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Article in *Journal of herpetology* · December 2016

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Source: South American Journal of Herpetology, 11(3):149-156.

Published By: Brazilian Society of Herpetology

DOI: <http://dx.doi.org/10.2994/SAJH-D-16-00008.1>

URL: <http://www.bioone.org/doi/full/10.2994/SAJH-D-16-00008.1>

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# Calling Site Selection by the South American Tree-frog *Hypsiboas pulchellus* (Anura, Hylidae) in Subtropical Wetlands

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**Abstract.** The selection of appropriate calling sites is a key aspect in the reproductive strategy of nearly all anurans. We evaluated if males of the South American tree frog (*Hypsiboas pulchellus*) select calling sites in undisturbed subtropical wetlands based on specific habitat cues. The study was designed to represent a snapshot of the male calling activity under low densities of intra- and interspecific competitors and little variation of climatic conditions. We characterized calling sites by measuring the vegetation attributes and flood levels of calling sites occupied by 59 males and comparing them to available microhabitats. We found that males exhibit some degree of selectivity for calling sites, often selecting microhabitats with greater density of vegetation > 50 cm tall. Calling site selection was not affected by water depth or area flooded. Most individuals vocalized in sites near the ground ( $\leq 25$  cm), a pattern that is the contrary to that expected to maximize sound propagation. We suggest that, due to the open habitat of the studied area, the choice of calling sites is more related to the need for shelter from predation and avoidance of desiccation and heat loss than to bioacoustic performance.

**Keywords.** Behavior; Reproduction; Vegetation; Vocalization; Wetlands.

## INTRODUCTION

Animals generally exhibit preference for microhabitats containing specific environmental characteristics, including the vegetation architecture, substrate composition and microclimatic conditions (Reinert, 1993; Tozetti et al., 2010). One of the most evident advantages of microhabitat selectivity is avoidance of competition (Schoener, 1974; Diaz and Valencia, 1985; Lüddecke et al., 2000), which can result in niche segregation among species (Crump, 1974; Cardoso et al., 1989; Rossa-Feres and Jim, 1994). Microhabitat preferences can be affected by seasonal events, such as the reproductive cycle. During the breeding season, microhabitat requirements of male anurans are thought to be related to calling site selection (Wells, 2007). Calling site selection is one of the most important components of anuran life history because it is related to reproductive success (Hödl, 1977; Wells, 2007).

General patterns of calling site configuration (e.g., site descriptions) are available for many anuran species of South America (see Rossa-Feres and Jim, 2001; Conte and Machado, 2005; Heard et al., 2008; Santos et al., 2008; Silva et al., 2008). Many studies focused on the bioacoustics characteristics of microhabitats, revealing that species are able to select specific sites that enhance call propagation (Patricelli and Blickley, 2006) and increase the chances of attracting females (Wells and Schwartz, 1982; Greer and

Wells, 1980). Calling site selection is also based on many other microhabitat features that, in general, have been poorly investigated for Neotropical anurans. Several biotic and abiotic factors may exert influence on site selection (Cardoso et al., 1989; Silva and Giaretta, 2008), including extent of competition, predation risk, and density of calling males, as well as climatic conditions such as rainfall and temperature (Longland and Price, 1991; Resetarits et al., 1991; Wells, 2007).

The synergistic influence of several inputs on the selection of calling sites makes the data from field-based studies difficult to be analyzed. A field survey designed to obtain data on relevant variables would facilitate understanding of the role of environmental cues on male decisions. The subtropical wetlands of southern Brazil provide a good opportunity for such studies for several reasons. First, the relatively homogeneous landscape has the predominance of field grasses with sparse scrubs, forming a vegetation cover with low structural complexity, especially regarding to the vertical stratum (Tozetti et al., 2009; 2010). In this situation, the characterization of a male calling site is simpler than in a forest habitat. Second, the regular rainfall regime of subtropical wetlands produces temporary water bodies (i.e., potential reproductive sites) throughout the year (Waechter, 1985; Ximenez and Tozetti, 2015). Finally, the occurrence of species that are reproductively active during most of the

