Seasonal Reproductive Dynamics of a Lek-Breeding Neotropical Treefrog is not Organized by Male Size (Anura, Hylidae)

Authors: Leão Pompeu, Caio Carneiro, de Sá, Fábio P., and Haddad, Célio F.B.

Source: South American Journal of Herpetology, 18(1) : 33-41

Published By: Brazilian Society of Herpetology

URL: https://doi.org/10.2994/SAJH-D-17-00111.1

South American Journal of Herpetology, 18, 2020, 33–41

Seasonal Reproductive Dynamics of a Lek-Breeding Neotropical Treefrog is not Organized by Male Size (Anura, Hylidae)

Caio Carneiro Leão Pompeu[1,*], Fábio P. de Sá[1], Célio F.B. Haddad[1]

[1] *Universidade Estadual Paulista, Instituto de Biociências, Departamento de Biodiversidade e Centro de Aquicultura, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil.*
* *Corresponding author. Email: caioclpompeu@gmail.com*

Abstract. Social structure in anurans is directly related to reproductive traits such as chorus organization, male territoriality, pair formation, breeding site choice, and temporal breeding pattern. The Neotropical treefrog *Dendropsophus sanborni* is an excellent model for studies on reproductive dynamics because it is a prolonged-breeder and usually occurs in high densities. Here, our goals were to better understand the factors that lead to social organization and influence seasonal reproductive dynamics of males of the species. We addressed the hypotheses that (1) the seasonal dynamics of *D. sanborni* is locally delimited by climatic conditions throughout its breeding season and (2) territorial males are structured spatially and temporally based on body size. We carried out monthly field sampling between October 2015 and September 2016 in an ecotone region of Brazil that originally comprised Semideciduous Seasonal Forest and Cerrado (savannah vegetation). We specifically analyzed environmental conditions, population abundance, size of calling males, and microhabitat use. Our results showed that environmental conditions drive the seasonal reproductive pattern and social structure of calling males is not organized by size. We did not find significant variation in male size among months of the breeding season or among perch heights and types. Our findings suggest a prolonged seasonal reproductive pattern associated with climatic factors without a social structure based on body size.

Keywords. Anura; Breeding recruitment; Breeding season; *Dendropsophus sanborni;* Social organization; Social structure; Atlantic Forest; Cerrado.

INTRODUCTION

Among anurans, social organization is directly related to body size and reproductive traits such as chorus structure, male territoriality, pair formation, breeding site choice, and temporal breeding pattern (Wells, 1977; Martin et al., 2011; Rosa and Andreone, 2012; Sousa and Ávila, 2015; Berec, 2017). Moreover, temporal and spatial breeding patterns are affected by abiotic (e.g., climate and availability of reproductive resources) and biotic (e.g., habitat use, abundance of individuals, reproductive strategies, and adult life span) factors (Crump, 1974; Gally and Zina, 2013; Akmentins et al., 2015; Hurme, 2015; Luna-Gómez et al., 2017; Leivas et al., 2018). The majority of the anuran species from tropical areas with well-defined seasons possess seasonal reproductive dynamics associated with the hotter and rainier periods of the year (Shahriza et al., 2010; Van Sluys and Guido-Castro, 2011; Waldez et al., 2011; Schalk and Saenz, 2016).

Seasonal reproductive patterns observed among anurans can be classified along a continuum between two basic types, prolonged and explosive (Wells, 1977). Prolonged breeding is most common among anurans and is characterized by long breeding periods and evident male territorial behavior (Wells, 1977; Vilaça et al., 2011; Brunetti et al., 2014; Dias et al., 2017). The lek system is considered typical of long-breeding species and involves males that call from within territories that serve as exhibition arenas for the attraction of females, who choose their mates (Wells, 2010; Höglund and Alatalo, 2014; Dias et al., 2017). Females visit the territories of males and choose mates on the basis of the quality of the breeding site, acoustic characteristics of calls, and morphological characteristics (such as body size; Jaquiéry et al., 2010; Roff, 2015; Botto and Castellano, 2016; Zhu et al., 2016; Cayuela et al., 2017a,b).

In anuran species with a lek mating system and a prolonged breeding, males compete and defend resource-based territories as breeding sites, with disputes occurring mainly via calls, endurance, warning displays, and physical combats (Wells, 1977; Rosa and Andreone, 2012; de Sá et al., 2016; Ospina-L. et al., 2017). Body size is also an important male trait associated with territory defense, thus influencing intrasexual competition. Differences in size can promote advantages among males during acoustic disputes, endurance, choices made by females, and physical combats (Zheng et al., 2010; Höglund and Alatalo, 2014; Méndez-Narváez and Amézquita, 2014; Laird et al., 2016; Zhu et al., 2016; Berec, 2017; Ospina-L. et al., 2017; Turin et al., 2018).

