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Seasonality in anuran activity and calling season in a Brazilian subtemperate wetland

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Abstract

Background: Most tropical regions have a climate characterized by marked seasonal rainfall patterns, and these seasonal patterns of rainfall directly affect anuran activity. However, in regions with temperate climates, the main aspect of climate related to anuran activity is the thermal regime. Thus, transitional climate regions represent good opportunities to study the effect of abiotic factors on anuran activity. In this study, we present new data on the activity pattern and calling season of Neotropical anurans in a subtemperate climate. Anuran activity was assessed based on the rate of capture of specimens in pitfall traps and calling surveys. The field study was conducted between May 2010 and April 2011 in wetlands in southernmost Brazil.

Results: An analysis based on directional (circular) statistics showed that general activity in the studied anurans was significantly seasonal. In addition, the general activity pattern of most species was regulated by temperature, not by rainfall, and approached that observed in regions with a temperate climate. However, we did not record a well-defined peak in the number of species displaying calling activity. This parameter did not exhibit any influence of temperature variations or rainfall.

Conclusions: The observed general activity pattern is different from that expected for the majority of anurans inhabiting eastern South America. The present study showed that the general activity patterns of most anurans in the wetland region in southernmost Brazil are regulated by temperature and not rainfall, similar to the pattern of anuran assemblies from temperate climates. However, the nonexistence of a significant relationship between calling activity and any of the environmental variables tested suggests the presence of a different environmental factor (e.g., photoperiod or the length of the hydroperiod of the relevant water bodies) as a trigger for the levels of general calling activity.

Keywords: Anuran; Behavior; Calling; Temperature; Wetlands

Background

Many environmental factors act on such anuran activity patterns as reproduction, movements, and foraging. For example, reproductive activity depends on the acoustic quality of the habitat, availability of females, and presence and density of males at the breeding site (Both and Grant 2012). Nevertheless, reproduction is primarily associated with climate-specific abiotic factors (Bertoluci 1998; Oseen and Wassersug 2002; Xavier and Napoli 2011). Although some Neotropical anuran species breed throughout the year, general activity and reproduction

typically exhibit remarkable seasonality (Jorgensen 1992; Bertoluci 1998). Other activities performed by anurans, such as dispersion, migration, or foraging, also appear to respond primarily to climatic variables. A wide range of methods are currently available for evaluating anuran activity, and the capture rate is the most frequently used indicator of general activity (Oliveira et al. 2013; Martins et al. 2014). Indeed, capture rate is an indirect measure of any activity performed by animals on the surface of a substrate (e.g., foraging, habitat exploration, dispersal, and migrations), as such activities increase their capture probability.

Associations between peaks of general activity and a particular behavior driven by physiological or metabolic events are poorly studied in the wild, especially in Neotropical anurans. An exception is reproductive activity,

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which can be evaluated through calling surveys. Environmental factors such as light intensity, relative humidity, and air temperature are relatively well-documented habitat cues that affect the calling activity of anurans (Fukuyama and Kusano 1992; Hatano et al. 2002; Almeida-Gomes et al. 2007). In contrast, photoperiod is a less well-studied climatic factor relative to seasonal changes in anuran behavior (Bradshaw and Holzapfel 2007). There is evidence that amphibians in subtemperate wetlands could be tracking photoperiod (as previously reported for temperature and rainfall) to determine their seasonal variations in activity (Canavero and Arim 2009). In addition, there has recently been significant improvement in the number of ecological studies of amphibians in the Neotropics, though most of these studies are concentrated in forested or tropical open habitats. Less attention has been dedicated to subtemperate open habitats, such as wetlands. Southern Brazilian wetlands possess unique climatic characteristics, such as colder winters, in comparison with other Brazilian regions (Huckembeck et al. 2012; Oliveira et al. 2013). Given the divergent opinions regarding the effects of climatic factors on the activity patterns of anurans (Oseen and Wassersug 2002; Saenz et al. 2006), transitional climatic regions represent an important natural laboratory for testing ecological hypotheses concerning the evolutionary process in ectotherms. In most Brazilian habitats (and other tropical areas), there is a small annual thermal amplitude (Maluf 2000), and precipitation appears to be the main determining factor of anuran activity patterns (Heyer 1973; Boquimpani-Freitas et al. 2007; Oliveira et al. 2013). However, in temperate climate regions, annual temperature variation appears to be the main factor that determines ectothermic activity (Gilbert et al. 1994; Navas and Bevier 2001; Oseen and Wassersug 2002). However, it is important to emphasize that studies performed in transitional regions between tropical and temperate climates have yielded conflicting results (Bernarde and Anjos 1999; Bernarde and Machado 2001; Conte and Rossa-Feres 2006).

