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An austral anuran assemblage in the Neotropics: seasonal occurrence correlated with photoperiod

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The study describes habitat use and temporal occurrence of calling males for an austral anuran assemblage in the Neotropics, southern Brazil. Three study sites (S1 – a permanent river and a stream, S2 – a dam and backwater, S3 – two permanent ponds periodically connected) were sampled between August 2005 and July 2006. The site S3 presented the richest and most diverse assemblage and habitat use within studied sites, and was partitioned by species groups. Richness and abundance of calling males for overall assemblage were seasonal, concentrated in spring and summer and correlated with photoperiod. Temperature, rainfall and air humidity were not correlated with the richness and abundance of calling males. Photoperiod also explained the calling seasons when species were analyzed individually. Habitat use and temporal occurrence were complementary in the partitioning of breeding resources, explaining species coexistence.

Keywords: Anura; assemblages; habitat use; seasonality; Neotropics

Introduction

It has been reported that anuran species of tropical wet regions have long reproductive periods, whereas species of tropical seasonal and temperate regions have interrupted reproductive cycles (Crump 1974; Duellman and Trueb 1994). Therefore, we can expect that amphibian reproductive activity in tropical and subtropical regions will be related to rainfall, whereas in temperate regions it will be correlated with temperature (Duellman and Trueb 1994; Pough et al. 2001). Other climatic variables, such as air humidity and photoperiod are also considered important for the breeding activity of amphibians (Duellman and Trueb 1994). Photoperiod can often act as an environmental cue to entrain amphibian rhythms such as estivation, spermatogenesis (see Feder and Burggren 1992) or anuran calling (see Hatano et al. 2002).

The influence of climatic variables on anuran reproductive activity has been studied for assemblages in tropical (seasonally or unseasonally wet) and temperate zones (e.g. Crump 1974; Heyer 1979; Aichinger 1987; Prado et al. 2005; Vasconcelos and Rossa-Feres 2005), but no studies have been made on austral assemblages in subtropical zones, where only temperature and photoperiod are cyclical.

Rio Grande do Sul (RS), a state in southern Brazil, is located in a subtropical zone with evenly distributed rainfall throughout the year. Approximately 82 anuran species have been confirmed to occur in the state (Braun and Braun 1980; Kwet

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2001; Garcia and Vinciprova 2003; Kwet and Faivovich 2001; Lingnau et al. 2006). Eighty of them belong to one of the following seven anuran families: Bufonidae, Cycloramphidae, Hylidae, Leiuperidae, Leptodactylidae, Microhylidae and Ranidae. The other two species belong to the order Gymnophiona. Di-Bernardo et al. (2004) estimated more than one hundred species in the state.

Anuran diversity in the central state region has been scarcely studied. The only available publications are a check list (Braun and Braun 1980), a faunal inventory (Cechin et al. 2002a) and three notes on the distribution of range extensions for single species (Cechin et al. 2002b; Kopp et al. 2002; Both et al. 2006). Our study area is located in the municipality of Itaara, in a transition zone between a mesophytic deciduous forest, highland steps, and the Pampean steps (Quadros and Pillar 2002).

We describe an anuran assemblage from a subtropical region in southern Brazil, central Rio Grande do Sul state and report on its habitat use. We also evaluate the occurrence and seasonality of calling males and assess the influence of climatic factors on breeding activity.

Material and methods

Study site

Our study was conducted at the Rodolfo Costa e Silva dam and neighbouring areas, municipality of Itaara (29°32′15 S; 53°47′30 W), at 420 m mean height. The locality shows a secondary succession stage, with natural regeneration impaired by agricultural activities (Spathelf et al. 2000). The climate is classified as subtropical wet (Maluf 2000), with evenly distributed rainfall throughout the year (1500–1750 mm) (Pereira et al. 1989) and seasonality determined by temperature (Figure 1).

Three sites were sampled:

- S1: Permanent river, adjacent to dam wall and temporary stream. River banks are rocky, steep and surrounded by trees. The temporary stream has a clay bottom, grassy vegetation on the borders and temporary ponds along the banks.
- S2: Dam and backwater, with flat or steep banks and swampy regions near the backwaters. Bank vegetation is grazed by cattle and soybean is grown during part of the year. Most of the dam has little aquatic vegetation. Backwater aquatic coverage is denser.
- S3: Permanent ponds periodically connected, with banks covered by arboreal species on one side and by crops and grazing land on the other. After rainfall, small temporary ponds and swamps are formed.

Samples

All study areas were sampled monthly, from August 2005 to July 2006. Time-constrained acoustic and visual encounter surveys, methods largely used for rapid inventory assessments (Rödel and Ernst 2004), were used. Three hours of observations on average were made per month at each site, and the samples were taken by two observers who walked throughout the sites. The time spent in each site varied according to habitat size and complexity (Scott and Woodward 1994). Species abundance was recorded by considering calling males only. Calling male abundance can be overestimated in the presence of large specimen aggregations (Zimmerman