The diversity of reproductive strategies among anurans might be more a reflection of environmental attri-

How to cite this article: Pompeu C.C.L., de Sá F.P., Haddad C.F.B. 2020. Seasonal reproductive dynamics of a lek-breeding neotropical treefrog is not organized by male size (Anura, Hylidae). *South American Journal of Herpetology* 18: 33–41. http://doi.org/10.2994/SAJH-D-17-00111.1

Submitted: 06 December 2017
Accepted: 11 December 2018
Available Online: 26 October 2020

Handling Editor: Taran Grant
http://doi.org/10.2994/SAJH-D-17-00111.1

butes than phylogenetic history (e.g., Haddad and Prado, 2005; Müller et al., 2013; Akopyan et al., 2018; O'Brien et al., 2018). The breeding season of an anuran species is limited by seasonal climatic factors in association with its social behavior, reproductive traits, and intraspecific competition. However, the selective pressures that favor prolonged breeding patterns are still not totally clear. Despite wide reports of mating advantages for large males in anurans with prolonged breeding patterns and lek mating systems (e.g., Berec, 2017; Clause, 2017; Ospina-L. et al., 2017), this is not the case for all species (e.g., Gutiérrez and Lüddecke, 2002; Friedl and Klump, 2005; Jacobs et al., 2016; Yu et al., 2016; Zhu et al., 2016).

Dendropsophus sanborni (Schmidt, 1944) is a Neotropical treefrog of the family Hylidae Rafinesque, 1815 that possesses a prolonged reproductive pattern with territorial males organizing lek mating systems (Cardoso, 1981; Martins and Jim, 2003; Toledo et al., 2003; Both et al., 2008; Santos et al., 2008). This species is an excellent model for better understanding the factors that lead to social organization and that influence reproductive dynamics over time. By studying calling males of *D. sanborni* over a 1-year period, we aimed to better understand the seasonal reproductive dynamics of this species by explaining how climatic conditions drive its reproduction. We wanted to determine how calling males are socially organized in space and how their organization is variable throughout the breeding season by specifically exploring population abundance, body size, and microhabitat use. Our hypotheses are that (1) the seasonal dynamics of *D. sanborni* are conditioned by climatic conditions and (2) throughout its breeding season, territorial males are organized spatially and temporally based on body size.

MATERIALS AND METHODS

Study species

Dendropsophus sanborni is a relatively small Neotropical treefrog of the family Hylidae that exhibits a prolonged reproductive pattern with territorial males that use vegetation surrounding flooded areas as calling sites where they organize lek mating systems (Cardoso, 1981; Martins and Jim, 2003; Toledo et al., 2003; Both et al., 2008; Santos et al., 2008; Haddad et al., 2008). The species usually occurs in high abundances, which makes this hylid an excellent model for studying social organization and reproductive dynamics over time.

Study area and data collection

We conducted our study at the Cantaclaro ranch (22°19′30″S, 47°42′52″W, 620 m above sea level), located in the Distrito de Itapé, municipality of Rio Claro, state of São Paulo, southeast Brazil. The ranch is about 20 km northwest of Rio Claro and about 15 km southeast of municipality of Itirapina. The relief of this rural region comprises hills and valleys and was originally an ecotone between Semideciduous Seasonal Forest and Cerrado (savannah vegetation), but it is currently extensively modified by agricultural and livestock activities. According to the classification of Koeppen, the climate of the region is of the type Cwa, marked by two defined seasons: a dry cold season, usually from April to September, and a rainy hot season, usually from October to March (Zaine and Perinotto, 1996). The study area encompassed a zone located along a slow-flowing stream in a valley, where a 90-m transect was demarcated with 10 wooden stakes, numbered 0–9, spaced at 10-m intervals.

We conducted fieldwork during the course of 1 year, starting in October 2015 and ending in September 2016, with one field visit per month. To determine the length of the species' breeding season we recorded the presence or absence of calling males every month (reproductively active males). We also estimated the monthly abundance of calling males by performing one auditory count per month. These auditory counts were performed with intervals of ca. 30 d between them and always at around 22:00 (a time that has high activity of calling males), thus avoiding subsequent sampling while also standardizing data collection in the field. These counts were performed while walking along the transect at a constant speed and registering every calling male heard (Heyer et al., 2001). Our activities in the field were conducted from 18:00–01:00, depending on the activity of calling males. We captured calling males via acoustic tracking to measure snout–vent length (SVL; mm) with digital calipers (Mitutoyo, model MIP/E-102, to the nearest 0.01 mm).