The southernmost region of Brazil is in a transition zone between subtropical and temperate climates (Maluf 2000), thus constituting an important study area for understanding the activity patterns (reproductive or not) of Neotropical anurans. The relatively low temperatures, by tropical standards, and unpredictable rainfall can act as abiotic filters to limit activity and the establishment of species in this region. Studies on anuran general activity are important for species conservation purposes (Eterovick et al. 2005) and typically yield information about the species' ecology and natural history (Santos et al. 2008). In Brazil, especially in Rio Grande do Sul State, the science of anuran general activity has not yet been pursued (Oliveira et al. 2013); thus, there is a lack of knowledge of this subject.

The present study aimed to evaluate the role of abiotic factors in the general activity pattern during the vocalization season in species associated with subtemperate wetlands in southernmost Brazil.

Methods

Study site

The study was conducted between May 2010 and April 2011 in an area formed by a mosaic of temporary wetlands (32° 08' S and 52° 11' E) located in Rio Grande, Rio Grande do Sul, southernmost Brazil. The samples were concentrated in an area of approximately 200 ha, which included a portion of the most extensive water bodies with the longest hydroperiods found at the study site. The predominant vegetation consisted of native field grass, which was relatively well preserved (Oliveira et al. 2013). The local climate was classified as humid subtemperate with an annual average temperature of 18.1 °C and an average temperature of 12.7 °C during the coldest month. The climatic seasonality in the study area was characterized by warm and cold seasons, which differed from much of the Brazilian territory climatic seasonality marked by dry and wet seasons (Maluf 2000; Tozetti et al. 2010).

During sampling, the mean minimum temperature of the air during the warm season ranged from 13.08 to 21.25 °C. During the cold season, the mean minimum temperature of the air ranged from 6.45 to 16.43 °C. The rainfall accumulation was 347.7 mm. Because of the small monthly variation in rainfall, the wettest period was defined by plotting the rainfall data (16.7 mm). June, July, October, and December of 2010 and January and April of 2011 were defined as dry months. The humid months were May, August, September, and November of 2010 and February and March of 2011. The climatological data were obtained from Meteorological Station 83,995 of Rio Grande, located 5 km from the study area.

Evaluation of anuran activity

Anuran activity was divided into two types: (1) general activity and (2) calling activity. These forms of activity were evaluated using the following two methods: general activity was evaluated in terms of the capture rate in pitfall traps with drift fences (Greenberg et al. 1994), and calling activity was evaluated through calling surveys. The capture rate in this study was considered an indicator of general activity. General activity corresponded to any activity by the animals on the surface of the substrate (e.g., foraging, habitat exploration, searching for partners, and migration) and increased the probability of capture. Because these methods are common in herpetology, they will be described only briefly in this paper.

We used two pitfall sets, each with two 40-m-long lines, distributed at selected locations around the water bodies (preferential sampling; Krebs 1999), with a distance of 3 km

between them. These sites were defined in a manner so that flooding of the buckets was avoided. Each line had four 100-L buckets united by drift fences, for a total of 16 buckets (for more details, see Ximenez et al. 2014). The traps remained open for four consecutive days per month between May 2010 and April 2011. Each captured animal was identified and measured. Whenever possible, the sex of the specimen was determined. The animals were then marked by toe clipping and released 5 m away from one of the ends of the capture trap. The markings used aimed to differentiate between captures and recaptures. Recaptures represented less than 0.001 % of the captures.