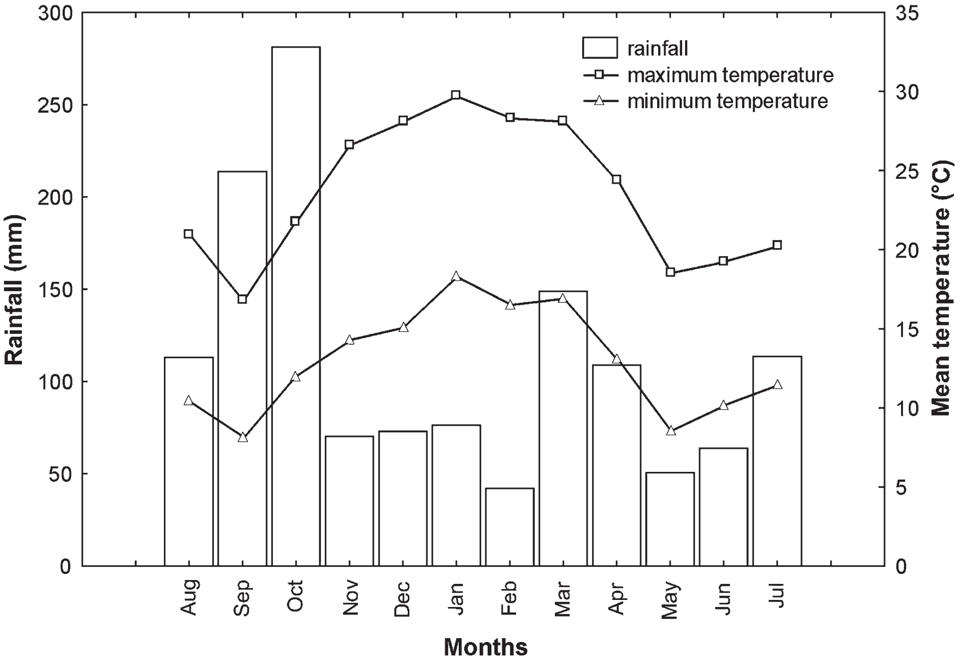

Figure 1. Monthly rainfall and maximum and minimum mean air temperatures throughout the period of study, August 2005–July 2006.

1994). Episodes of high abundance of calling males occurred during the study, but species distribution in several habitats within study sites minimized potential biases. Voucher specimens were deposited in the Herpetological Collection at the Universidade Federal de Santa Maria. The habitat use of each species was recorded qualitatively. In the three sampled sites the following habitats were observed: temporary ponds, permanent ponds, stream, open dam, dam backwater, swampy regions near permanent ponds and rocks.

Temperature (maximal and minimal means), rainfall, and relative air humidity data were obtained from www.cptec.inpe.br, Centro de Previsões Climáticas do Tempo e Clima. These data are recorded at the meteorological station of the municipality São Martinho da Serra, 10 km from the study site. Temperature and rainfall data were based on five days per month (sample day and four previous days), and relative air humidity on sample day. Photoperiod data were obtained from http://euler.on.br/ephemeris/index.php, Observatório Nacional Brasileiro.

Statistical analysis

Sample efficiency was evaluated by a mean collector curve generated by 500 random additions from the samples, using EstimateS 7.5 (Colwell 2005). The diversity of anuran assemblages of the three sites was compared using the Shannon-Wiener index (H' log, *e* base) (Magurran 1988; Krebs 1999), and their Pielou (e) equitability assessed by the bootstrapping method (Ryan et al. 1995), using the Past 1.13 software (Hammer et al. 2005). In this method, 1000 random samples are pooled for each sample (each area, in this study), and the samples are compared in pairs.

Comparisons are made with 200 pairs and the same numbers of individuals as the original samples. For each replicate pair, diversity indices and equitability are computed. The number of times diversity or equitability exceeds or equals the observed value indicate the probability that the observed difference occurred by random sampling of one parent population, as estimated by the pooled sample. A small probability ($P<0.05$) indicates significant difference in the diversity indices between the two samples (Ryan et al. 1995). To avoid overestimates in the analysis, we considered the maximal calling male abundance for the total of 12 samples in each site (Santos et al. 2007).

Similarities in habitat use and temporal occurrence of calling males were analyzed through cluster analysis using Unweighted Pair-Group Method of Arithmetic Averages (UPGMA) (Krebs 1999) based on the Jaccard Similarity Index (C_j) and Morisita-Horn Index (C_H), respectively. The cophenetic correlation coefficient (r) measured loss of information in the similarity matrix represented by cluster analyses (Romesburg 1984). Values of $r \geqslant 0.9$ were considered a very good fit, $0.8 \leqslant r < 0.9$ a good fit, $0.7 \leqslant r < 0.8$, a poor fit, and $r<0.7$ a very poor fit (Rohlf 2000). The analyses were performed using NTSYS 2.1 (Rohlf 2000).

The temporal occurrence of males in calling activity was analyzed through a circular statistical analysis (Zar 1999), using ORIANA 2.02 (Kovach 2004). Months were converted into angles (intervals of 30°) and richness and abundance of calling males in each month were taken as frequencies of each angle (month) observed (see Prado et al. 2005). Through this method we estimated: a) the mean angle (α), which represents the mean time of the year during which most species were in breeding activity; b) the circular standard deviation (SD) related to α; c) the length of the mean vector (r), a measure of data concentration around the circle (year), ranging from 0 (scattered data) to 1 (concentrated data on the same direction).