year (Tozetti et al., 2010; Oliveira et al., 2013; Ximenez and Tozetti, 2015), as is the case of the South American tree frog, *Hypsiboas pulchellus* (Duméril and Bibron, 1841). Species that show continuous or prolonged patterns of activity facilitate acquisition of reproductive data even on cold nights. On cold nights, *H. pulchellus* is often the only species with actively calling males (Ximenez and Tozetti, 2015), which are observed at low densities in Brazilian southern wetlands. This condition generates a good scenario for studying anuran calling behavior under a low level of interference of male competitors and background noise generated by other frog species. Here, we evaluated whether males of *H. pulchellus* exhibit calling site selectivity based on the structural attributes of microhabitat. The species breeds throughout the year; however, calling activity is more common during colder months (e.g., Langone, 1994; Ximenez and Tozetti, 2015). Based on this, we carried out an intensive sampling effort during a short period of the breeding season of *H. pulchellus*, representing a snapshot study of male behavior under minimum variation of local climatic conditions.

## MATERIALS AND METHODS

### Study area and study species

Data were collected between November and December 2012 in undisturbed wetlands at the Estação Ecológica do Taim (ESEC Taim), a conservation area located on the coastal plains of Rio Grande do Sul state, southern Brazil (32°20′–33°00′S, 52°20′–52°45′W). The region is included within the Uruguayan Savanna eco-region (Olson et al., 2001) and is characterized by a system of lagoons and ephemeral ponds surrounded by well-preserved grasslands and wetlands (Josende et al., 2015). Sampling was concentrated in an area of 2,000 ha that encompasses one of the most important lagoons of ESEC Taim. The local climate is classified as humid subtropical, with an mean annual air temperature of 18.1°C, coldest month mean temperature of 12.7°C, and mean annual rainfall of 1,162 mm (Maluf, 2000). Dry periods can occur in spring, whereas there is a higher incidence of rainfall during the winter (Vieira, 1983). Because of the presence of a climatic transition between tropical and subtropical regimes and the presence of sand dunes and a marine influence, the climatic characteristics of the region are peculiar, such as a colder winter in comparison to other Brazilian regions (Maluf, 2000; Oliveira et al., 2013). During fieldwork, air temperature varied from 10.3–34.2°C (mean = 20.9°C ± 5.7°C) and accumulated rainfall summed 41.4 mm. Meteorological data were obtained from a meteorological station located 10 km from the study site.

The South American tree frog, *Hypsiboas pulchellus*, is a medium-sized hylid that is common and abundant

throughout its geographic range, which extends from southeastern Brazil, Uruguay, and southeastern Paraguay through eastern, central and northern Argentina (Faivovich et al., 2005; Frost, 2013). This hylid is one of the most common anuran species from open habitats of South America, occupying a wide range of habitats, including altered areas (e.g., Langone, 1994; Achaval and Olmos, 2007; Maneyro and Carreira, 2012). The generalist calling behavior of male *H. pulchellus*, which occupies a wide variety of calling habitats, provides a good opportunity to evaluate the match between calling site attributes and environmental structure (Ziegler et al., 2011).

### Data collection

We concentrated our sampling effort in the period of lowest density of calling males at the study region (during the colder summer days) in order to avoid the additional influence of effects such as the interspecific male–male competition and the background noise generated by other frog species on the selection of calling sites by male *Hypsiboas pulchellus*. We located active males in the wetlands at night, between 19:00 and 01:00, through auditory surveys (Heyer et al., 1994). Once located, individuals were captured manually, weighed using a digital scale, and measured (snout–vent length; SVL) with a caliper.