A calling survey was performed twice per month between 1800 and 2300 h from May 2010 to April 2011 for a sample total of 120 h. To standardize the sampling effort, all samples were collected in a predefined area of approximately 1 ha located in the vicinity of the pitfall traps, for a total of two sampling sites. An estimate of the number of calling males was made during each sampling night for each site. The data were grouped into one of the following abundance classes (adapted from Bertoluci and Rodrigues 2002): a) 1–4 individuals in calling activity, b) 5–9 individuals, c) 10–20 individuals, or d) >20 individuals. In terms of the duration of the vocalization season, the species were classified as follows: 1) annuals—species that vocalized more than 70 % of the year or were recorded for at least 2 months in each season (warm and cold); 2) warm season—species that vocalized only during the warm months (November to April); and 3) cold season—species that vocalized only during the cold months (May to October). We calculated the frequency of calling occurrence, which corresponded to the number of samples (= months) in each vocalizing species divided by the total number of samples (12) of each species.

Data analysis

For all statistical analyses, we used data on anuran abundance to evaluate general activity and richness indices to evaluate calling activity. To evaluate general activity, only species with ten or more captured individuals were considered, thus making the analysis more robust. Additionally, arboreal species and/or species with “digital discs” were excluded from the analysis of general activity because they were able to escape from the traps (Enge 2001; Oliveira et al. 2013).

A circular statistical analysis (Zar 1999) was applied to evaluate the existence of a seasonal pattern in both general (estimated by the capture rate in traps) and calling activities (estimated by the number of calling species). The months were represented numerically by angles (intervals of 30 °C), and both the number of captures in the traps and number of calling species each month were used as frequencies for each month observed (Prado et al. 2005; Both et al. 2008). The following parameters were

considered in the analysis: 1) the median angle (μ), which corresponded to the average period of the year (sampled days) in which most of the species were active and 2) the length of the mean vector (r), which indicated the clustering level of observations around μ . This value varied from 0 (least clustering) to 1 (greatest clustering), and 3) the circular standard deviation (SD). The seasonality tendencies for both activities were assessed using a non-parametric Rayleigh test (z). A significant Rayleigh test indicated the seasonal activity of the anuran assemblage studied. The niche breadth of the calling season of each species was calculated using the inverse of the Simpson diversity index (Simpson 1949):

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

In the equation, p is the proportion of use (calling registers) of temporal category i (month survey), and n is the total number of categories. The values obtained for the diversity index as applied in our study range from 1 to 10, in which 1 corresponds to exclusive calling in only 1 month (specialists) and 10 corresponds to the use of all months in the same proportion (generalists; see Pro-tázio et al. 2014). For a temporal niche analysis, we used the minimum number of calling males previously defined in each abundance class category in the sample (adapted from Bertoluci and Rodrigues 2002). Niche overlap was calculated using Pianka’s overlap index (Pianka 1973). The overlap index between species 1 and 2 (O_{12}) with temporal calling activities p_{1i} and p_{2i} , respectively, was calculated as follows:

$$O_{12} = O_{21} = \sum_{i=1}^n p_{2i}p_{1i} / \sqrt{\sum_{i=1}^n (p_{2i}^2)(p_{1i}^2)}$$

In the equation, p represents the proportion of calling males in each month category i , n is the number of categories (months), and j and k represent compared species. The possible overlap scores range from 0 (no overlap) to 1 (complete overlap). We used a null model to investigate the presence of nonrandom patterns in the temporal distribution of calling. This null model was based on the niche overlap module of EcoSim (Gotelli and Entsminger 2003). For these null models, a data matrix with species, months, and the proportion of the number of calling males in each month was created. We performed 1000 randomizations of the data set to simulate random patterns that would be expected in the absence of seasonality in calling behavior (Gotelli and Graves 1996).

Comparisons of the capture rates between the months were analyzed using a Kruskal-Wallis analysis of variance followed by a Kruskal-Wallis post hoc test when necessary (Zar 1999). We applied a Mann-Whitney test to evaluate

the variation in general activity between the warm/cold and dry/humid months (i.e., a Mann–Whitney *U* test: Zar 1999). A multiple regression was performed to detect possible associations between the climatic variables and the general and calling activities of the anurans (Zar 1999). The following climatic variables were considered for all regressions: maximum air temperature, minimum air temperature, relative air humidity, and accumulated rainfall. All statistical tests were performed with a significance level of 0.05 using the program Statistica 8.0.