We captured a large number of calling males during each expedition and along the transect (Table 1), without

Table 1. Abundance of calling males recorded by monthly auditory counts (one count per month of the number of males calling; see Materials and Methods for details) and total number of calling males captured at the Cantaclaro ranch, Itapé, Rio Claro, São Paulo, Brazil. The ratio row shows how representative our monthly samples were.

	2015			**2016**								
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**
Abundance	15	15	37	55	33	3	0	0	0	0	0	3
Captures	10	9	16	19	13	2	0	0	0	0	0	3
Ratio	66%	60%	43%	34%	39%	66%	-	-	-	-	-	100%

prioritizing any specific area, to ensure that the choice of the individuals sampled was random. In order to document the temporal distribution of individuals during the breeding season, we marked and captured males using a standardized method consisting of the ablation of digits in a sequential order (see Martof, 1953). Recaptures were randomized by following the same method employed for captures. In addition to marking, we also recorded characteristics of calling sites (height and type of perches). These methods also allowed us to determine how the sizes of calling males are organized in space, considering that social structure is based on size. After marking and measuring, we released the calling males exactly where we found them.

Given that anurans are ectothermic and have life cycles that are strongly associated with water, we selected specific climatic traits that could potentially influence or limit the reproductive activity of males of the species, with a focus on understanding the seasonal reproductive dynamics of *Dendropsophus sanborni* (Saenz et al., 2006; de Sá et al., 2014; Caldart et al., 2016; Plenderleith et al., 2018). During each field visit we also recorded the meteorological conditions of air and water temperature and relative air humidity using a digital thermohygrometer (Incoterm, model 7429, to the nearest 1°C and 5% relative air humidity). We complemented our meteorological data with information about the total monthly rainfall and monthly air temperature of the study region collected by the weather station of the Centro de Análise e Planejamento Ambiental (CEAPLA/IGCE) at UNESP, Rio Claro, SP, Brazil, located ca. 18 km from the study area.

Correlations between abundance of calling males and environmental factors were analyzed using Spearman coefficients (*rs*) because abundance of calling males was not normally distributed. To test for variation in monthly mean SVL of calling males, we performed an analysis of variance (ANOVA). Likewise, we used ANOVA to test for variation in mean SVL of calling males among distinct perch heights. We checked for homogeneity of variances and normality of residuals to validate the test. We considered statistical significance at the level of 5% (Zar, 1999) and used the statistical software BioEstat 5.3 (Santos, 2007).

RESULTS

Monthly abundance of calling male *Dendropsophus sanborni* varied considerably over the year. At the beginning of our study in October 2015, calling males were already reproductively active. The number of calling males increased progressively every month until January 2016, when we recorded the highest number of calling males ($n = 55$ individuals). The abundance of calling males subsequently declined to 33 individuals in February and only 3 in March; no reproductively active males were recorded from April to August. Finally, in September 2016 we documented the commencement of the breeding season by recording 3 calling males (Table 1; Fig. 1).

