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Spatial and temporal organization in three syntopic species of the *Scinax ruber* group (Anura: Hylidae) in the Atlantic rainforest, southeastern Brazil

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Coexistence of anuran species might lead to acoustic interference among communications, especially where species are closely related. This problem might be minimized through resource partitioning. To test this idea, we analysed calling with respect to temporal and physical space usage in three syntopic, closely related species (*Scinax cuspidatus*, *Scinax* aff. *hayii* and *Scinax* aff. *x-signatus*) in a temporary pond in the Atlantic rainforest. The chorus attendance of each species resulted from a different combination of factors in the rainy season. Although there was some temporal overlap of daily activity among species, peak activity time differed, particularly between the two species whose calls were most similar. Although all three species tend to aggregate in open microhabitats, their coexistence is apparently facilitated by differential use of vertical strata and organization of calling sites near the sites of conspecifics. Together, these factors apparently reduce acoustic interference among heterospecific calls.

Keywords: advertisement call; resource partitioning; *Scinax*; spatial distribution; temporal distribution

Introduction

Studies on anuran communities in the Atlantic rainforest, with focus on the spatial and/or temporal distribution of species and resource partitioning, have increased in the last 15 years (e.g. Rossa-Feres and Jim 1994, 1996; Pombal 1997; Bertoluci 1998; Bertoluci and Rodrigues 2002; Pombal and Haddad 2005; Prado and Pombal 2005; Abrunhosa et al. 2006). A general tendency observed is that coexisting species tend to use environmental resources differently (Donnelly and Guyer 1994; Pombal 1997; Garcia-Rutledge and Narins 2001; Gillespie et al. 2004; Gottsberger and Gruber 2004; Abrunhosa et al. 2006). Such a partition can be explained either ecologically or historically. From an ecological perspective, resource partitioning could result in character displacement caused by interspecific competition. An alternative, historical explanation would consider the phylogenetic history of the species considered. Distinguishing which explanation better describes what is structuring a community

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*Corresponding author. Email: pabrunhosa@gmail.com and quantifying the importance of each factor, represents the core objective for community ecologists (Brooks and McLennan 1991).

When one asks the question "what guarantees the coexistence among sympatric and closely related species?", the investigator assumes the importance of historical factors influencing community structure. Because a group of closely related focal species have a similar evolutionary history, they should share a number of morphological, physiological and behavioural characteristics. If closely related species occur in sympatry and syntopy, they should be involved in a vast array of interactions, because they tend to use resources more similarly than non-related species (MacNally 1979; Schwartz and Wells 1983, 1985; Given 1990). Any possible differences in resource use by them should be better explained ecologically.

In anuran communities, acoustic communication plays an important role in social interactions (Wagner 1989). Accordingly, one expectation is that in larger aggregates of different species, the acoustic interference should be considerably higher than in smaller ones (Wollerman and Wiley 2002). Therefore, in seasonal tropical communities, where breeding activities of several species are concentrated in the warm and rainy season, simultaneous conspecific and heterospecific calls must generate significant background noise, which is a potential problem for efficient intraspecific communication (Gerhardt and Huber 2002).

Several mechanisms have been noted as important to attenuate such acoustic interference among species. Included are divergence in the acoustic properties and changes in behaviour and ecological traits of the species (Gerhardt and Schwartz 1995), making signal transmission more efficient. Evidence includes: (1) differences in the use of time on a seasonal scale (days or months) or on a daily scale (hours); (2) the temporal fine adjustment on call rate (e.g. vocalization in antiphony: seconds or milliseconds); (3) differences in acoustic space use (e.g. dominant frequency of the call); and (4) differences in physical space use, including microhabitat selection and spatial distribution pattern (Hödl 1977; Littlejohn 1977; Schwartz and Wells 1983; Gerhardt and Schwartz 1995; Garcia-Rutledge and Narins 2001; Gerhardt and Huber 2002; Abrunhosa et al. 2006).

Here we report on ecological aspects and behavioural mechanisms associated with attenuation of interference among three species of the genus *Scinax* that reproduce in a temporary pond of the Atlantic Forest of the State of Rio de Janeiro. *Scinax cuspidatus*, *Scinax* aff. *x-signatus* and *Scinax* aff. *hayii* are included in the same clade of the *Scinax ruber* species group (*sensu* Faivovich 2002), and their calls are similar in structure and frequency. Their advertisement calls are pulsed with total or partial overlap of dominant frequency (see Pombal et al. 1995a for *S. cuspidatus*; and the present study). In the Reserva Biológica União, State of Rio de Janeiro, southeastern Brazil, these species are sympatric and occur in syntopy. Based upon the premise that call is one of the most important specific recognition factors (e.g. Hödl 1977; Schwartz 1987; Márquez et al. 1993; Pombal 1997), and its specificity is an efficient mechanism of reproductive isolation, it is expected that among syntopic and closely related species some kind of partitioning: of the acoustic, physical and/or temporal space will occur. The aims of this study are: (1) evaluate the level of acoustic similarity among *S. cuspidatus*, *S.* aff. *hayii*, and *S.* aff. *x-signatus*; (2) verify whether acoustic activities are temporally partitioned; (3) examine the influence of environmental variables on the reproductive activity of each species; (4) verify whether spatial portioning occurs between species; (5) analyse the influence of social variables on the spatial distribution of each species; and (6) examine how the species are spatially organized in a temporary pond of the Atlantic rainforest, southeastern Brazil.

Materials and methods

Study area

The study was conducted in a temporary pond (22°25'03″ S, 42°02'10″ W) in a clearing area located at the Reserva Biológica União (ReBio União), in the Atlantic Forest domain (Ab'Saber 1977), Municipality of Rio das Ostras, State of Rio de Janeiro, southeastern Brazil. ReBio União is the largest continuous coastal lowland forest in Rio de Janeiro state. The reserve has a total area of 3126 hectares, of which 65% is dense rainforest. The study site has an area of approximately 650 m^2 and a very heterogeneous physiognomy, from open areas with little emergent vegetation to areas with much shrub and trees. The adjacent forest is well preserved.

Data collection

Fieldwork was conducted monthly from September 2002 to May 2003 and from August 2003 to July 2004. Each visit usually lasted seven consecutive nights, which resulted in 97 nights and 473 hours of observation. Fieldwork started before sunset (at about 5 p.m.) and finished when the activity of the studied species ended, except for five nights when we recorded the temporal distribution of the species on a nightly scale, and fieldwork lasted the whole night.

Nine environmental variables were measured daily at the study site: daytime weather condition, night-time weather condition, 1-night previous weather condition, 2-night previous weather condition, pond depth (cm), maximum air temperature (°C), mean air temperature (°C), minimum air temperature (°C) and air humidity (%). The weather condition was a categorical measure: 1 = no rain, 2 = drizzle, 3 = rain, 4 = heavy rain. Mean air temperature was measured at 9 p.m. with a mercury thermometer to 0.5°C precision, and the values of minimum and maximum air temperature, and air humidity were obtained with an alcohol thermo-hygrometer; both measures were taken at about 1.50 m height above the ground. The monthly precipitation was collected and provided by the *Programa de Translocação da Associação Mico-Leão-Dourado*.

Call recording and analysis

The calls were recorded during a 1-minute sequence using a Marantz PMD 222 professional cassette recorder with a unidirectional Le Son SM-48 microphone held at 50 cm from the calling male. After the call of a male was recorded, the individual was captured, toe-clipped (see Martof 1953), measured to the nearest 0.1 mm with callipers, weighed (body mass was taken to the nearest 0.1 g with a mechanical balance), and immediately released at the same site. Air temperature was also recorded after each recording session.

Vocalizations were analysed using a Pentium PC at a sampling frequency of 22.05 kHz, 16-bit resolution, using the software Avisoft-Sonagraph Light 1 (Berlin, Germany) and Sound Ruler Version 0.9.4.1 (Gridi-Papp 2003–2007). Call terminology follows Duellman and Trueb (1986).