Results

General activity

The circular statistical analysis revealed that anuran general activity was significantly seasonal ($P < 0.001$; Table 1). We captured 535 individuals belonging to nine species (Table 2). General activity was greater during warm months ($N = 392$) than during cold ones ($N = 143$, $U = 160.50$, $P = 0.008$). Multiple regression revealed the existence of a significant and positive relationship between the general activity, relative humidity, maximum and minimum temperatures, and accumulated rainfall ($R^2 = 0.22$, $P = 0.05$; Table 2). However, general activity did not vary significantly between dry and humid months (Table 2). When the species were evaluated separately, the relationship between general activity and abiotic variables was only significant for *Physalaemus biligonigerus* ($R^2 = 0.40$, $P < 0.001$), *Pseudopaludicola falcipes* ($R^2 = 0.25$, $P = 0.02$), *Leptodactylus gracilis* ($R^2 = 0.23$, $P = 0.03$), and *Elachistocleis bicolor* ($R^2 = 0.51$, $P < 0.001$; Table 1).

General activity was significantly higher during warm months for *E. bicolor* ($N = 103$), *L. gracilis* ($N = 27$), and *P. biligonigerus* ($N = 53$) than during cold months ($N = 1$, $N = 4$, $N = 13$; $U = 77.50$, $P < 0.001$; $U = 130.00$, $P < 0.001$; $U = 130.00$, $P < 0.001$, respectively; Table 2). Only *P. falcipes* presented greater general activity during cold months ($N = 16$) than during warm months ($N = 1$; $U = 190.00$, $P < 0.01$; Table 2). The general activity of *Leptodactylus cf. latrans*, *Physalaemus gracilis*, and *Pseudis minuta*

did not vary significantly between warm and cold months (Table 2). There was no significant variation between dry and humid months for any of the species (Table 2). The multiple regression model showed a positive and significant relationship between the maximum air temperature, minimum air temperature, relative air humidity, accumulated rainfall, and activities of *P. biligonigerus* ($R^2 = 0.40$, $P = 0.0004$), *P. falcipes* ($R^2 = 0.25$, $P = 0.02$), *L. gracilis* ($R^2 = 0.23$, $P = 0.03$), and *E. bicolor* ($R^2 = 0.51$, $P = 0.000007$). The activity of the other species did not respond significantly to any of the climatic variables (Table 2).

Calling activity

The circular statistical analysis revealed that anuran calling activity was not significantly seasonal (Table 1). Calling records were obtained for 13 species distributed in six families (Fig. 1). Two periods with a higher number of calling species were detected: between August and November and between January and March. A peak in the number of calling species occurred during October ($N = 7$ species) and September, February, and March ($N = 6$) (Fig. 1).

Regarding calling activity, five species were classified as “annual” (*Dendropsophus sanborni*, *Hypsiboas pulchellus*, *Physalaemus* sp., *P. minuta*, and *Scinax squalirostris*), six as “warm season” (*Dendropsophus minutus*, *E. bicolor*, *L. gracilis*, *Odontophrynus maisuma*, *P. falcipes*, and *Rhinella dorbignyi*) and two as “cold season” (*L. cf. latrans* and *Scinax granulatus*). The species with a higher frequency of calling were *H. pulchellus* (83.33 %) and *S. squalirostris* (75 %), whereas *O. maisuma* and *L. cf. latrans* only called during 1 month (Fig. 1). The number of species exhibiting calling activity did not show a significant relationship to any of the environmental variables ($R^2 = 0.22$; $P = 0.53$; sample number = 12). Because of the difficulty in differentiating the vocalizations of *P. biligonigerus* and *P. gracilis*, these species were not differentiated and were recorded as *Physalaemus* sp.

For all species, a higher calling activity occurred during warm months, which coincided with a peak in the capture rate in the traps. However, when examining the species separately, the calling and general activity periods only overlapped for *E. bicolor*, *L. gracilis*, and *Physalaemus* sp. Males of *L. cf. latrans* had a calling activity peak (October) that occurred before the general activity peak (November to January). An identical result occurred for *P. minuta*, which had calling peaks in September, October, March, and April, and general activity peaks in November, December, June, and July. However, *P. falcipes* males concentrated their vocalizations during warm months (November and January) and presented the greatest general activity during cold months (August and September). It should be emphasized that this comparison between the

Table 1 Anuran activity patterns in subtemperate wetlands of Brazil. The seasonality evaluation of general (estimated by the number of captures) and calling activities of anurans in subtemperate wetlands in southernmost Brazil