The Rayleigh's Uniformity Test was used to calculate the probability of the null hypothesis that the data are uniformly distributed around the analyzed cycle ($P>0.05$) (Zar 1999). A significant result of the Rayleigh test ($P<0.05$) indicates that the data are not uniformly distributed and there is a significant mean angle or mean direction (Kovach 2004); i.e., there is seasonality in breeding activities of the studied anuran assemblage.

The influence of climatic factors on richness and abundance of calling males was tested with Spearman's correlation coefficient (r_s) (Zar 1999), using BioEstat 4.0 (Ayres et al. 2005). The same analysis was performed separately for species with abundance higher than 20 individuals. Because the maximal and minimal temperatures were themselves correlated, only the maximal temperature was considered in correlations. The absence of independence between temporally consecutive samples can be considered to be a problem in statistical tests and Type I errors can increase (Legendre and Legendre 1998). Currently, several methods can be used to remove autocorrelation between samples (Legendre and Legendre 1998; Rangel et al. 2006) considered a result of sampling bias for consecutive months. However, the temporal structure of data can be a result of temporal dependence between samples and, as in this case, naturally produced by physical or biological processes (Legendre and Legendre 1998). For this study, we assume that natural processes have an important influence on anuran calling activity. By considering group features (e.g. ectothermy, water-dependent reproduction, endogenous cycles), we expected a concentration of species breeding activity during the warmest and rainiest months, thus producing a temporal-dependent pattern among samples (months).

Results

Richness and diversity

During the 12 months of sampling, 18 anuran species belonging to six families were recorded: Bufonidae, Cycloramphidae, Hylidae, Leiuperidae, Leptodactylidae and Microhylidae. The family Hylidae was the richest in species (nine), followed by the families Leiuperidae and Leptodactylidae (each with three species). The families Bufonidae, Cycloramphidae and Microhylidade were represented by a single species (Table 1).

The mean collector curve calculated for all the three sites reached an asymptotic format with few variations (Figure 2), and we can therefore expect to find an increase in the number of species in the future. The highest diversity was observed in S3 ($H'=2.21$), followed by S1 ($H'=1.34$) and S2 ($H'=1.15$). The bootstrap comparison showed that S3 diversity was significantly higher than the diversity reported for the other sites ($P<0.01$, for both comparisons). There was no difference between S1 and S2 ($P>0.05$). Equitability decreased from S1 ($e=0.76$) to S3 ($e=0.53$) and S2 ($e=0.39$). The equitability of S1 was statistically higher than that of S2 ($P<0.001$). There was no significant difference in comparisons between S1 and S3 and/or S2 and S3 ($P>0.05$, for both comparisons).

Habitat use

Habitat use analysis for the 18 species recorded in calling activity at the three study sites showed six groups of species with overlap up to 70% (Figure 3):

- Species in permanent ponds: *Aplastodiscus perviridis*, *Pseudis minuta*, *Scinax fuscovarius* and *S. squalirostris*;
- Species in permanent ponds and neighbouring swampy regions: *Pseudopaludicola falcipes* and *Leptodctylus fuscus*;
- Species in permanent ponds and dam backwater: *Dendropsophus minutus*, *D. sanborni* and *Hypsiboas faber*;
- Species in permanent ponds, open dam and dam backwater: *H. pulchellus* and *L. ocellatus*;
- Species in permanent and temporary ponds: *S. granulatus* and *Elachistocleis bicolor*;
- Species in permanent and temporary ponds and dam backwater: *L. gracilis* and *P. cuvieri*.

The three species that also vocalized in streams, *C. achavalli, L. macroglossa* and *P.* cf. *gracilis*, were not grouped with other species.

Calling activity

The circular statistical analysis showed that richness and abundance of males in calling activity was seasonal (Rayleigh test) and concentrated between September and February (9.67 ± 1.97 species and 228.83 ± 69.48 individuals, respectively). An isolated peak in male abundance was recorded in April (Figure 4B), when 150 males

Table 1. Habitat use of 18 species of anurans in three sites in the municipality of Itaara, southern Brazil. Black bars=presence of calling males, grey bars=only visual record, (***)=species recorded afterwards the present study.

Family / Species	**S1**	**S2**	**S3**
Bufonidae	░	█	█
Chaunus achavali			
Melanophryniscus sp.	***		
Cycloramphidae			
Limnomedusa macroglossa	█		
Odontophrynus americanus	***		
Hylidae			
Aplastodiscus perviridis			█
Dendropsophus minutus		█	█
Dendropsophus sanborni		█	█
Hypsiboas faber		█	█
Hypsiboas pulchellus	█	█	█
Pseudis minuta			█
Scinax fuscovarius		░	█
Scinax granulatus	█		█
Scinax squalirostris			█
Leiuperidae			
Physalaemus cf. *gracilis*			█
Physalaemus cuvieri	█	█	█
Pseudopaludicola falcipes			█
Leptodactylidae			
Leptodactylus fuscus			█
Leptodactylus gracilis	█	█	█
Leptodactylus ocellatus	░	█	█
Microhylidae			
Elachistocleis bicolor			█
Species richness	**9**	**9**	**17**
Species recorded in calling activities	**5**	**8**	**17**