We recorded the distance between individual calling sites and the ground, considering the ground or the water surface to be zero. Height measurements were grouped into four categories (0–25 cm, > 25–50 cm, > 50–75 cm, and > 75 cm) that were post-defined based on visual optimization of the data in a histogram. To characterize the microhabitat used by calling males, we established a virtual quadrant of 4 m<sup>2</sup> around each individual for recording the percentage of the quadrant containing the following variables (adapted from Huckembeck et al., 2012; Tozetti and Martins, 2008): (a) vegetation taller than 50 cm, (b) vegetation shorter than 50 cm, (c) percentage of flooded substrate, and (d) water depth when substrate was flooded. To evaluate microhabitat availability within the landscape, the same variables were measured in two 4 m<sup>2</sup> quadrants randomly distributed in a grid of 121 quadrants (11 × 11 quadrants), considering the observed males to be the center of the grid.

Parameters used for evaluating the available and occupied microhabitats were defined based on the local habitat configuration. The vegetation cover of the study site was characterized by the relatively homogeneous areas of grass fields with shrubs. Additionally, the local vegetation cover was associated with a planar surface of the terrain and the absence of rocks, fallen logs, trees, or other similar elements, factors which combined characterize a habitat with low structural complexity (Friedlander and Parrish, 1998). Because of the simplified habitat configuration,

**Table 1.** Characterization of microhabitats occupied by calling males of *Hypsiboas pulchellus* and available microhabitats at Estação Ecológica do Taim, southern Brazil. Values are followed by the results of a Wilcoxon paired test for each variable.

Variable	% occupied habitat <i>n</i> = 59 (mean ± SD)	% available habitat <i>n</i> = 118 (mean ± SD)	Wilcoxon rank	<i>P</i>
vegetation > 50 cm tall	22.2 ± 23.6	7.2 ± 15.7	879.5	0.01
vegetation < 50 cm tall	40.9 ± 12.8	47.7 ± 23.0	776.0	0.18
flooded substrate	37.4 ± 19.1	44.1 ± 25.8	587.5	0.09
water depth	18.7 ± 5.8	17.9 ± 6.9	874.0	0.09

the predominant variation in the local landscape was due to the presence of two well-defined vegetation strata: one composed of plants < 50 cm tall and the other composed of plants between 50 and 100 cm tall. An additional source of local habitat heterogeneity was the flood level of the soil.

### Data analysis

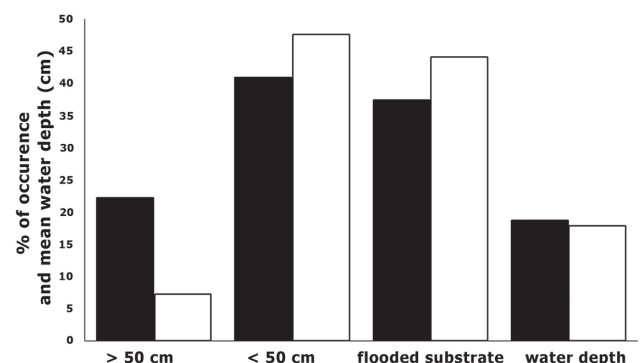
To identify possible differences in microhabitat configuration between occupied and available microhabitats, we performed a principal component analysis ordination (PCA), which was generated using a correlation measure matrix in the Multiv 3.13b software (Pillar, 2006). We tested whether males of *Hypsiboas pulchellus* used microhabitats differentially, comparing the 59 microhabitats occupied by individuals with another 118 randomly available microhabitats, using the Wilcoxon paired test in the PAST software (Hammer et al., 2001). We also determined the frequency of occurrence, presence, and absence of vegetation taller and shorter than 50 cm and tested whether the frequency differed between microhabitats available or occupied by tree frogs using an analysis of variance (ANOVA) via randomization tests between sample units (i.e., each microhabitat), following the procedures described by Pillar (2006). This analysis was also used to compare the presence and absence of males among the three height categories of calling sites. Additionally, we performed a linear regression to describe the relationship between the height of the calling sites and the vegetation cover and further tested the model using randomization tests in the Multiv 3.13b software (Pillar, 2006). We used 10,000 randomizations for all randomization tests (linear regression and ANOVA). For all statistical tests, we employed a significance level of  $P < 0.05$ .