Variables	Annual cycle 2010–2011	
	General activity	Calling activity
Number of observations (<i>N</i>)	535	55
Mean vector (μ)	335.172°	315.000°
Mean vector length	0.449	0.159
Circular deviation pattern (SD)	72.523°	109.952°
Rayleigh test (<i>P</i>)	<0.001	0.251

Table 2 Associations between anuran activity and different abiotic variables

Family	Captures		Annual activity variation		Activity variation between seasons				Activity and climatic factors	
	N(warm/cold)	N(dry/humid)	Kruskal-Wallis results		Mann-Whitney results for				Multiple regression results	
			H	P	Warm/cold		Dry/humid		R ²	P
Hylidae										
<i>Pseudis minuta</i> (Günther, 1858)	29/16	25/20	10.59	0.48	287.50	0.99	279.50	0.86	0.09	0.48
Leiuperidae										
<i>Physalaemus biligonigerus</i> (Cope, 1861)	53/13	27/39	24.03	0.01*	130.00	<0.001*	232.50	0.25	0.40	0.0004*
<i>Physalaemus gracilis</i> (Cope, 1861)	34/18	30/22	19.66	0.05*	252.50	0.43	283.50	0.92	0.13	0.26
<i>Pseudopaludicola falcipes</i> (Hensel, 1867)	1/16	4/13	15.75	0.15	190.00	<0.01*	256.00	0.51	0.25	0.02*
Leptodactylidae										
<i>Leptodactylus gracilis</i> (Duméril and Bibron, 1840)	27/4	14/17	20.54	0.03*	130.00	<0.001*	248.00	0.41	0.23	0.03*
<i>L. cf. latrans</i>	141/63	133/71	35.47	0.0002*	285.50	0.96	242.50	0.35	0.10	0.43
Microhylidae										
<i>Elachistocleis bicolor</i> (Guérin-Méneville, 1838)	103/1	50/54	40.07	0.0001*	77.50	<0.001*	259.59	0.56	0.51	0.000007*
Bufoidea										
<i>Rhinella dorbignyi</i> (Duméril and Bibron, 1841)	2/8	3/7	-	-	-	-	-	-	-	-
Cycloramphidae										
<i>Odontophrynus maisuma</i> (Rosset, 2008)	4/2	3/3	-	-	-	-	-	-	-	-
All species	535	535	31.59	<0.01*	160.50	0.008*	265.00	0.63	0.22	0.05*

A comparison and correlation between anuran activity (evaluated by the number of captures) and different abiotic variables between May 2010 and April 2011 in subtemperate wetlands in southernmost Brazil. The number of samples (n samples) used for all statistical tests was 48. See "Methods" section for a detailed explanation