Eight acoustic parameters of the advertisement calls were measured: call rate (number of calls per minute), call duration (s), call interval (s), pulses per call, peak time (s) (Tárano 2001; time from the beginning of the call to the point of maximum amplitude), proportional rise time (ratio between peak time and call duration, which provides an envelope form: linear, exponential or inverse exponential; see Gerhardt 1998), frequency modulation (kHz; difference between the final dominant frequency and the initial dominant frequency) and dominant frequency (kHz). Waveforms and power spectra were produced using the Sound Ruler Version 0.9.4.1, and sonograms were produced using the Avisoft-Sonagraph Light 1 software (FFT = 256 points; $O = 87.5$; Hamming window).

We performed discriminant function analysis to test for differences among the calls of *S. cuspidatus*, *S.* aff. *hayii,* and *S.* aff. *x-signatus* and to identify the acoustic parameters that contribute to this differentiation.

Temporal distribution

Temporal distribution of the species was considered on a nightly and a seasonal scale. To evaluate the reproductive period of each species on a seasonal scale, we recorded the period when males were calling, presence of gravid females and pairs in amplexus. To evaluate the time spent by males in calling activity (nightly scale), we counted the number of males acoustically active for each species at each hour, during the whole night ($n = 5$ nights).

The temporal reproductive pattern of each species was defined according to the time spent by individuals of that species attending the chorus in the pond. Therefore, each of the species was classified as either a prolonged, opportunistic or explosive breeder (*sensu* Abrunhosa et al. 2006). Choruses were arbitrarily defined as three or more individuals calling.

In order to examine whether specific choruses differed among species in relation to environmental variables, we performed a covariance analysis (Zar 1999). A multiple regression analysis (Forward Stepwise; Zar 1999) identified the relationship among the environmental variables and the chorus attendance, and among the environmental variables and the number of calling males for each species. We investigated possible differences among the three species with regard to the initial time and end of the calling activity, chorus duration and activity peak (the time when the largest number of males present at the pond was calling) using multivariate analysis of variance (MANOVA; Zar 1999). To assess whether the presence of the three species of *Scinax* alters the calling activity time of each species, influencing the degree of activity overlap in activity times, we analysed these data using two different conditions: (1) nights when only one species formed a chorus and (2) nights when the three species were heard calling.

Spatial distribution

We measured quantitative and qualitative variables relating to five pond microhabitats to evaluate differences among them. Quantitative variables measured were as follows: depth of the water column in cm, measured at the edge and the centre of the microhabitat; percentage of the canopy cover at the centre of the microhabitat and area of the microhabitat in m^2; and qualitative variable was the type of vegetation dominant in the area (if grass, herbaceous, shrub and/or arboreal vegetation). Five sampling points were randomly selected each month during the year to measure pond depth at the edge and centre of the microhabitat. Canopy cover percentage was quantified according to the number of quadrants (a grid of 30 × 30 cm, divided into 100 quadrants) occupied by the vegetation. To test for differences between the microhabitats we used analysis of variance. Data measured in percentage were transformed (arc-sin) for this analysis.

To evaluate the spatial distribution of each species and their possible microhabitat selection, we marked points of reference at 1-m intervals along the whole pond with adhesive plastics. Quantitative measures of calling sites were taken: height from the water surface (cm), point of capture according to the adhesive plastics, and microhabitat type. We used the ratio between proportion of males found in each microhabitat and the proportion of the area of each microhabitat (in relation to the total area of the pond) because the size of each microhabitat was not similar.

To evaluate the influence of other species on the microhabitat selection and vertical occupation by each species, we considered the different states observed for that species (if calling in the presence or absence of one or two congener species). Each state was defined as a different species condition: only males of *S. cuspidatus* calling; only males of *S.* aff. *hayii* calling; only males of *S.* aff. *x-signatus* calling; males of *S. cuspidatus* + *S.* aff. *hayii* calling; males of *S. cuspidatus* + *S.* aff. *x-signatus* calling; males of *S.* aff. *hayii* + *S.* aff. *x-signatus* calling; males of *S. cuspidatus* + *S.* aff. *hayii* + *S.* aff. *x-signatus* calling.

We performed analyses of variance (ANOVA; Zar 1999) to test for differences in the distribution of each species among the different microhabitats and among the heights of the calling sites. To examine the possible social influence in the calling site height occupied by each species, we conducted a Student's *t*-test.

The spatial distribution pattern of each species (if random, uniform or aggregated) was tested by the Poisson distribution using variance-to-mean ratio test (see Brower and Zar 1984). We plotted on a schematic map the positions of actively calling males under a variety of conditions for each species: (1) presence of only one species, (2) presence of two species, and (3) presence of all species. According to the variance-to-mean ratio, a value of the coefficient of dispersal (I) < 1.0 indicates uniform distribution and $I > 1.0$ indicates aggregated distribution. The chi-squared test was used to assess the level of significance of the observed dispersion coefficients.

Statistical treatment

All data were tested for normality and homogeneity of variances and non-parametric tests were used when these assumptions were not met. In some cases, data were log-transformed to meet basic assumptions of the parametric tests. Descriptive statistics are given as mean ± standard deviation (range) (n).

Results

Climate was seasonal. The hydroperiod of the pond fluctuated according to rainfall, whereas air temperature varied between seasons with low values during the dry period

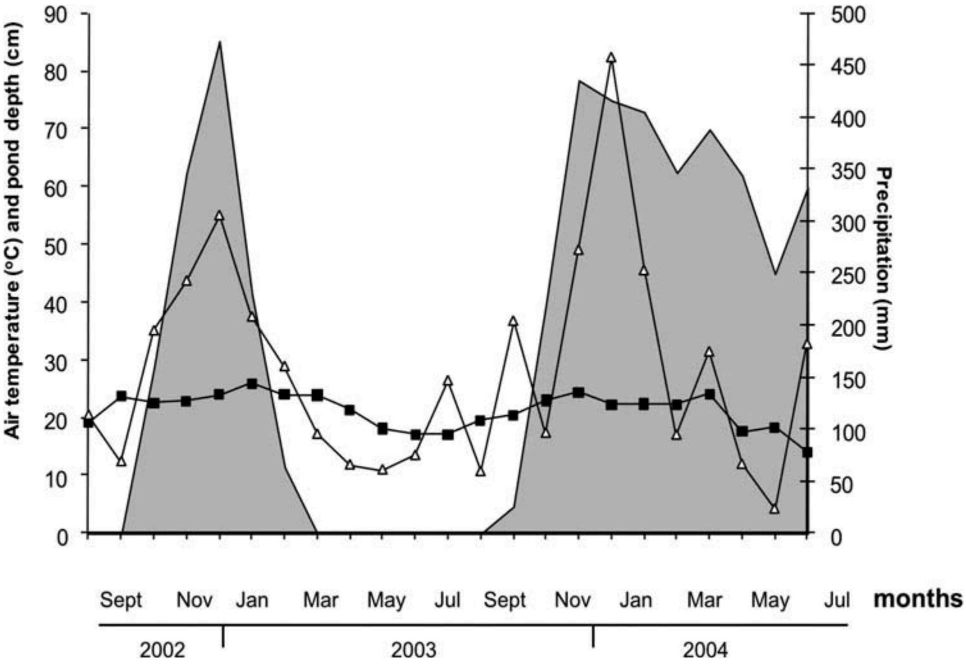

Figure 1. Mean air temperature (square), mean pond depth (grey area), and monthly precipitation (triangle) at the study site, ReBio União, Rio de Janeiro, Brazil from September 2002 to June 2004.

(from May to September) and high values during the rainy period (from December to February) (Figure 1).

Acoustic parameters

Table 1 shows a descriptive summary of the acoustic parameters of the advertisement calls of *S. cuspidatus*, *S.* aff. *hayii*, and *S.* aff. *x-signatus*.

The advertisement call of *S. cuspidatus* (Figure 2A, B) is a pulsed note. Pulses are regularly spaced and the mean duration of the last one is twice (0.04 ± 0.003; n = 10) as long as the others (0.02 ± 0.003; n = 10) (Figure 2A). Call duration is positively correlated with the number of pulses per call (r = 0.90; p = 0.001; n = 334) and call interval and call rate are highly variable (range = 3.3–37.6 s; range = 2–85 calls per minute, respectively). The call has an ascendant-linear envelope form (Figure 2A). The call has sidebands (Figure 2B) and the dominant frequency can vary among the three first bandwidths (from a total of four to five bands). The first bandwidth (72%; n = 334) is the most common dominant frequency, followed by the third (14%; n = 334). Some calls had the first two bandwidths with the same energy concentration (11%; n = 334). The call is not frequency modulated (t = –1.32; p = 0.20; n = 10 individuals).