### RESULTS

We described the calling sites of 59 males of *Hypsiboas pulchellus*. Mean mass was 3.99 g (DP = 0.994, min = 2.00 g, max = 7.00 g) and mean SVL was 4.0 cm (DP = 3.7, min = 3.4 cm, max = 5.2 cm). We sampled 118 quadrants of available microhabitats (quadrants without males). Microhabitat characteristics differed between the

used and available sites, mainly with regard to vegetation height. Despite the low availability of taller vegetation, calling males tended to select sites with predominant taller vegetation (> 50 cm; Fig. 1). The selected calling sites presented larger percentages of vegetation > 50 cm tall (mean = 22.2; DP = 23.6;  $n = 59$ ) relative to available microhabitats (average = 7.2, DP = 15.7;  $n = 118$ ;  $W = 879.5$ ;  $P < 0.01$ ; Table 1, Fig. 1). The percentage of flooded substrate and water depth did not differ between available and occupied microhabitats, suggesting that these variables exert low influence on calling site selection (Table 1, Fig. 1). Statistics of other non-significant variables are summarized in Table 1. Despite the association between quadrants with calling males and vegetation > 50 cm tall, there was a weak relationship between the perch height used by calling males and the vegetation cover > 50 cm ( $r^2 = 0.026$ ;  $P = 0.397$ ), suggesting that the height of calling site is not related to this class of vegetation cover percentage.

The first two PCA axes accounted for 82.76% of the total variation in the characteristics of available and occupied microhabitat (Fig. 2, Tables 2–3). In the ordination, the vectors indicate the trend of similarity between the characteristics of occupied and available microhabitats (quadrants with and without calling males, respectively). In general, the distribution of available microhabitats was associated with a broad set of variables relative to occupied sites, a difference that suggests greater homogeneity in the configuration of selected calling sites. Most of the variation in occupied microhabitats was related to the first PCA component, while most of the variation



**Figure 1.** Water depth and percentage of microhabitats available (open bars) and occupied by calling males of *Hypsiboas pulchellus* (dark bars) at Estação Ecológica do Taim, southern Brazil.

**Table 2.** Eigenvalues of the Principal Component Analysis explained by the four principal components (1–4) of the percentage of variance of vegetation cover > 50 cm tall, percentage of vegetation cover < 50 cm tall, percentage of flooded substrate area, and water depth associated with microhabitats occupied by calling males of *Hypsiboas pulchellus* and available microhabitats at Estação Ecológica do Taim, southern Brazil.

	Component 1	Component 2	Component 3	Component 4
eigenvalues	18.123	14.982	0.641	0.049
percentage	45.307	37.455	16.019	1.219
cumulative %	45.307	82.762	98.781	100