N the number of captures in pitfalls, NA not applicable

*Significant variation

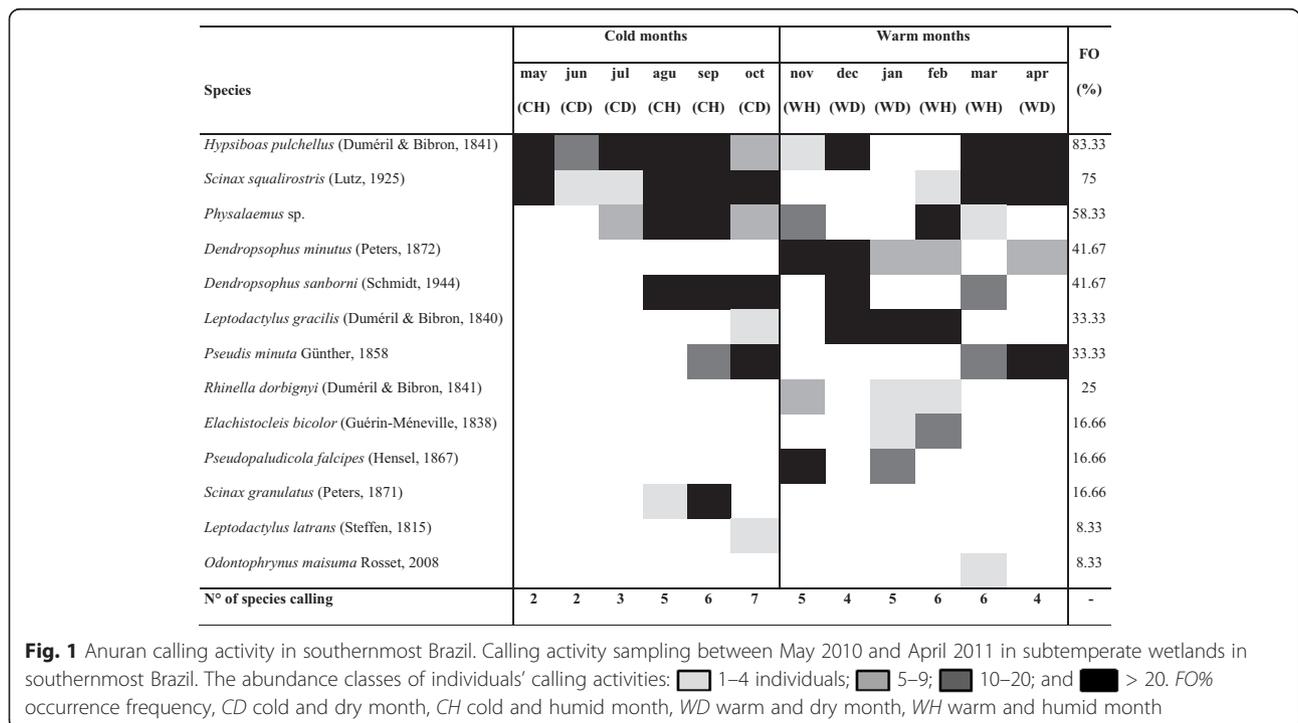


Fig. 1 Anuran calling activity in southernmost Brazil. Calling activity sampling between May 2010 and April 2011 in subtemperate wetlands in southernmost Brazil. The abundance classes of individuals' calling activities: □ 1–4 individuals; ▒ 5–9; █ 10–20; and █ > 20. FO% occurrence frequency, CD cold and dry month, CH cold and humid month, WD warm and dry month, WH warm and humid month

calling and general activity periods was not possible for *R. dorbignyi* and *O. maisuma* because of the low number of captures (<10), similar to the hylids because of their ability to climb and escape from the traps (with the exception of *P. minuta*).

Greater values of temporal niche breadth were observed for *H. pulchellus* ($B = 6.72$), followed by *D. sanborni* ($B = 4.81$), and *Physalaemus* sp. ($B = 4.13$) (Table 3). Lower values were observed for *E. bicolor*, *L. cf. latrans*, and *O. maisuma* ($B = 1$). A niche overlap analysis revealed that the patterns varied from complete overlap to no overlap between species (Table 3). The mean overlap was 0.227 ± 0.267 , and only 10.4 % of all species pairs showed a temporal overlap greater than 0.6. Greater overlap values were observed for *R. dorbignyi* and *P. falcipes* (0.9845988), *Physalaemus* sp. and *S. fuscovarius* (0.731399), and *S. squalirostris* and *H. pulchellus* (0.9035631). The null model showed that the observed temporal niche overlap index (0.227) did not vary significantly more than expected by chance (0.218) ($P > 0.05$). This suggests that the assemblage calling activity is randomly distributed.

Discussion

Our data suggest that the general activity of the studied anuran populations exhibits a seasonal pattern predominantly related to air temperature but not rainfall. This pattern was different from that expected for the majority of eastern South America (Bertoluci 1998; Vasconcelos et al. 2010). The relatively harsh winter in southernmost Brazil possibly imposes limitations on anuran activity due to a reduction in metabolic rate (Lillywhite 1974). During the coldest months, there would be a decreased in mobility and, consequently, in the probability of capture in traps (Toledo and Haddad 2005; Saenz et al. 2006).

The potential for cold as a factor limiting general activity was reinforced by the fact that captures during cold months were higher on days with higher minimum temperatures. In addition, species are expected to exhibit different ranges of optimal operative body temperature (Huey 1991). Although this hypothesis is speculative, it could explain the peak of activity during warm months in *E. bicolor*, *L. gracilis*, and *P. biligonigerus*, whereas *P. falcipes* presented a higher general activity during colder months. Another aspect of life history that affects general activity is the differences in the level of dependency on aquatic habitats. After an intense rain, the habitat could remain flooded for many weeks, promoting a long period of intense activity in some species and with no relationship to the precipitation rate. This effect appears to occur in *L. cf. latrans*, *P. gracilis*, and *P. minuta*, which exhibited no seasonal variation in activity pattern.