The advertisement call of *S.* aff. *hayii* (Figure 2C, D) is composed of a pulsed note, repeated at very variable intervals (range = 0.2–15.3 s), with a mean of 10 calls per minute (n = 9). Call duration is positively correlated with the number of pulses

Table 1. Acoustic parameters of the advertisement call of *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus*.

	Scinax cuspidatus	*Scinax* aff. *hayii.*	*Scinax* aff. *x-signatus*
Call duration (s)	0.20 ± 0.02 (0.14–0.27) (334)	0.25 ± 0.04 (0.14–0.36) (56)	0.13 ± 0.01 (0.10–0.18) (160)
Call interval (s)	2.16 ± 1.84 (0.34–37.60) (328)	3.50 ± 3.56 (0.60–23.97) (44)	0.93 ± 0.50 (0.25–15.31) (160)
Number of pulses	9 ± 1 (6–14) (334)	7 ± 1 (5–11) (56)	4 ± 1 (3–4) (160)
Dominant frequency (kHz)	2.38 ± 0.08 (2.09–2.54) (334)	3.30 ± 0.24 (2.77–3.72) (50)	2.83 ± 0.12 (2.52–3.38) (160)
Frequency modulation (kHz)	0.05 ± 0.05 (0.05–0.10) (50)	0.47 ± 0.31 (0.19–0.84) (20)	0.20 ± 0.09 (0.10–0.38) (50)
Envelope form	0.57 ± 0.08 (0.32–0.88) (50)	0.87 ± 0.04 (0.69–0.96) (20)	0.83 ± 0.12 (0.51–0.93) (50)
Call rate	33 ± 22 (2–85) (36)	10 ± 5.11 (4–19) (9)	57 ± 16 (25–84) (16)
Number of individuals recorded	36	9	16

Note: Results are presented as mean ± standard deviation, (range), and (n).

per call (r = 0.84; p = 0.004; n = 56). Pulses are regularly spaced and similar in duration (Figure 2C). The call shows amplitude modulation, with very little intensity in initial pulses and final pulses with a peak of amplitude, characterizing an ascendant-exponential amplitude modulation (Figure 2C). The call structure comprises a dominant frequency bandwidth around 3.3 kHz and sidebands, which is less evident above and below this range (Figure 2D). The initial dominant frequency is different from the final dominant frequency (t = –2.66, p = 0.04, n = 5 males), featuring a call frequency modulation of about 0.5 kHz. However, this modulation is evident in each pulse of the call in a similar way, and does not appear as a gradual increase in frequency over the call.

The advertisement call of *S.* aff. *x-signatus* (Figure 2E, F) is composed of a pulsed note, regularly emitted at intervals of 0.9 s, totalling 57 calls per minute. The duration of the call is positively correlated with the number of pulses per call (r = 0.90, p < 0.001, n = 160). The number of pulses per call varies between three and four; they are regularly spaced and similar to each other with regard to duration (Figure 2E). The call shows an ascendant-exponential amplitude modulation, with peak amplitude in the third or fourth pulse (Figure 2E). The mean dominant frequency of the call is 2.8 kHz. Sidebands are visible, appearing below and above the dominant frequency bandwidth (Figure 2F). Although not visually detected in the sonogram (Figure 2F), the initial and final dominant frequencies were significantly different (t = –2.94,

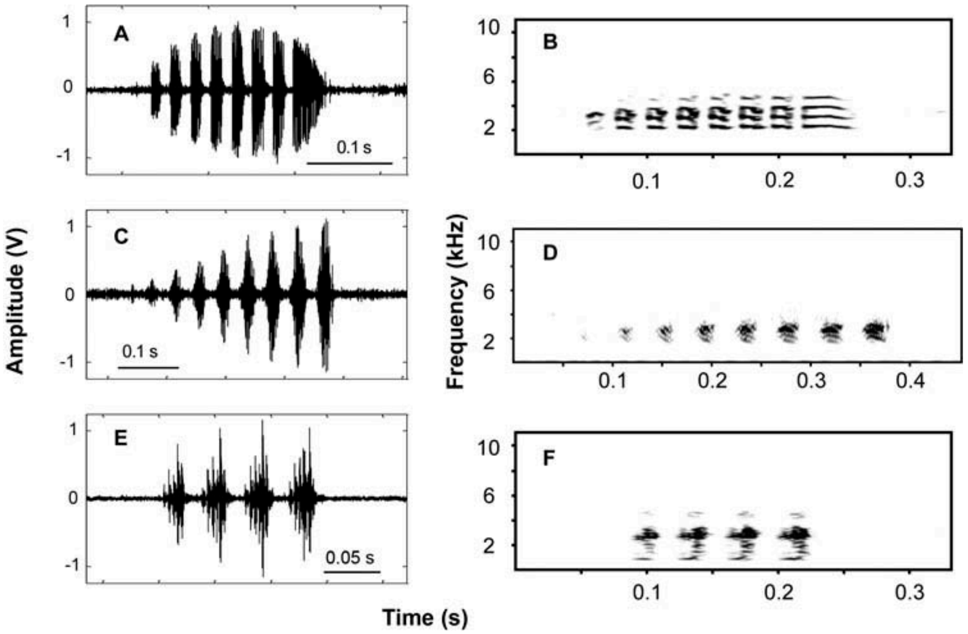

Figure 2. Oscillogram (left) and sonogram (right) of the advertisement call of (A, B) *Scinax cuspidatus*, (C, D) *Scinax* aff. *hayii*, and (E, F) *Scinax* aff. *x-signatus*. ReBio União, Rio de Janeiro, Brazil.

$p = 0.009$, $n = 10$ males), indicating a rather discrete frequency modulation (about 0.2 kHz). However, this modulation is evident in each pulse of the call in a similar way, and does not appear as a gradual increase in frequency over the call.

Discriminant analysis

Despite the large overlap in the properties of the call spectrum and the structure of the acoustic signal of the three species of *Scinax*, the stepwise forward discriminant analysis was highly significant (Wilks' $\lambda = 0.02$; $F_{[18, 1078]} = 346.72$; $p < 0.0001$; $n = 550$). Figure 3 shows the discrimination among the species that is due mainly to differences in the number of pulses per call and dominant frequency (Table 2). The first canonical function explained 79% of the differences among the calls of these species, while the second function explained the remaining 21%.

Temporal distribution

On a seasonal scale, the reproductive activity of the three species was restricted to the rainy season (from November 2002 to March 2003 and from December 2003 to March 2004, Figure 4), starting with the first rains.

We recorded 35 breeding aggregations of *S. cuspidatus* (17 during the first year and 18 during the second), 31 of *S.* aff. *x-signatus* (17 during the first year and 14 in