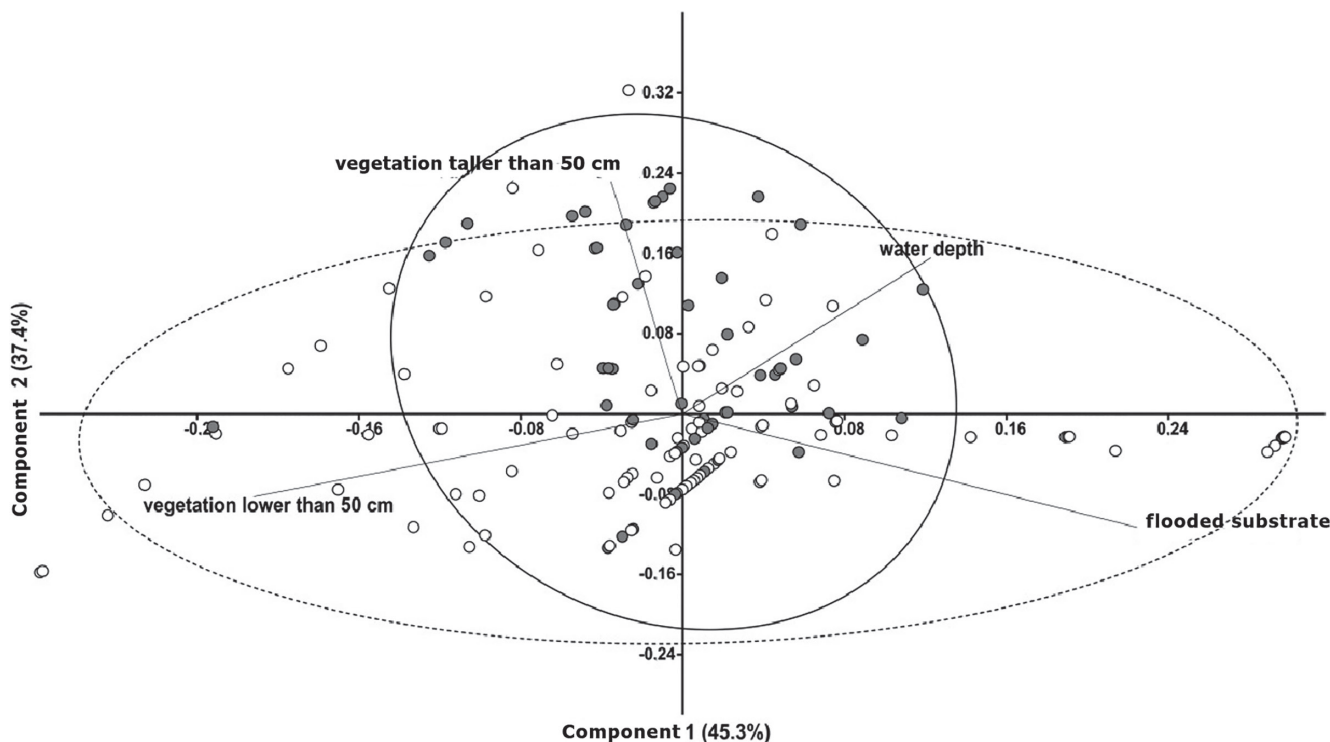
**Table 3.** Eigenvectors of the Principal Component Analysis depicting the four principal components (1–4) of the percentage of variance of vegetation cover > 50 cm tall, percentage of vegetation cover < 50 cm tall, percentage of flooded substrate area, and water depth associated with microhabitats occupied by calling males of *Hypsiboas pulchellus* and available microhabitats at Estação Ecológica do Taim, southern Brazil.

Variables	Component 1	Component 2	Component 3	Component 4
vegetation > 50 cm tall	-0.13943	0.74539	0.43426	0.48619
vegetation < 50 cm tall	-0.65441	-0.24144	-0.43402	0.57016
flooded substrate	0.66703	-0.3374	0.051889	0.66222
water depth	0.32769	0.52179	-0.78762	-0.0024995

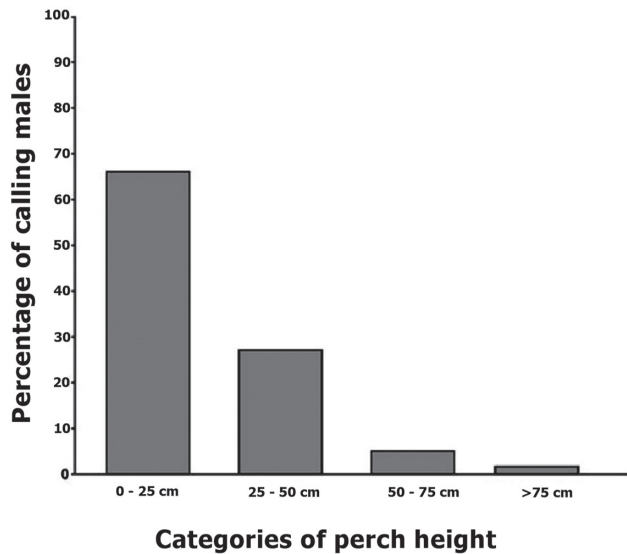
between microenvironments was related to the second component. The major variation in the first component was related to vegetation < 50 cm tall and to the presence of floodwaters. In the second component, most of the variation was related to the vegetation > 50 cm tall and water depth. The PCA results suggest that males tend to occupy microhabitats with larger percentages of vegetation cover > 50 cm tall and to avoid flooded areas.