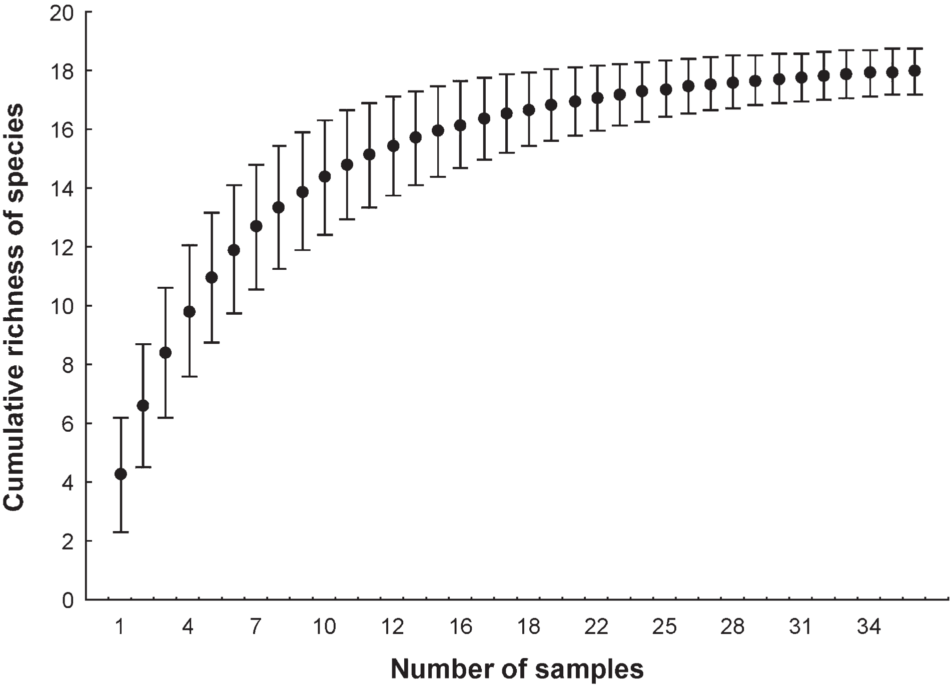

Figure 2. Collector's curve for anuran species recorded between August 2005 and July 2006 in the municipality of Itaara, southern Brazil. The central points represent the mean curve and the vertical bars represent their respective range (confidence interval of 95%).

of *H. pulchellus* were calling. The mean angle of the breeding activity was registered in November (Table 2, Figures 4A, 4B), although the length of the mean vector (r) did not show strong concentration in the same direction as the studied cycle (Table 2).

In general, richness and abundance of males in calling activity was greatest in spring (September to November), and decreased progressively in summer (December to February) and autumn (March to May). The lowest values were observed in winter (June to August) (3.33 ± 1.15 species and 61 ± 21.07 individuals) (Table 3).

Correlation analysis showed that photoperiod was the only climatic factor correlated with richness and abundance of calling males (r_s=0.70 and P=0.01; r_s=0.73 and P<0.01, respectively) (Figure 5). Seven of eight species analyzed (87%) correlated significantly with photoperiod (Table 4). The activity pattern of *H. pulchellus* was negatively related to photoperiod and temperature. The species *S. squalirostris* was not related to any variable. Photoperiod was positively correlated with mean maximal temperature (r_s=0.65; P=0.02).

Similarity analysis of temporal occurrence yielded four groups with overlap equal or over 70%, representing species groups with calling activities distributed in seasons (Figure 6):

- Species that called mainly during spring and summer: *D. sanborni, S. granulatus, P. minuta, P. cuvieri, P. falcipes,* and *L. gracilis*;
- Species that called only during summer: *H. faber* and *L. ocellatus*;