Although the peaks in calling activities correspond to warmer and moister months (Navas and Bevier 2001),

many studies noted the importance of evaluating the effects of environmental variables independently for each species (Steelman et al. 2010). This pattern is reinforced by our data, which showed particular behaviors in certain species, such as *P. falcipes*, whose general activity was higher during colder months. However, this pattern may have been a secondary response because some of the coldest months had isolated rainfall peaks, which may have increased the species' reproduction (Carvalho-e-Silva et al. 2000; Loebmann and Haddad 2010; Barreto et al. 2012).

Despite the occurrence of isolated peaks of rainfall during the coldest months, the region displayed a relatively homogeneous distribution pattern of rain throughout the year (Santos et al. 2008; Lingnau 2009; Oliveira et al. 2013). This pattern could further reinforce the effects of other factors, affording humidity only a secondary role as a moderator of anuran activity in southernmost Brazil. This scenario reduces the accuracy of predictions on activity patterns based on air temperature and humidity (Steelman et al. 2010). There was no significant relationship between calling activity and any of the environmental variables tested. We did not record a well-defined peak in the number of species showing calling activity. Such a peak has been demonstrated for other anuran communities in other locations in Brazil (Bertoluci 1998; Eterovick and Sazima 2000) and Uruguay (Canavero et al. 2008), including environments climatically similar to our study area (Bernarde and Anjos 1999; Conte and Machado 2005; Santos et al. 2008). Note that different species could respond differently to abiotic variables that influence reproductive activity (Hartel et al. 2007; Wells 2007). In addition to climatic variables, these triggers include other environmental parameters, such as photoperiod (Both et al. 2008; Canavero et al. 2009), which can make the detection of a general pattern of answers to the climatic variables difficult. In an attempt to predict mathematically the activity patterns of an anuran community in subtemperate wetlands in Uruguay, Canavero et al. (2008) observed that the annual pattern of calling activity is determined by a response to a set of seasonal variables or a variable that synthesizes the entire seasonal variation, such as photoperiod. This principle reinforces the fact that not all species respond to specific variables such as temperature or rainfall. Photoperiod appears to be a good predictor of activity in *H. pulchellus*, *P. minuta*, and *P. gracilis*. As also observed by Canavero et al. (2008), these species also presented a broad period of activity almost throughout the year in the present study.

The relatively low values of niche breadth suggest that many species presents a short season of calling activity. Consequently, species would have a smaller overlap during reproductive periods, as occurred, e.g., between *L. latrans*, *D. minutus*, *E. bicolor*, and *O. maisuma* and between *O. maisuma*, *E. bicolor*, and *L. gracilis*. Finally, this behavior would reduce the overlap between species during the

Table 3 Values of niche overlap (*O*) and niche breadth (*B*) in calling activities for 13 anuran species in subtemperate wetlands in southernmost Brazil

	<i>Dmin</i>	<i>Dsan</i>	<i>Ebic</i>	<i>Hpul</i>	<i>Lgra</i>	<i>Llat</i>	<i>Omai</i>	<i>Pfal</i>	<i>Phys</i>	<i>Pmin</i>	<i>Rdor</i>	<i>Sfus</i>	<i>Ssqu</i>
<i>Dmin</i>		0.3367491	0.1905002	0.09861692	0.6654356	0	0	0.6622442	0.1925226	0.1391423	0.666469	0	0.0695677
<i>Dsan</i>			0	0.5644163	0.3296402	0.4821027	0.2651565	0	0.6667762	0.4935692	0	0.4978963	0.6974541
<i>Ebic</i>					0.4459272	0	0	0	0.3566882	0	0,09901475	0	0.01404555
<i>Hpul</i>					0.0008878645	0.05973157	0.4778526	0.01158963	0.5650231	0.6384265	0.01182861	0.3745081	0.9035631
<i>Lgra</i>						0.01486424	0	0.1442043	0.1606475	0.007599841	0.1030245	0	0.0106476
<i>Llat</i>							0	0	0.1070065	0.5112835	0	0	0.2949566
<i>Omai</i>								0	0.01783441	0.2678165	0	0	0.5618221
<i>Pfal</i>									0,1903211	0	0.9845988	0	0
<i>Phys</i>										0.3200138	0.2295631	0.731399	0.5588524
<i>Pmin</i>											0	0.3649998	0.660339
<i>Rdor</i>												0	0.001390717
<i>Sfus</i>													0.2994721
<i>Ssqu</i>													
<i>O(mean)</i>	0.34	0.10	0.33	0.36	0.11	0.12	0.12	0.28	0.26	0.21	0.18	0.34	0.34
<i>B(mean)</i>	3.63	4.81	1.00	6.72	2.97	1.00	1.00	1.47	4.13	3.51	1.41	1.07	5.63