We also observed males of *Hypsiboas pulchellus* vocalizing within a wide range of distances above the

ground. Calling height varied from 0 cm (i.e., floating and resting on emergent aquatic vegetation) to 82 cm (mean = 19.6 cm). However, 92% of males called from heights < 50 cm (Fig. 3). The category 0–25 cm included 66% (39) of males, whereas the categories > 25–50 and > 50–75 cm included 26% (15) and 7% (4) of the calling males, respectively (Fig. 3). Although we found evidence of selection of microhabitats presenting a larger percentage of vegetation > 50 cm tall, most calling males occupied lower position in the vegetation. The perch height



**Figure 2.** Representation of the first two components of the Principal Component Analysis between the quadrants of microhabitats occupied by calling males of *Hypsiboas pulchellus* (gray dots), quadrants of available microhabitats (white dots), and the four habitat variables measured at Estação Ecológica do Taim, southern Brazil. The continuous ellipsis indicates 95% of the quadrants used by *H. pulchellus* and the dotted ellipsis indicates 95% of the quadrants available in the water body.



**Figure 3.** Percentage of microhabitat use for three perching height categories used by calling males of *Hypsiboas pulchellus* at Estação Ecológica do Taim, southern Brazil.

category 0–25 cm presented significantly more calling males than the other categories (ANOVA: Sum of squares = 13.22;  $P = 0.0001$ ).

## DISCUSSION

Our evidence suggests that males of *Hypsiboas pulchellus* actively search for calling sites based on vegetation structure. Our data revealed that microhabitats with greater densities of taller vegetation were used in a higher proportion than its availability in the environment. This suggests that males select microhabitats with predominantly higher vegetation (> 50 cm) as calling sites. Calling site position might be related to male visual detectability by females, visual communication, and territory defense, as observed in *Phyllomedusa burmeisteri* Boulenger, 1882 (Abrunhosa and Wogel, 2004). The ability to select specific perch heights for calling is important to avoid competition and constitutes a mechanism to prevent interspecific mating among closely-related species (Martins et al., 2006). Some studies have shown that by occupying higher and more open microhabitats males can enhance call propagation, thereby improving reproductive success, as observed in *Centrolenella fleischmanni* (Boettger, 1983) (Greer and Wells, 1980; Wells and Schwartz, 1982). Nonetheless, even though male *H. pulchellus* selected sites with higher densities of taller vegetation, most calling males vocalized at low heights of 0–25 cm. This pattern is contrary to what is expected in terms of sound propagation (Narins and Hurley, 1982) and is probably due to the vast majority of perch heights in this vegetation being lower. Similar behavior has been observed in males of *Hyla parviceps* (Boulenger, 1882)

(Ellinger and Hödl, 2003; Penna and Solis, 1998; Richards and Wiley, 1980).

However, many other variables than perch height affect the efficiency of sound propagation, including vegetation architecture (Greer and Wells, 1980; Lardner and bin Lakim, 2002; Slabbekoorn and Peet, 2003), air temperature, humidity and wind speed (Michelsen, 1978; Wells and Schwartz, 1982). In fact, studies on anurans suggest that the efficiency of sound production tends to be very low (Prestwich et al., 1989). If this statement also applies to *Hypsiboas pulchellus*, male reproductive success should depend more on calling effort, including the amount of acoustic energy produced per call (Sullivan, 1983) and the number of nights of calling activity (Dyson et al., 1992; Sullivan and Hinshaw, 1992). In fact, *H. pulchellus* is one of the anuran species that has the longest calling season in the subtropical Brazilian region (Ximenez and Tozetti, 2015). The vegetation at our study site was composed of sparse masses of grass reaching up to a maximum height of 1 m. Consequently, the vertical component of the habitat structure is poorly stratified, being much less complex than other Brazilian open coastal habitats (e.g., the *Restingas*). A combination of homogeneous habitat characteristics can increase the efficiency of sound propagation and reception.