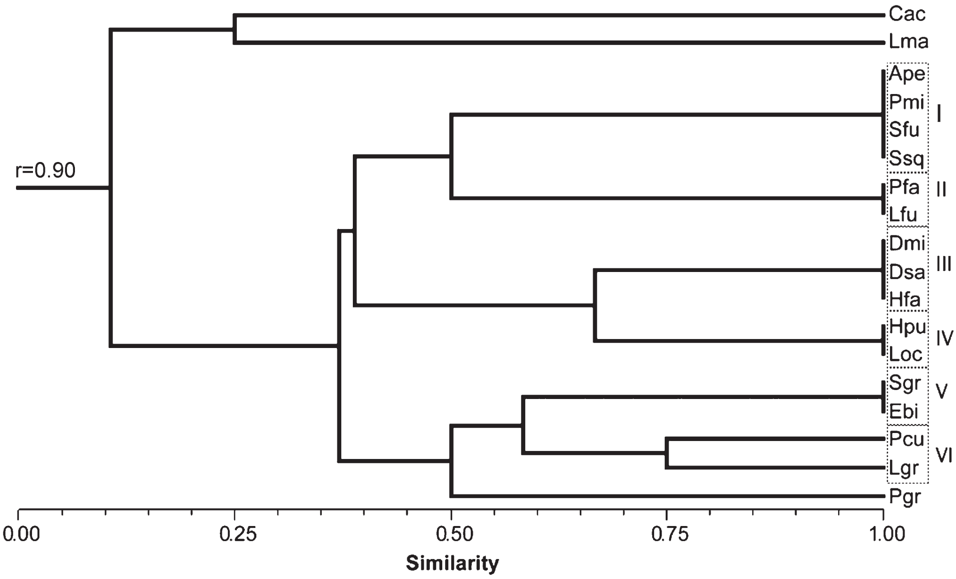

Figure 3. Similarity of habitat use for males of 18 anuran species recorded in three sites in the municipality of Itaara, southern Brazil. The rectangles indicate groups with overlap up to 90%. r=cophenetic correlation coefficient. Group I: species in permanent ponds; group II: species in permanent ponds and neighbouring swampy regions; group III: species in permanent ponds and dam backwater; group IV: species in permanent ponds, open dam and dam backwater; group V: species in permanent and temporary ponds; group VI: species in permanent and temporary ponds and dam backwater. Species: *Aplastodiscus perviridis* (Ape), *Chaunus achavali* (Cac), *Dendropsophus minutus* (Dmi), *D. sanborni* (Dsa), *Elachistocleis bicolor* (Ebi), *Hypsiboas faber* (Hfa), *Hypsiboas pulchellus* (Hpu), *Leptodactylus fuscus* (Lfu), *L. gracilis* (Lgr), *L. ocellatus* (Loc), *Limnomedusa macroglossa* (Lma), *Physalaemus* cf. *gracilis* (Pgr), *P. cuvieri* (Pcu), *Pseudis minuta* (Pmi), *Pseudopaludicola falcipes* (Pfa), *Scinax fuscovarius* (Sfu), *S. granulatus* (Sgr), *S. squalirostris* (Ssq).

- Species that called during spring: *D. minutus* and *S. fuscovarius*;
- Species that called throughout the year, except in summer: *H. pulchellus* and *S. squalirostris*.

Six species were not included in any groups. Males of *Chaunus achavali* were only active in winter (Table 3). Males of *Limnomedusa macroglossa* were active in late winter and early spring. Males of *E. bicolor* and *Physalaemus* cf. *gracilis* called in spring and late summer (February). Males of *A. perviridis* and *L. fuscus* called in one month and in low abundance.

Discussion

Richness, diversity and habitat use

Most of the species recorded during this study are typical of grasslands (*sensu* Duellman 1999). *Hypsiboas faber* is associated with the Atlantic Forest and occurs also on forest borders or gaps, and sometimes at impacted areas (Haddad 1998). *Aplastodiscus perviridis* has been reported previously only for northwestern Rio Grande do Sul (Kwet 2001); its southern distribution range was recently expanded to

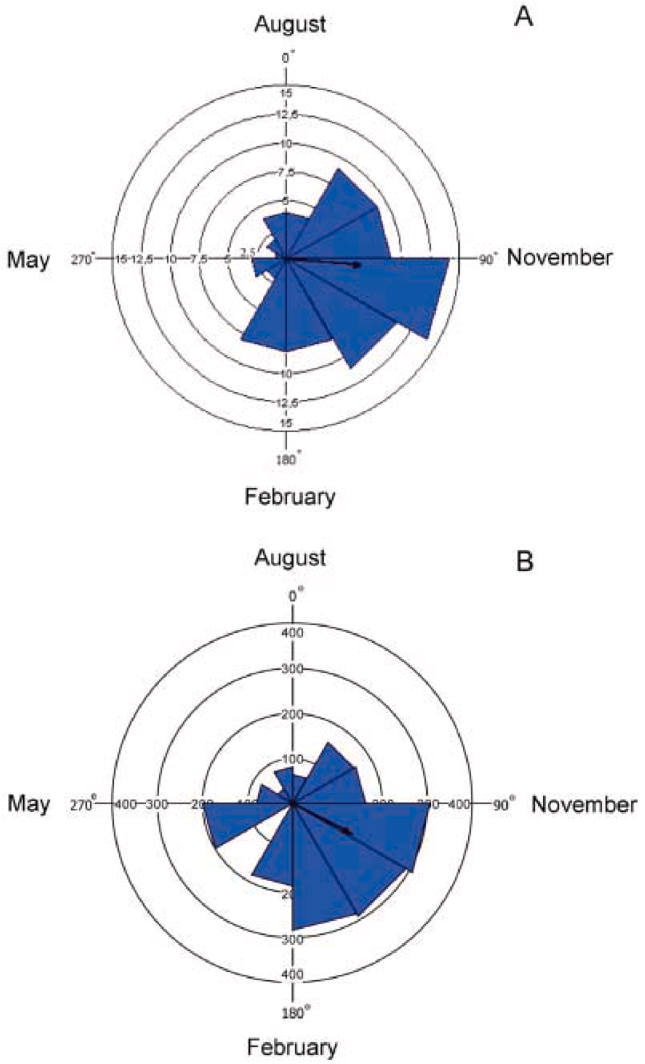

Figure 4. Rose diagram of circular analysis of richness (A) and abundance (B) of calling males of 18 anuran species in calling activity between August 2005 and July 2006 in the municipality of Itaara, southern Brazil. The angles represent the months. The length of the mean vector (r) is a measure of concentration of data around the year.

our study area (Both et al. 2006). *Physalaemus* cf. *gracilis* has also been previously reported only for the northeastern portion of Rio Grande do Sul (Kwet 2001). The occurrence of species that are typical of other geographic regions in our study area emphasizes its importance as a transition zone between zoogeographical domains, as described by Lema (1984).