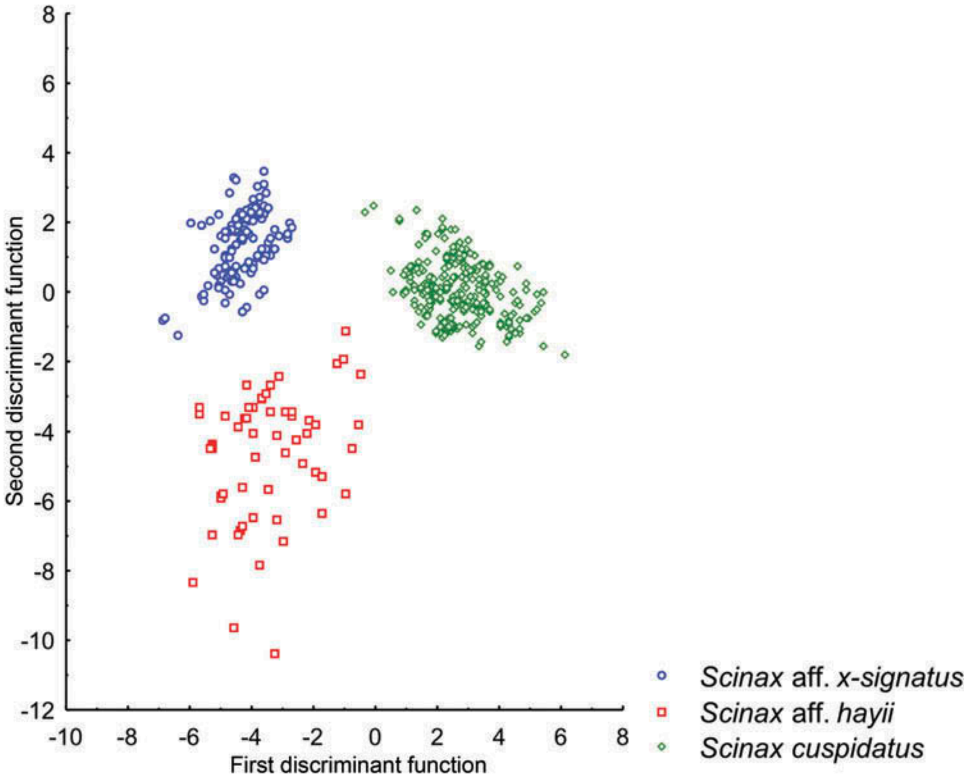

Figure 3. Scatterplot of the discriminant functions of acoustic parameters of three syntopic species of *Scinax*. ReBio União, Rio de Janeiro, Brazil.

Table 2. Canonical coefficients for the nine variables in the forward discriminant analysis among the advertisement calls of *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus*.

Selected variables	Function 1	Function 2
Pulses per call	0.90	−0.23
Dominant frequency	−0.61	−0.61
Calls per minute	−0.28	0.41
Call duration	−0.19	−0.47
Final dominant frequency	−0.35	−0.42
Peak time	−0.08	−0.33
Proportional rise time	0.04	0.24
Frequency of the most energetic pulse	−0.16	−0.04
Initial dominant frequency	0.07	0.26

the second) and 14 aggregations of *S.* aff. *hayii* (11 in the first year and only three in the second) during the study period. Only males of *S.* aff. *x-signatus* were heard calling in the four possible conditions: alone, only with *S. cuspidatus*, only with *S.* aff. *hayii*, and together with the two other congeneric species. We did not record nights where males of *S. cuspidatus* and *S.* aff. *hayii* were found in calling activity

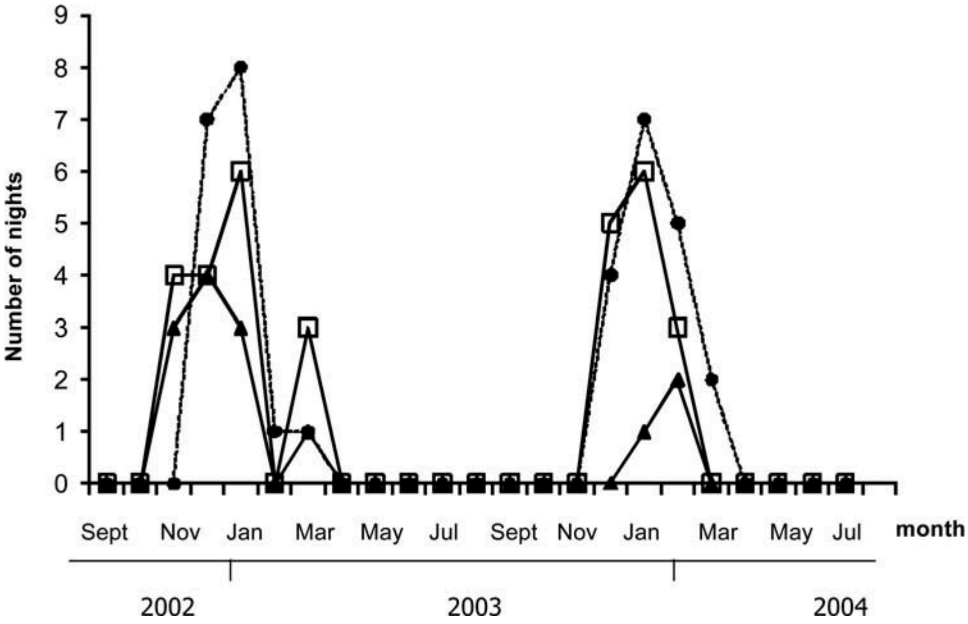

Figure 4. Breeding season of *Scinax cuspidatus* (filled circles), *Scinax* aff. *hayii* (filled triangles), and *Scinax* aff. *x-signatus* (open squares) from September 2002 to July 2004, according to the number of nights that each species formed a chorus in the study area, ReBio União, Rio de Janeiro, Brazil.

without *S.* aff. *x-signatus*; and on only one night we find calling males of *S.* aff. *hayii* without the other two species.

We observed an interspecific reproductive dynamic during the reproductive season. Male *S. cuspidatus* attended chorus most often, attending even on nights without rain. Males of *S.* aff. *hayii* were absent from the pond most frequently and their behaviour differed between the 2 years of the study. In the first year, reproductive activity occurred up to 3 days after heavy rains and in the second year, chorusing aggregations were formed only on nights with heavy rains. Reproductive aggregations of males of *S.* aff. *x-signatus* were large after nights with heavy rains, but chorus attendance also occurred when there was no rain or just drizzle. However, in these conditions, the number of active males was low and females were not observed.

The analysis of covariance indicated that chorus attendance of the three species of *Scinax* was differently influenced by environmental variables ($F_{[2.90]} = 4.40$, $p = 0.01$). Tables 3 and 4, respectively, show the results of the regression analysis of environmental variables on the chorus formation and on the number of males in calling activity for each species, indicating the predictor variables for each species.

Despite the partial or total overlap in the time of calling activity, on a daily scale, when the three species were present, the time of activity peak was different among species (*S. cuspidatus*: 9:00 p.m., *S.* aff. × −*signatus*: 10:00 p.m., *S.* aff. *hayii*: 1:00 a.m., $n = 5$), especially for the pairs *S. cuspidatus* – *S.* aff. *hayii* and *S.* aff. *hayii* – *S.* aff. *x-signatus* (Figure 5). The onset of activity for *S.* aff. *hayii* males (about 11:00 p.m.) coincided with a decrease in the number of active males of the other species.

Table 3. Parameters of the forward multiple regression explaining the chorus attendance in *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus* according to environmental variables in the ReBio União, Rio de Janeiro, Brazil.

Scinax cuspidatus	$R^2 = 0.76$; $F_{(4,48)} = 16.15$; $p = 0.000001$		
Predictor variables	slope ± SE	*t*-test (31)	*p*
Pond depth	0.01 ± 0.002	7.51	0.0000001
One-night previous weather condition	0.08 ± 0.07	1.15	0.26
Scinax aff. *hayii*	$R^2 = 0.29$; $F_{(3,30)} = 4.02$; $p = 0.01$		
Predictor variables	slope ± SE	*t*-test (30)	*p*
Maximum air temperature	−0.01 ± 0.01	−0.97	0.34
One-night previous weather condition	0.14 ± 0.09	1.58	0.12
Day weather condition	0.08 ± 0.06	1.22	0.23
Scinax aff. *x-signatus*	$R^2 = 0.45$; $F_{(5,28)} = 4.58$; $p = 0.003$		
Predictor variables	slope ± SE	*t*-test (28)	*p*
Day weather condition	0.27 ± 0.08	3.35	0.002
Pond depth	0.008 ± 0.003	2.85	0.008
Night weather condition	−0.26 ± 0.11	−2.26	0.03
One-night previous weather condition	0.24 ± 0.11	2.24	0.03
Maximum air temperature	0.04 ± 0.02	2.08	0.04

For each predictor variable the parameters shown are the slope ± SE, *t*-test, and significance level. For multiple regression of each chorusing species, *F*-test, and the resulting *P*-value is also shown.

Table 4. Parameters of the forward multiple regression explaining the abundance of calling males in *Scinax cuspidatus, Scinax* aff. *hayii*, and *Scinax* aff. *x-signatus* according to environmental variables in the ReBio União, Rio de Janeiro, Brazil.

