic partitioning among anuran species appear to be reflected in divergences in the dominant frequency and in the call duration of species that present a high spatial and temporal overlap, as observed by Salas et al. (1998). This result agrees with our findings: *P. cuvieri* and *P. kroyeri* showed a marked differentiation in the call duration and dominant frequency. Dominant frequency is considered a static acoustic trait, shaped by stabilizing selection, and with an important role in the species recognition, in the reproductive isolation and sexual selection (Gerhardt 1994b, Nityananda & Bee 2011), whereas call duration plays an important role in female preference and also sexual selection (Wilczynski et al. 1999, Gerhardt & Brooks 2009). Thus, the acoustic divergence observed between *P. cuvieri* and *P. kroyeri* may allow both the recognition of males by the female and the selection of those with the best fitness.

Finally, partitioning in the acoustic signal can operate by involving multimodal channels, with a synergy of several biological aspects that not only involve interaction (Gerhardt 1994b). For example, males can alter their position to improve the reception of a specific signal or even alter the timing of their call to avoid temporal overlap (Schwartz & Wells 1983, Chek et al. 2003). Thus, we believe that the acoustic partitioning observed between *P. cuvieri* and *P. kroyeri* may involve other aspects of the advertisement call of both species. However, approaches considering the varying degrees of different ecological traits of sympatric and allopatric populations of the two species may help define the real importance of the advertisement call in the interaction. Our results reveal that acoustic niche partitioning is an important mechanism of niche segregation, and seems to be of primary importance to avoid hybridization and reduce competition for food and space, ensuring co-occurrence of the two species in the studied ponds.

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Author contributions

HSNB conceived the study, collected and analyzed the data, interpreted the results and wrote the manuscript; MVSAV collected the data and contributed to the final version of the manuscript; TAFS collected the data and contributed to the final version of the manuscript; AiSP interpreted the results and contributed to the final version; ArSP idealized the study, collected and annalysed the data, interpreted the results and wrote the manuscript.