The rarefaction curve pointed to a greater number of species than the number recorded during our study, which was actually confirmed during fieldwork conducted after the present study ended. In September 2006, after heavy rain, we recorded *Melanophryniscus* sp., an undescribed species (Baldo, D., unpublished data)

Table 2. Results of circular statistical analysis testing seasonality in calling activity of anurans (richness and abundance of males) registered in the central region of Rio Grande do Sul, Brazil.

Variable	Richness	Abundance
Observations (n)	75	1842
Mean angle (α)	95.265°	117.925°
Length of mean vector (r)	0.427	0.361
Circular standard deviation (SD)	74.798°	81.798°
Rayleigh test of uniformity (*P*)	<0.01	<0.01

Table 3. Records of calling activities for 18 anurans species between August 2005 and July 2006. Black bars=record of calling activity, gray bars=visual record.

	2005					**2006**						
Months	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**
Species												
Aplastodiscus perviridis				■	■							
Chaunus achavali	■	▨	▨			▨					■	■
Dendropsophus minutus	■	■	■	■	■							
Dendropsophus sanborni		■		■	■	■	■					
Elachistocleis bicolor			■	■	■		■					
Hypsiboas faber						■	■					
Hypsiboas pulchellus	■	■	■	■	■			■	■	■	■	■
Leptodactylus fuscus				■								
Leptodactylus gracilis				■	■	■						
Leptodactylus ocellatus	▨	▨	▨	▨	■	■	■	▨				
Limnomedusa macroglossa	■	▨	▨	■	■	■	▨	▨	▨	▨		
Physalaemus cuvieri			■	■	■	■	■					
Physalaemus cf. *gracilis*		■	■				■					
Pseudis minuta		■	■	■	■	■	■		■			■
Pseudopaludicola falcipes		■	■	■	■	■						
Scinax fuscovarius	▨	■	■	■								
Scinax granulatus		■		■	■	■	■					
Scinax squalirostris		■	■	■		▨	■	■				■
Species richness	**4**	**9**	**9**	**14**	**11**	**8**	**8**	**2**	**3**	**1**	**2**	**4**
Total abundance	**63**	**156**	**160**	**304**	**289**	**281**	**183**	**6**	**199**	**81**	**39**	**81**

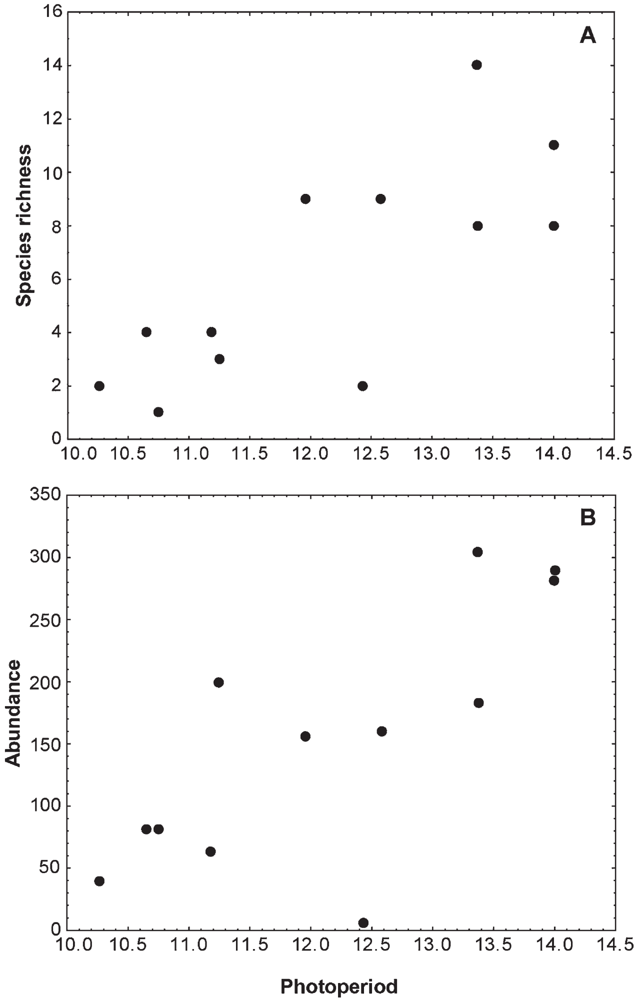

Figure 5. Scatter diagrams representing the correlation of the photoperiod with richness (A) and with abundance (B) of anurans in calling activities (r_s=0.70 and P=0.01; r_s=0.73 and P<0.01, respectively) between August 2005 and July 2006.

Table 4. Correlations between abundance of eight anuran species in calling activities and environmental variables between August 2005 and July 2006. The species analyzed presented abundance higher than 20 individuals. (*) follows significant correlations (P<0.05). Species abbreviations follow Figure 3.