Niche overlap was estimated by Pianka's overlap index and niche breadth by the inverse of the Simpson diversity index (*B*). *Dmin*, *Dendropsophus minutus*; *Dsan*, *Dendropsophus sanborni*; *Ebic*, *Elachistocleis bicolor*; *Hpul*, *Hypsiboas pulchellus*; *Lgra*, *Leptodactylus gracilis*; *Llat*, *Leptodactylus* cf. *latrans*; *Omai*, *Odontophrynus maisuma*; *Phys*, *Physalaemus* sp; *Pmin*, *Pseudis minuta*; *Pfal*, *Pseudopaludicola falcipes*; *Rdor*, *Rhinella dorbignyi*; *Sfus*, *Scinax fuscovarius*; *Ssqu*, *Scinax squalirostris*

breeding seasons, thus reducing the possibility of competition for physical and acoustic space and diluting the effect of predators on nests (Kopp et al. 2010; Sinsch et al. 2012).

The majority of the species showed calling activity that was restricted to the warm season (46.15 %) or extended throughout the entire year (38.46 %). Even species that presented calling activity restricted to the cold season (*L. cf. latrans* and *S. granulatus*) were active during the transitional months between the cold and warm seasons. This result reinforces the finding that temperature was the predominant climatic factor for determining anuran calling activity. Note, however, that the calling season of *S. granulatus* may have been underestimated because of the low abundance of individuals in the studied area (personal observations).

The species with the longest calling periods were *H. pulchellus* and *S. squalirostris*. This pattern was most likely enhanced by their relatively high tolerance to low temperatures (Both et al. 2008). Species with higher tolerance to low temperatures may have greater reproductive success (Martins 2009), which could explain why those species were two of the most abundant in the study region. The prolonged calling pattern of *H. pulchellus* has also been recorded in other populations in southern South America (Achaval and Olmos 1997; Trindade et al. 2010) and in Uruguay (Canavero et al. 2008). However, the calling period of *S. squalirostris* in other subtemperate regions was concentrated during the warmer months between September and April (Achaval and Olmos 1997; Kwet and Di-Bernardo 1999). This result suggests a certain plasticity of the species regarding seasonality and reproductive activity. Such plasticity also appears to occur in *P. minuta*, whose reproductive activity was previously identified as brief (Santos et al. 2008) or long (Langone 1994; Melchior et al. 2004). The low values of niche overlap reinforce the potential of the entire community to keep calling through all the year. Another important aspect of our work was that our results showed a temporal disjunction between the general and calling activities for some species (*L. cf. latrans*, *P. minuta*, and *P. falcipes*). The limitation of an ecological interpretation of activity data often occurs because of the low availability of basic information on the biology of the observed species, particularly regarding reproductive biology.

Conclusions

The present study is one of the first to describe anuran general activity in southern Brazil. The study showed that the general activity patterns of most anurans in the studied wetland habitats appear to be regulated by temperature and not rainfall, similar to the pattern of anuran assemblages in temperate climates (Oseen and Wassersug 2002; Saenz et al. 2006). The nonexistence of

a significant relationship between calling activity and any of the environmental variables tested suggested the presence of a different environmental factor (e.g., photoperiod or the length of the hydroperiod of water bodies) or some untested biotic elements as a trigger for the levels of general calling activity. Nevertheless, the observed general activity pattern is different from that expected for most of eastern South America.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

SSX was responsible for the field samples, performed most of the statistical analyses, and drafted the first version of the manuscript. AMT conceived the study, determined the sampling design, and reviewed the manuscript. All authors read and approved the final manuscript.

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