Further, microhabitats located near the ground within dense vegetation may act as calling and retreat sites, thereby reducing the need for daily movement what would be important in habitats with high predation pressure (Rebelato et al., in press). This pattern has been observed in *Phyllodytes luteolus* (Wied-Neuwied, 1821) (Eterovick, 1999) and *Hypsiboas faber* (Wied-Neuwied, 1821) (Oliveira et al., 2016). From another perspective, calling near the ground could be a strategy for avoiding the direct incidence of wind (a relevant habitat component at our study site), which can cause desiccation and heat loss (Robertson, 1986), as males calling from more exposed sites may experience higher dehydration rates (Prado and Pombal, 2005). Thermal changes are one major predictor of ectotherm activity in subtropical coastal habitats of southern Brazil (Tozetti et al., 2009; Martins et al., 2014).

A previous study indicated that competition among conspecific males is the most decisive biotic feature related to calling site selection in *Hypsiboas pulchellus* (Ziegler et al., 2011). By keeping a minimum distance from conspecific males, a given male can experience increased mate encounters, reduced negative effects of calling interference, and minimized aggressive interactions (Whitney and Krebs, 1975; Shepard, 2004; Nali and Prado, 2012). In the present study we did not test the effects of social interactions on calling site selection. Instead, our sampling was designed to limit the interference of social interactions over our results. Hence, we believe that male–male competition did not interfere in

our study, because (1) *H. pulchellus* was the only species engaged in calling activity during the sampling period and (2) calling males of *H. pulchellus* were observed in the lowest density of the entire breeding season (male density < 1/700 m<sup>2</sup>). During peak reproductive activity, male density is 3–4 times greater than during the period of the present study (pers. obs.). This particular situation offers a possibility to reduce the variables during our snapshot study, and we highlight that in higher densities of calling males habitat selection is likely to differ. We have assumed this trade-off between number of calling males and environmental variables in order to facilitate data interpretation.

Despite the existence of data on ecological aspects of *Hypsiboas pulchellus* (Maneyro and Rosa, 2004; Ziegler et al., 2011; Both et al., 2008), detailed information about calling site microhabitat is lacking (Conte and Machado, 2005). As shown in the PCA results, the occupied microhabitats exhibited greater homogeneity in structural features than the available microhabitats, suggesting some degree of selectivity in male calling site choice. The pattern we have described highlights the notion that even a widespread and abundant species, such as *H. pulchellus*, can exhibit selectivity when its microhabitat is examined in detail. Further comparative studies are necessary to achieve a better understanding of the processes related to habitat use. Preferences for a specific habitat type can be an evolutionarily conservative characteristic leading to similarities among phylogenetically-related species, which in turn can result in geographically distant populations sharing similar habitat preferences over their geographical range (Heyer et al., 1990; Ptacek, 1992; Rossa-Feres and Jim, 2001; Martins et al., 2006). However, a common set of local habitat features and biotic pressures can also drive local habitat selection. Data for different populations of widespread anuran species would generate baseline information for the understanding of evolutionary process related to calling site selection.

#### ACKNOWLEDGMENTS

We thank many students from Universidade do Vale do Rio dos Sinos, Laboratório de Ecologia de Vertebrados Terrestres for their field assistance. We also thank the Instituto Chico Mendes de Conservação da Biodiversidade, particularly Ana Carolina Canary, for granting access to the study area. Financial support for this study was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #446910/2014-7) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES #2556/10) for financial support and Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul for a scholarship.

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