	Dsa	Hpu	Pmi	Sgr	Ssq	Pcu	Pfa	Ebi
Rainfall	−0.13	−0.04	0.08	−0.16	0.33	−0.15	−0.12	0.36
Relative air humidity	−0.34	0.21	−0.10	−0.30	0.15	−0.19	−0.03	−0.26
Maximal temperature	0.52	−0.72*	0.22	0.40	−0.36	0.52	0.06	0.45
Minimal temperature	0.44	−0.77*	0.08	0.36	−0.53	0.41	0.01	0.31
Photoperiod	0.83*	−0.78*	0.76*	0.80*	−0.12	0.84*	0.71*	0.68*

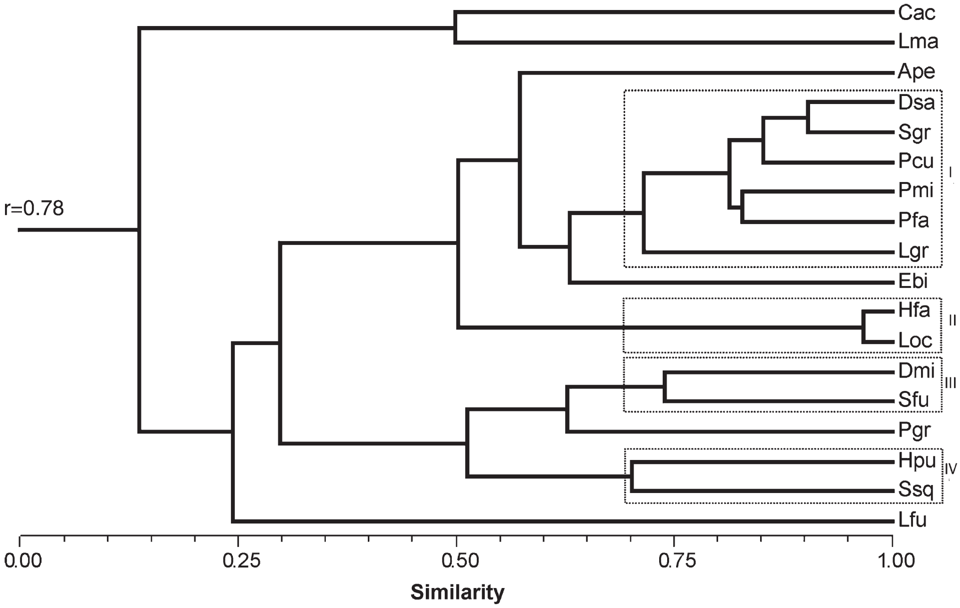

Figure 6. Similarity of calling season for males of 18 anuran species recorded between August 2005 and July 2006. The rectangles indicate groups with overlap greater than 70%. r=cophenetic correlation coefficient. Group I: species that called mainly during spring and summer; group II: species that called only during summer; group III: species that called during spring; group IV: species that called throughout the year, except in summer. Species abbreviations follow Figure 3.

and *Odontophrynus americanus* in S1. Approximately 90 males of the first species were reported during a single night. On the same night we also recorded 20 males of *O. americanus*, which had been previously found in the proximities of S2 during our study.

The greatest diversity was observed in S3, and this may be associated with site heterogeneity, such as water body types and the complexity of vegetation structure on banks and ponds. Heterogeneity is considered important for the coexistence of anuran species by several authors (e.g. Cardoso et al. 1989; Rossa-Feres and Jim 1996; Parris and McCarthy 1999; Hazell et al. 2001). This study area is the only one with water bodies that keep water for a long time and with several temporary ponds.

Reproduction that relies on lentic water bodies for spawning or for tadpole development is one of the most primitive modes usually found in anurans (Duellman and Trueb 1994). Most of the species recorded in S3 show some dependence on lentic water. Reproductive modes (*sensu* Haddad and Prado 2005) 1 and 11 (eggs and exotrophic tadpoles in lentic water and foam nest floating on pond; exotrophic tadpoles in ponds, respectively) are typical of 12 species studied. *Hypsiboas faber* exhibits mode 4 (eggs and early larval stages in natural or constructed basins, subsequent to flooding, exotrophic tadpoles in ponds or streams), *A. perviridis* mode 5 (eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds or streams), and *L. fuscus* and *L. gracilis,* mode 30 (foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds). All the modes mentioned have some degree of proximity with lentic water bodies. Only *L. macroglossa* and *C. achavali* (mode 2, eggs and exotrophic tadpoles in lotic water) were associated with and found near lotic water bodies.

Site S2, the least diverse and equitable, is part of the dam. Dam habitats have intermediate features between lotic and lentic environments, and harm the reproduction of many species (Esteves 1998). The destruction of marginal ponds and the changes in physical and chemical features of water are the main harmful characteristics of dams (Esteves 1998). In the open dam, only *H. pulchellus* and *L. ocellatus* were observed engaging in calling behavior. All other species were observed in backwaters (Figure 3).

The diversities of S1 and S2 did not differ, but S1 equitability was greater. We observed *L. macroglossa* exclusively in this area. This species showed lower spatial overlap with other species. *Limnomedusa macroglossa* was usually found on rocks and superficial soils near the water course and temporary ponds, habitats available at S1. This species can be a bioindicator of these habitat types (Gudynas and Gehrau 1981), and is cited as endangered for Uruguay (Maneyro and Langone 2001). Segalla and Langone (2004) noticed the disappearance of this species from dammed-up rivers due to construction of a hydroelectric plant in Paraná state. The dam sampled for this study was designed for water supply and is small if compared with dams built for hydroelectric plants. In spite of its small size and the proximity between S1 and S2, we did not find individuals of *L. macroglossa* in S2. The absence of *L. macroglossa* in S2 supports the idea that dams are harmful to the species. Studies on dam impact on *L. macroglossa* populations in Rio Grande do Sul are nonexistent, but our observations may be a stimulus for their development.