Scinax cuspidatus	$R^2 = 0.64$; $F_{(5,28)} = 9.99$; $p = 0.00001$		
Predictor variables	slope ± SE	*t*-test (28)	*p*
Pond depth	0.14 ± 0.02	5.96	0.000002
Night weather condition	−2.04 ± 1.07	−1.90	0.07
1-night previous weather condition	1.73 ± 0.98	1.76	0.09
Mean temperature	−0.84 ± 0.48	−1.75	0.09
Day weather condition	−1.12 ± 0.78	−1.44	0.16
Scinax aff. *hayii*	$R^2 = 0.37$; $F_{(3,30)} = 5.96$; $p = 0.003$		
Predictor variables	slope ± SE	*t*-test (30)	*p*
1-night previous weather condition	4.88 ± 1.40	3.49	0.001
Day weather condition	2.50 ± 1.04	2.41	0.02
Night weather condition	−3.33 ± 1.50	−2.21	0.03
Scinax aff. *x-signatus*	$R^2 = 0.34$; $F_{(3,30)} = 5.10$; $p = 0.006$		
Predictor variables	slope ± SE	*t*-test (30)	*p*
Pond depth	0.07 ± 0.02	2.84	0.008
Day weather condition	1.70 ± 0.77	2.20	0.04
Night weather condition	−1.85 ± 1.15	−1.61	0.12

For each predictor variable the parameters shown are the slope ± SE, *t*-test, and significance level. For multiple regression of each chorusing species, *F*-test, and the resulting *P*-value is also shown.

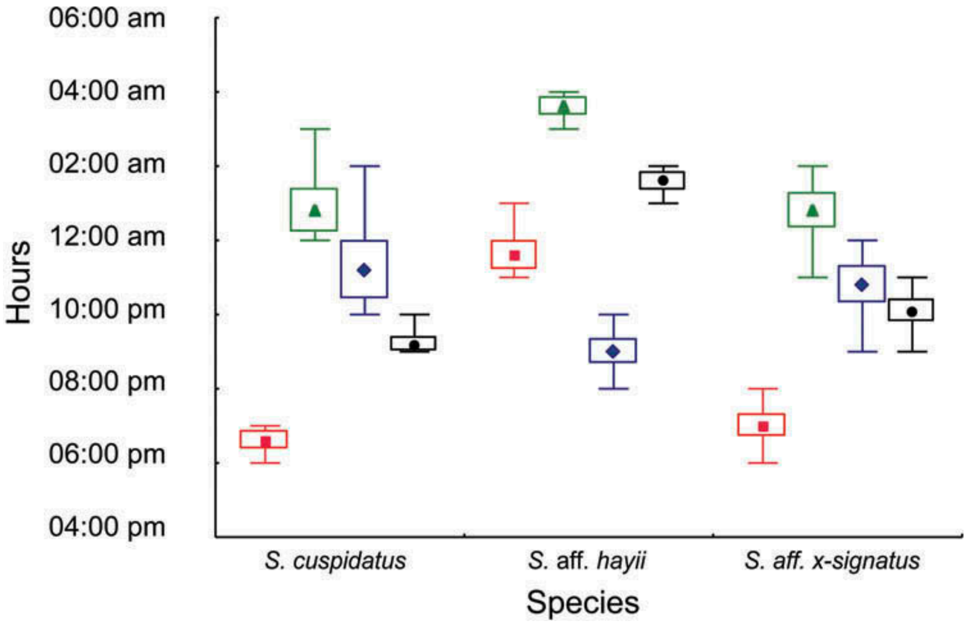

Figure 5. Distribution of the daily temporal activity in *Scinax cuspidatus*, *Scinax* aff. *hayii* and *Scinax* aff. *x-signatus*, showing the start time (square) and end time (triangle) of calling activity, chorus duration (diamond) and activity peak (circle) at the study area, ReBio União, Rio de Janeiro, Brazil. The parameters shown are the mean ± SD (n = 5).

According to the multivariate analysis of variance, which considered different conditions (presence of only one and three species calling), we found differences in relation to some parameters of daily temporal activity (Table 5). The results indicated that when one of the species was heard calling (*S. cuspidatus* or *S.* aff. *x-signatus*) without another congeneric species, there was no significant difference with respect to the time of starting and time of ending of calling activity, chorus duration, and activity peak (Wilks' $\lambda = 0.30$, $R_{[4.2]} = 0.58$, $p = 0.74$). However, when the three species were active, we found a significant difference between the set of variables (time of starting,

Table 5. Mean values of some parameters (time of starting and time of ending of calling activity, chorus duration and activity peak) of the daily temporal activity of *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus* according to presence of only one (alone) and three species calling (together) in the ReBio União, Rio de Janeiro, Brazil.

Condition	*S. cuspidatus*		*S.* aff. *hayii*	*S.* aff. *x-signatus*	
	Alone (n = 4)	Together (n = 5)	Together (n = 5)	Alone (n = 2)	Together (n = 5)
Start time	6:00 pm	6:00 pm	11:00 pm	7:00 pm	6:00 pm
End time	1:00 am	3:00 am	4:00 am	4:00 am	2:00 am
Chorus duration	8 hours	10 hours	6 hours	10 hours	9 hours
Activity peak	9:00 pm	9:00 pm	1:00 am	11:00 pm	10:00 pm

time of ending, chorus duration and activity peak) (Wilks' λ = 0.02, $R_{[8.18]}$ = 15.31, p = 0.000001). The planned contrast between *S. cuspidatus* and *S.* aff. *x-signatus* maintained the differences found in this condition ($R_{[4.9]}$ = 5.99, p = 0.01). Analysis of variance performed separately for each variable in this condition confirmed the results (time of starting: $F_{[2,12]}$ = 77.19, $p < 0.001$; time of ending: $F_{[2.12]}$ = 4.20, p = 0.04; chorus duration: $F_{[2,12]}$ = 42.55, p = 0.001; time of activity peak: $F_{[2,12]}$ = 12.25, p = 0.001). As males of *Scinax* aff. *hayii* were not heard calling without other congeneric species (except for one night), no tests were performed.

Spatial distribution

Quantitative and qualitative physical characteristics of each microhabitat are shown in Table 6. According to the cluster analysis, which considered vegetation structure, vegetation cover, depth of pond in the centre, and edge of each site (Figure 6), microhabitats 2 and 3 were more similar, while microhabitat 1 was the most different. The percentage of canopy cover and the depth of the water column at the edge and at the centre of the microhabitat were different among the microhabitats (ANOVA: Wilks' λ = 0.20; $F_{[12,47]}$ = 3.40; p = 0.001).

Microhabitat selection

In general, microhabitat 4 was the most used by the three species, followed by microhabitat 1 for *S. cuspidatus* and *S.* aff. *x-signatus*, and microhabitat 5 for *S.*

Table 6. Physical parameters of microhabitats of temporary pond located in the ReBio União, Rio de Janeiro, Brazil.

Microhabitat	Canopy cover (%)	Edge pond depth (cm)	Centre pond depth (cm)	Vegetation structure	Area (m^2)
1	46.2 ± 3.59 (20.8–60.1) (45)	40.6 ± 18.6 (20.0–62.0) (5)	62.6 ± 10.01 (51.0–76.0) (5)	Grasses dominant and sparse trees	245
2	58.6 ± 17.9 (18.0–77.0) (45)	28.0 ± 14.2 (16.0–48.0) (5)	49.0 ± 3.67 (45.0–52.0) (5)	Grass and herbaceous	88
3	59.0 ± 18.1 (27.0–75.1) (45)	26.0 ± 5.7 (22.0–36.0) (5)	37.8 ± 8.9 (27.0–50.0) (5)	Herbaceous and shrub	114
4	50.8 ± 17.5 (23.4–69.0) (45)	18.8 ± 1.6 (17.0–21.0) (5)	33.6 ±6.7 (24.0–41.0) (5)	Herbaceous and arboreal	113
5	79.6 ± 12.9 (52.6–97.6) (45)	28.6 ± 17.3 (12.0–51.0) (5)	47.4 ± 14.6 (27.0–62.0) (5)	Shrubs and arboreal	97

The values of pond depth refer to the greatest values obtained during the samples (February 2004).
Note: Values are presented as mean ± SD (range) (*n*).