Spatial overlap in habitat use was high and 15 species (83%) showed spatial overlap higher than 70% with at least one other. Of all species belonging to the six groups with spatial similarity higher than 70%, only *P. cuvieri* and *L. gracilis* were also grouped on the temporal axis. Thus, spatial and temporal resource partitioning can be considered complementary.

Calling activity

The calling activity observed in this study was seasonal, and circular analysis results indicate greater activity between September and February. These months had the highest temperatures and longest photoperiods. Similar results of circular analyses were obtained for three years of the four-year study conducted in Pantanal, where greater calling activity was correlated with the rainy season (November through January) (Prado et al. 2005).

Anuran breeding activity is influenced by climatic factors, mainly rainfall, air humidity, temperature and photoperiod (e.g. Hatano et al. 2002; Conte and Machado 2005; Canelas and Bertoluci 2007; Santos et al. 2007). Rainfall and temperature are the climatic factors considered determinant for breeding activities of anurans in tropical and subtropical regions in Brazil (e.g. Bernarde and Machado 2001; Bertoluci and Rodrigues 2002a; Conte and Machado 2005; Prado et al. 2005; Vasconcelos and Rossa-Feres 2005). However, neither rainfall nor temperature correlated with breeding season in at least two studies (Pombal 1997; Bernarde and Anjos 1999). In the present study, anuran calling activity (richness and abundance) of the assemblage was explained only by photoperiod, but this climatic factor was closely correlated with maximal temperature. Most of the analyzed species (n=7) followed the assemblage pattern and their calling activity was positively associated with photoperiod. Only *H. pulchellus* was negatively correlated with photoperiod and temperature, indicating that calling activities of this species were related to winter (low temperature and shorter days).

We expected an absence of correlation between breeding activities and rainfall. Because rain is well distributed throughout the year, it does not characterize a seasonally variable factor that would explain anuran breeding activity in the study area. We expected the same result for relative air humidity, which has no seasonal variation and whose mean was over 70% (www.cptec.inpe.br).

As opposed to rainfall and humidity, temperature has a seasonal variation characterized by warm (spring and summer) and cold (autumn and winter) periods, likely to correspond to higher or lower anuran calling activity in the study area. Thus, we might have expected a correlation between temperature and calling activities, but this was not seen. The presence of species with greater thermal tolerance (e.g. *C. achavali, H. pulchellus* and *S. squalirostris*), which also called during cold months, could have inhibited the expected correlation. However, the correlations obtained for the most abundant species corroborate the assemblage pattern. Therefore, the hypothesis above was unsupported because only the calling activity of *H. pulchellus* was correlated (negatively) with temperature.

The strong correlation of anuran calling activity with photoperiod may be due to the use of that climatic factor as a cue of environmental conditions suitable for reproduction (e.g. higher temperatures for calling activities and/or embryonic and larval development). A complex interaction between photoperiod and temperature controls anuran biological rhythms by triggering hormonal stimuli linked to reproduction, including gametogenesis (Duellman and Trueb 1994; Saidapur and Hoque 1995) and calling activities (see references in Hatano et al. 2002). These two climatic factors play important roles in the timing of reproductive cycles of amphibians, mainly among species from temperate zones because of their predictable seasonal changes (Pough et al. 2001). However, photoperiod is considered the most common cue for seasonal change for ectotherms in temperate environments because it gives relatively noise-free information about the time of the year, whereas variation in temperature is highly non-predictable (Gotthard 2001).

The lack of studies on temporal occurrence of anurans in high Neotropical latitudes, where precipitation is not seasonal, restricts the interpretation of our results. In the Pampean area of the most southern Brazil, Santos et al. (in press) found greater species richness in the warmest period of the year, although rainfall and temperature explain little about seasonal anuran occurrence. Therefore, breeding activity patterns of austral assemblages may have more similarity with those of assemblages in temperate regions, for which variations of photoperiod and temperature are important for the breeding activity of species (Duellman and Trueb 1994; Pough et al. 2001).

Although we found groups of species with calling activity related to seasons of the year in the similarity analysis, we also found a high overlap of species activity in spring and summer. The overlap across species during this period was recorded for tropical (e.g. Bertoluci 1998; Cardoso and Haddad 1992; Pombal 1997) and subtropical assemblages (e.g. Basso 1990; Di-Bernardo et al. 2004; Conte and Machado 2005). This pattern indicates that calling season is less important for partitioning anuran reproductive resources (Basso 1990) in seasonal regions (Santos et al. 2007) although this interpretation is not always supported (see Eterovick and Sazima 2000; Kopp and Eterovick 2006). In the present study, calling season and habitat use, together explained breeding resources partitioning and species coexistence. Other studies have also recorded differential habitat use for anuran species (e.g. Collins and Wilbur 1979; Bernarde and Anjos 1999; Bertoluci and Rodrigues 2002b; Santos et al. 2007), which can be related to ecophysiological adaptations and/or evolutive constraints (Heyer et al. 1975; Eterovick and Sazima 2000).

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