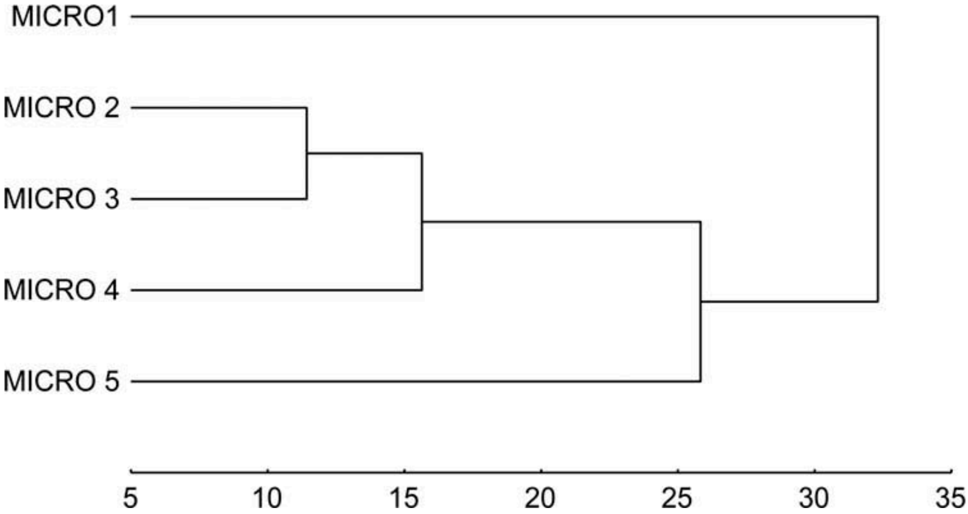

Figure 6. Cluster analysis of the microhabitats of the pond, based on the parameters canopy cover, vegetation structure and depth of the water column at the edge and the centre of each microhabitat. UPGMA method and Euclidean distance. Vertical axis: microhabitats; horizontal axis: linkage distance. Rebio União, Rio de Janeiro, Brazil.

aff. *hayii*. Results from ANOVA showed that males of *S. cuspidatus* ($F_{[4,140]} = 12.63$, $p < 0.0001$) and *S.* aff. *x-signatus* ($F_{[4,146]} = 4.69$; $p = 0.001$) differed in the use of the microhabitats. However, results of ANOVA were not significant for males of *S.* aff. *hayii* ($F_{[4,66]} = 2.05$; $p = 0.10$). Planned contrasts between microhabitats 1 and 4 confirmed that *S. cuspidatus* ($F_{[1,140]} = 14.38$; $p = 0.0002$) and *S.* aff. *x-signatus* ($F_{[1,146]} = 4.89$; $p = 0.03$) were more common in microhabitat 4. We found different results when we discriminated the presence or absence of the congener species (Table 7).

The vertical spatial distribution of males from the three different species of *Scinax* revealed a great overlap among the calling sites (*S. cuspidatus*: range 0.30–5.0 m, *S.* aff. *hayii*: range 0.40–2.50 m, *S.* aff. *x-signatus*: range 0–2.0 m). However, ANOVA showed a different vertical distribution ($F_{[2,277]} = 67.49$, $p < 0.0001$; *S. cuspidatus*: median = 150 cm; *S.* aff. *hayii*: median = 120 cm; *S.* aff. *x-signatus*: median = 50 cm). This result was corroborated when we discriminated the microhabitats (1 and 4) under the condition that all the species were calling together ($F_{[2,27]} = 4.07$, $p = 0.03$; $F_{[2,29]} = 10.97$, $p = 0.0003$, for microhabitat 1 and 4, respectively; Table 8).

When we compared the microhabitats, we also found a different vertical distribution for *S. cuspidatus*: $F_{[4,106]} = 2.68$; $p = 0.04$ and for *S.* aff. *x-signatus*: $F_{[4,94]} = 4.15$; $p = 0.004$. Planned contrasts revealed that males of *S.cuspidatus* occupied lower perches in microhabitat 1 (about 1.50 m, $n = 67$) than in microhabitat 4 (about 2.00 m, $n = 22$) ($F_{[1.106]} = 9.89$, $p = 0.002$). In contrast, males of *S.* aff. *x-signatus* occupied higher perches in microhabitat 1 (80 cm, $n = 54$) compared with microhabitat 4 (50 cm, $n = 26$) ($F_{[1.94]} = 8.25$, $p = 0.005$). The mean height of the perches occupied by *S.* aff. *hayii* males was about 1.15 m ($n = 53$).

By assessing the intraspecific vertical distribution in different conditions (if calling alone, with one or two congeneric species), we found differences only for *S. cuspidatus*

Table 7. Results from analysis of variance (ANOVA) of the spatial distribution of *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus* calling males under different conditions at the study site, ReBio União, Rio de Janeiro, Brazil.

Condition	ANOVA	* Predominantly occupied microhabitats	ANOVA
S. cuspidatus			
Calling alone (n = 10 nights)	$F_{[4,45]} = 8.48$; $p = 0.00003$	Micro 1 and Micro 4	$F_{[1,45]} = 12.22$; $p = 0.001$
With *S.* aff. *x-signatus* (n = 12 nights)	$F_{[4,55]} = 1.48$; $p = 0.23$		
With the other congeneric species (n = 7 nights)	$F_{[4,30]} = 6.91$; $p = 0.0005$	Micro 1 and Micro 4	$F_{[1,30]} = 8.07$; $p = 0.008$
S. aff. *hayii*			
With *S.* aff. *x-signatus* (n = 6 nights)	$F_{[4,25]} = 1.44$; $p = 0.25$		
With the other congeneric species (n = 7 nights)	$F_{[4,30]} = 8.43$; $p = 0.0001$	Micro 4 and Micro 3	$F_{[1,30]} = 13.47$; $p = 0.0009$
S. aff. *x-signatus*			
Calling alone (n = 5 nights)	$F_{[4,20]} = 5.02$; $p = 0.26$		
With *S. cuspidatus* (n = 12 nights)	$F_{[4,55]} = 3.89$; $p = 0.007$	Micro 4 and Micro 1	$F_{[1,55]} = 4.91$; $p = 0.03$
With *S.* aff. *hayii* (n = 6 nights)	$F_{[4,25]} = 3.13$; $p = 0.03$	Micro 1 and Micro 5	$F_{[1,25]} = 7.44$; $p = 0.01$
With the other congeneric species (n = 7 nights)	$F_{[4,30\}} = 5.89$; $p = 0.001$	Micro 4 and Micro 1	$F[_{1,30]} = 1.07$; $p = 0.31$

Planned contrasts were performed between the two microhabitats with the highest number of individuals when $p < 0.05$.
Note: * decreasing order.

Table 8. Values of the height of the calling site of *Scinax cuspidatus, Scinax* aff. *hayii* and *Scinax* aff. *x-signatus* according to the microhabitats (MICRO) predominantly occupied by males in the condition all the species calling together in the ReBio União, Rio de Janeiro, Brazil.

	S. cuspidatus		*S.* aff. *hayii*		*S.* aff. *x-signatus*	
MICRO	1	4	1	4	1	4
Height	90 cm (50–200; 15)	170 cm (60–300; 6)	80 cm (70–90; 2)	110 cm (35–200; 18)	60 cm (20–100; 13)	60 cm (15–80; 8)

Note: Values presented as median (range; n).

($F_{[2.105]} = 6.70$, $p = 0.002$), indicating that the presence of any other species of *Scinax* interfered in the occupation of the stratum. Planned contrasts between the height of the calling sites in the conditions (1) calling alone × with the two other species ($F_{[1.105]} = 7.81$, $p = 0.006$) and (2) calling alone × with *S.* aff. *x-signatus* ($F_{[2.105]} = 6.70$, $p = 0.002$), corroborated such interference.

Table 9. Coefficient of dispersion (*I*, variance-to-mean ratio) for males of *Scinax cuspidatus, Scinax* aff. *hayii,* and *Scinax* aff. *x-signatus* attending choruses in different conditions (in the presence or absence of the other congeneric species) at the study site, ReBio União, Rio de Janeiro, Brazil.

	Date	Congeneric species	Variance-to-mean ratio		
			Chorus size	*I*	χ^2 *
S. cuspidatus	14/12/2002	Absence	10	2.88	365.4††
	17/12/2002	Absence	16	1.42	183.6†
	09/01/2003	Absence	10	2.00	265.4††
	21/02/2003	Absence	13	1.10	137.0
	19/01/2004	Absence	18	1.86	239.3††
	18/01/2004	*S.* aff. *x-signatus*	21	2.63	341.3††
	11/12/2002	*S.* aff. *hayii* and *S.* aff. *x-signatus*	16	2.00	258.5††
	15/01/2003	*S.* aff. *hayii* and *S.* aff. *x-signatus*	13	2.00	257.0††
S. aff. *hayii*	12/11/2002	*S.* aff. *x-signatus*	17	4.46	575.2††
	13/11/2002	*S.* aff. *x-signatus*	12	2.44	321.0††
	11/12/2002	*S. cuspidatus* and *S.* aff. *x-signatus*	5	1.25	170.0†
	15/01/2003	*S. cuspidatus* and *S.* aff. *x-signatus*	8	1.00	98.6
S. aff. *x-signatus*	18/03/2003	Absence	11	2.50	325.9††
	15/12/2003	Absence	7	2.00	252.5††
	18/01/2004	*S. cuspidatus*	10	1.50	190.4†
	12/11/2002	*S.* aff. *hayii*	16	1.83	233.6††
	13/11/2002	*S.* aff. *hayii*	15	1.17	158.47
	11/12/2002	*S. cuspidatus* and *S.* aff. *hayii*	10	0.80	114.5
	15/01/2003	*S. cuspidatus* and *S.* aff. *hayii*	17	2.08	267.5††

Notes: * $\chi^2_{0.05,\ 129} = 156.51$ (critical values of the chi-squared distribution). $^{\dagger}p < 0.05$; $^{\dagger\dagger}p < 0.001$.

In general, males of all species of *Scinax* had an aggregated distribution (Table 9). The variance-to-mean ratio test showed that all species showed a tendency to aggregate, regardless of the condition (calling alone, with one or two species of *Scinax*). The graphic analysis of the distance among calling males during the aggregations (Figure 7) showed that they tended to stay closer to conspecifics than heterospecifics.

Discussion

Acoustic parameters

The evolution of acoustic signals in frogs has been shaped by several factors, including historical limitations, active selective forces (through male interactions or female choice) or passive selective forces (e.g. effect from signal propagation through the

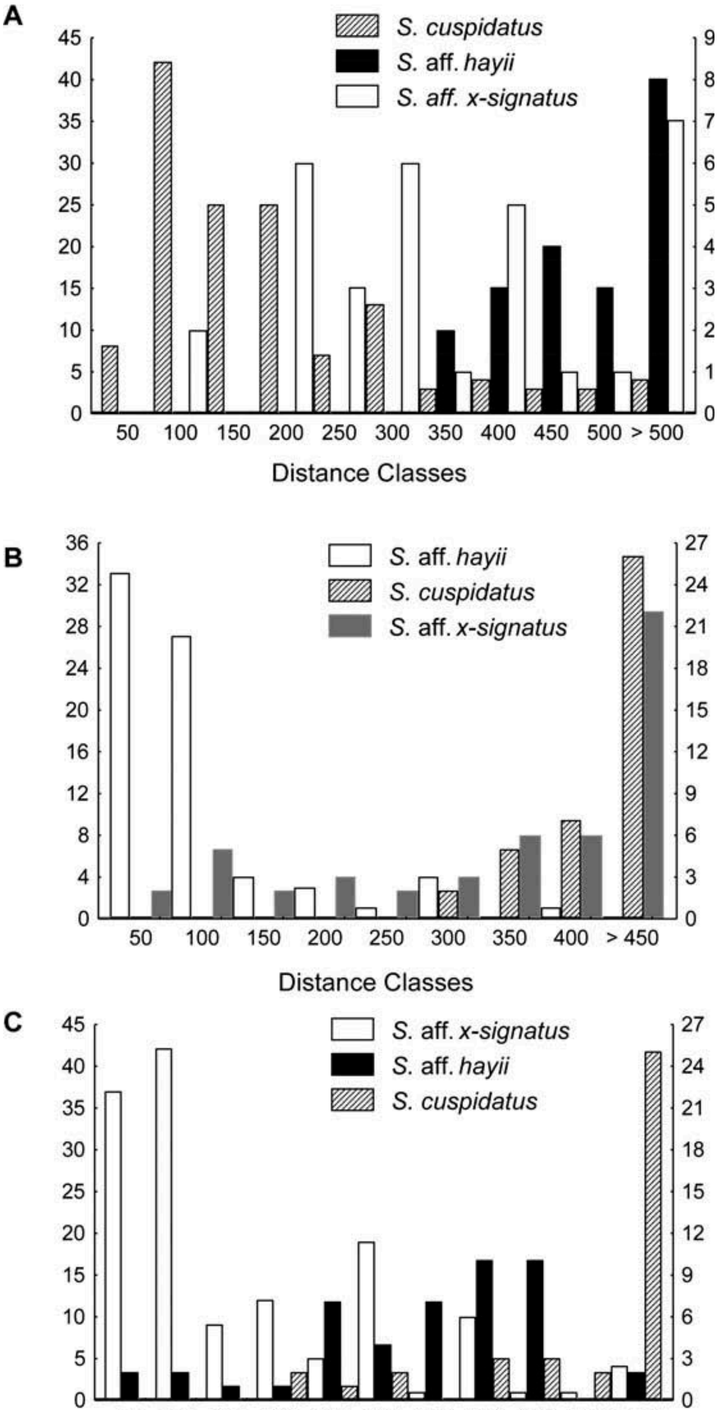

Figure 7. Distance among conspecific and heterospecific calling sites of (A) *Scinax cuspidatus*, (B) *Scinax* aff. *hayii* and (C) *Scinax* aff. *x-signatus*. The left y-axis corresponds to the number of observations for conspecifics, the right y-axis for heterospecifics. ReBio União, Rio de Janeiro, Brazil.

environment and from acoustic interference of the habitat) (Rand 1985). Acoustic characters shared by phylogenetically related species may represent historical evidence. This applies to species of the *Scinax ruber* group (Pombal et al. 1995a, 1995b; present study), the group of *Aplastodiscus albosignatus* (Abrunhosa et al. 2005), the genera *Bufo* and *Pseudacris* (Cocroft and Ryan 1995), and the genus *Chiasmocleis* (Wogel et al. 2004), among others.

Besides the pulsed call, which is common to all species in the *Scinax ruber* species group (Pombal et al. 1995a, 1995b; Magrini et al. 2011), the advertisement calls of *S. cuspidatus*, *S.* aff. *hayii,* and *S.* aff. *x-signatus* are composed of one note repeated at varying intervals. The calls possess sidebands and their spectral properties overlap (between 2 and 4 kHz). They are distinguished from each other by the number of pulses per call and the dominant frequency.

When we compared calls from the same species from different localities or the most closely related species of the *Scinax ruber* clade, for whom vocalizations are known, we found some differences. In the case of *S. cuspidatus*, the call differences can be related to different climatic or social variables at the time of recording that usually influence temporal acoustic parameters in several anuran species (Gerhardt 2012). The advertisement call of *S. cuspidatus* from Conceição da Barra, ES (Pombal et al. 1995a), is shorter (call duration = 0.12–0.15 s, pulses per call = 5–6 pulses per call; our study: 0.14–0.27 s of call duration, and 6–14 pulses per call) and according to the sonogram presented in this study, dominant frequency bandwidth (2.3–4.0 kHz) seems to correspond to the three first sidebands (dominant frequency in our study was represented by the third bandwidth = 2.09–2.54 kHz). In this study the duration of the advertisement call of *S.* aff. *hayii* exhibits great amplitude (0.14–0.36 s). This range includes values of call duration found in four other localities where *S. hayii* has been recorded [Jundiaí, SP (Pombal et al. 1995a): 0.19–0.32 s call duration; Boracéia, SP (Heyer et al. 1990): 0.20–0.26 s call duration; Itapeva, MG, and Atibaia, SP (Magrini et al. 2011): 0.19–0.28 s call duration]. However, calls of *S.* aff. *hayii* have fewer pulses per call (5–11) than *S. hayii* [Jundiaí, SP (Pombal et al. 1995a): 14–21 pulses per call; Boracéia, SP (Heyer et al. 1990): 15–20 pulses per call; Itapeva, MG, and Atibaia, SP (Magrini et al. 2011): 13–17 pulses per call] and the dominant frequency overlaps somewhat with the population from Jundiaí [our study: 2.77–3.72 kHz; Jundiaí, SP (Pombal et al. 1995a): 3.0–4.1 kHz dominant frequency; Boracéia, SP (Heyer et al. 1990): 1.20–2.80 kHz of dominant frequency; Itapeva, MG, and Atibaia, SP (Magrini et al. 2011): 1.08–2.06 kHz dominant frequency]. The advertisement call of *S.* aff. *x-signatus* cannot be compared to *S. x-signatus* because the vocalization is unknown. Given the existence of numerous cryptic species within the *Scinax ruber* group (Fouquet et al. 2007), vocalization is an important tool to diagnose and differentiate species.

The great acoustic similarity (calls with longer duration and greater number of pulses) between *S. cuspidatus* and *S.* aff. *hayii* could have led to mismatching, but no heterospecific pairs in amplexus were found during the two years of study. This suggests that the calls may contain information that provides pre-zygotic isolation, as seen in *Dendropsophus microcephalus*, *Dendropsophus ebraccatus* and *Dendropsophus phlebodes* (Fouquette 1960; Schwartz 1987). Alternatively, species are partitioning other resources, which ensures their reproductive isolation. Tárano (2010) showed that species' acoustic similarity was counteracted by habitat and/or microhabitat segregation or vice versa. The divergence in the microhabitat selection and the height of perches between *S. cuspidatus* and *S.* aff. *hayii* males corroborate this.

Temporal distribution

The reproductive activity of the three species of *Scinax* was concentrated in the warm and rainy season, which is quite common for Neotropical species (Gottsberger and Gruber 2004), especially from temporary ponds (Arzabe et al. 1998). The observed overlap in seasonal distribution is expected among syntopic species of the seasonal tropics and/or temporary environments (Heyer 1973; Donnelly and Guyer 1994; Rossa-Feres and Jim 1994; Arzabe et al. 1998), especially when species are related and have the same reproductive mode (Gottsberger and Gruber 2004).

Despite the great precipitation during the second year of study, resulting in a longer hydroperiod, the reproductive season of *S. cuspidatus* lasted 4 months, whereas for *S.* aff. *hayii* and *S.* aff. *x-signatus* it was longer in the first year, when temperatures were higher. These observations suggest that a combination of factors, not the rain alone, explains the reproductive activity of the species, which was supported by the regression analysis. Chorus attendance in *S. cuspidatus*, in general, was independent of weather conditions at night (with or without rain). This behaviour represents a typical pattern of prolonged breeding of anuran species with males exhibiting site fidelity, using vocalizations, and showing aggression towards intruders (Wells 1977). Males of *S.* aff. *hayi* and *S.* aff. *x-signatus*, which restricted their reproductive activities following nights of heavy rains, can be classified as opportunistic, with heavy rains being responsible for the activity of these species. Similar results of aggregations related to rain were observed in other anuran communities among prolonged or not prolonged breeders (e.g. Arzabe et al. 1998; Gottsberger and Gruber 2004; Abrunhosa et al. 2006).

Oseen and Wassersug (2002) found that explosive breeders respond to a few environmental variables when compared with the prolonged breeders, since they maximize efficiency instead of speed (Wells 1977). Although *S.* aff. *hayii* and *S.* aff. *x-signatus* were opportunistic breeders and spend less time at the reproductive aggregation compared with *S. cuspidatus* males, the analysis of regressions regarding environmental variables contradicted these expectations. Studies of Blankenhorn (1972) and Salvador and Carrascal (1990) corroborate the results found in our study.

When the three species were reproductively active, their daily temporal activities overlapped somewhat. However, the time of peak activity was distinct (*S. cuspidatus*: 9:00 p.m.; *S.* aff. *hayii*: 1:00 a.m.; *S.* aff. *x-signatus*: 10:00 p.m.), especially between the pair of species of greater acoustic similarity (*S. cuspidatus*, and *S.* aff. *hayii*). Other studies have also shown that species may limit their calling activity to the hours in which males of other species are less active (Crump 1974; Kuramoto 1980). In this case, the interference produced by heterospecific calls can be minimized.

The fact that peak activity of males of *S. cuspidatus* and *S.* aff. *x-signatus* was during the first half of the night can be related to the most suitable temperature and energy constraints, which affect both the sender and the receiver (Gerhardt and Huber 2002). In contrast, the activity time for *S.* aff. *hayii* was mainly concentrated in the second half of the night. The low intensity of its advertisement call may explain this phenomenon (pers. obs.). To start calling activity late at night may represent a mechanism that makes the intraspecific communication more efficient, because the other species tend to reduce their activity from then, providing less background noise for conspecific communication. Alternatively, this may be explained by temperature; perhaps males of *S.* aff. *hayii* are more tolerant to lower temperatures.

Analyses of daily activity time for *S. cuspidatus S.* aff. *hayii* and *S.* aff. *x-signatus* males revealed that on nights when all three congeneric species were present, there were significant differences with respect to the time of starting and time of ending of calling activity, chorus duration and activity peak from those nights when no other congeneric species were present. This suggests that the presence of congeneric species of the *Scinax ruber* group influences their activity times, probably reducing interference on the communication of conspecifics, as suggested by Crump (1982) in a study of anuran community ecology.

Spatial distribution

The tendency for species of *Scinax* to aggregate is common among anurans (eg MacNally 1979; Given 1990; Dyson and Passmore 1992). The preference for establishing calling sites near the sites of conspecifics (MacNally 1979; Given 1988, 1990), the increase in the efficiency of signal propagation, and the reduction of acoustic interference (Littlejohn 1977; MacNally 1979) have been noted as possible explanations for chorus formation in frogs. Intra- and interspecific organization of *Scinax* male calling sites suggests that the spatial arrangement minimizes interference by heterospecific calls. Several other studies observed this tendency (e.g. Given 1990; Gerhardt and Schwartz 1995; Gerhardt and Huber 2002). Changes in the distribution pattern on different nights may be associated with increased density in the chorus and decreased spacing between males (Fellers 1979; Gerhardt et al. 1989; Dyson and Passmore 1992).

Our data indicate that in the absence of temporal information, the three species of *Scinax* occupied microhabitat 4 most of the time. However, when temporal information is included in the analysis, the results indicated differential use of microhabitats: *S. cuspidatus* preferably occupied microhabitat 1, *S.* aff. *hayii* preferably occupied microhabitat 4, and *S.* aff. *x-signatus* occupied, equally, microhabitats 1 and 4. Microhabitats 1 and 4 were those with the lowest percentage of coverage by the canopy. Reduced signal degradation in open areas (Gerhardt and Huber 2002; Parris 2002) may explain the higher occupation of vertical strata by males of all species of *Scinax*. Although there was some overlap in the microhabitats selected (1 and 4), the vertical use was significantly different among species, suggesting spatial partitioning on a micro-scale. Regardless of the presence or absence of congeneric species, males of *S. cuspidatus* always called on higher perches than males of *S.* aff. *hayii*, which in turn, occupied higher calling sites than *S.* aff. *x-signatus*. This type of segregation strengthens the primary reproductive isolation (advertisement call), as observed for numerous species (Hödl 1977; Gerhardt and Schwartz 1995; Gillespie et al. 2004), resulting in more efficient communication among individuals.

Differences found in relation to the occupation of microhabitats and the vertical strata for *S.* aff. *x-signatus* and *S. cuspidatus*, respectively, according to the presence or absence of congeneric species, indicate possible heterospecific interference in the spatial distribution of species. Some studies of closely related species have demonstrated that interspecific interactions cause changes in spatial distribution, in vocal behaviour, and temporal distribution, especially if species are acoustically similar (Littlejohn and Martin 1969; Schwartz and Wells 1983, 1984; Odendaal and Bull 1986; Given 1990).

The spatial organization of *Scinax* species together with the distribution of activity throughout the night (daily temporal scale) reinforces the idea of coexistence through sharing of resources associated with reproduction. Therefore, each species retains an effective form of intraspecific communication to ensure their reproductive success without wasting investment.

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