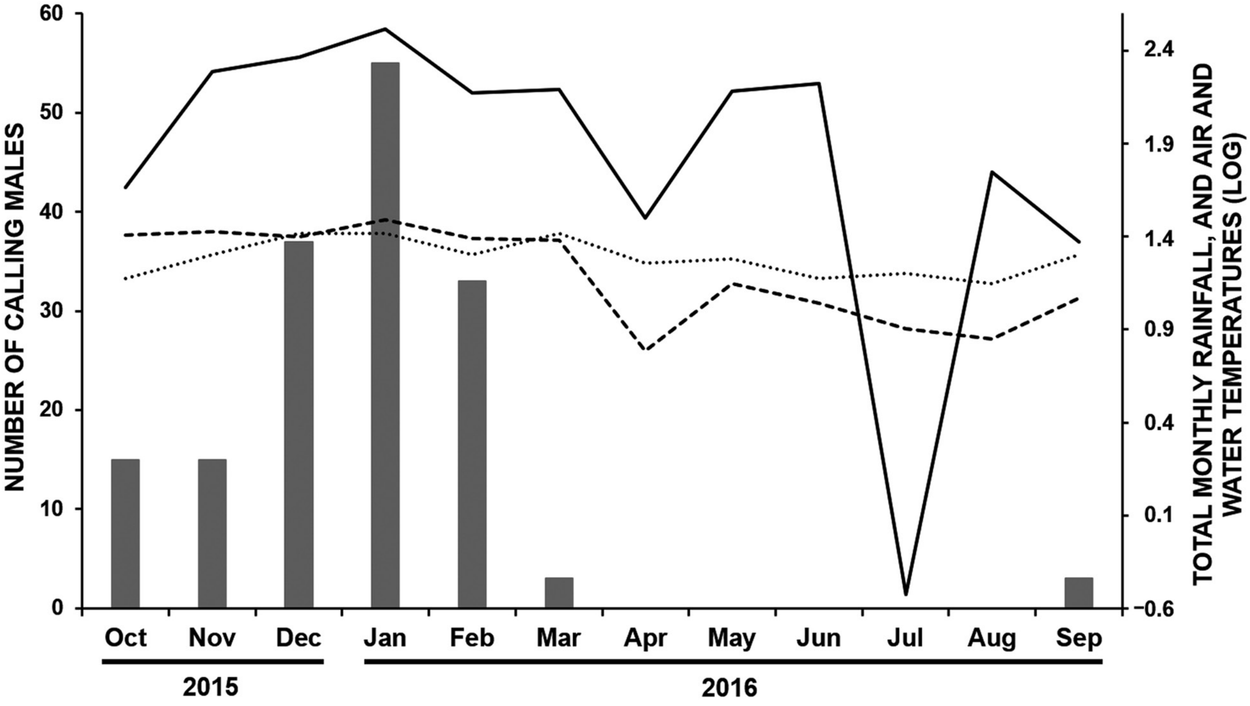

Figure 1. Number of calling male *Dendropsophus sanborni* per month (bars), total monthly rainfall (mm, line), and air (dashed line) and water (dotted line) temperatures (°C) per month at the Cantaclaro ranch, Itapé, Rio Claro, São Paulo, Brazil. We converted total monthly rainfall and temperatures to log scale for better visualization of the correlation of these variables with the abundance of calling males.

Total monthly rainfall and abundance of calling males varied gradually over the course of the rainy season. From the beginning of the species' breeding season, both abundance of calling males and total rainfall gradually increased, peaking in January, when we recorded the highest values for rain and active males; subsequently, they both decreased gradually. Total rainfall increased significantly between May and June 2016, but particularly between 16 May and 9 June, representing an unusual pattern for the region, which typically has pretty dry winters (Zaine and Perinotto, 1996). Despite this unexpected increase in the amount of rainfall in May and June, we recorded no calling males during these months or during the remaining months of the colder period of the year.

The abundance of calling males per month during the 2015/2016 breeding season was not normally distributed, according to Shapiro–Wilk's test (W = 0.76; $P = 0.0095$), and it was significantly correlated with abiotic factors (see Fig. 1), including those we measured directly: air temperature ($rs = 0.87$; $P = 0.0002$; $n = 12$), water temperature ($rs = 0.68$; $P = 0.014$; $n = 12$), and relative air humidity ($rs = 0.62$; $P = 0.02$; $n = 12$). Additionally, considering data for abiotic factors obtained from the weather station (located about 18 km from the study area), abundance of calling males per month was significantly correlated with mean monthly minimum air temperature ($rs = 0.89$; $P = 0.0001$; $n = 12$), monthly minimum air temperature ($rs = 0.83$; $P = 0.0008$; $n = 12$), monthly maximum air temperature ($rs = 0.56$; $P = 0.05$; $n = 12$), and total monthly rainfall ($rs = 0.56$; $P = 0.05$; $n = 12$). The abiotic factor that was not correlated with the number of calling males was mean monthly maximum air temperature ($rs = 0.54$; $P = 0.06$; $n = 12$), also obtained from the weather station.

We classified males into three size-categories—large, medium, and small—on the basis of the range of SVLs for all 72 males captured during our study (see Fig. 2). Figure 2 shows the distribution of SVLs for calling males per month. At the beginning (September) and end (March) of the breeding season, only medium-sized males were calling. With the exception of November (with only small- and medium-sized males being present), we registered calling males from all the size categories (i.e., representing the variability of sizes) in all other months of the breeding season. We found no statistically significant variation in the SVLs of captured calling males among months throughout the 2015/2016 breeding season (F = 1.02; $P = 0.41$, df = 5), indicating that there is no temporal organization or temporal structuring throughout the breeding season based on male size.

Only three calling males were recaptured, all at the end of the breeding season (February and March). These males were recaptured very close to the place where they were originally captured in the previous month (displacement of 5.5 m for one of the males and 2.4 m for the other two).

Table 2. Different perch heights used by male *Dendropsophus sanborni* as calling sites. We indicate the number of calling males (*n*) recorded in each perch height class and their respective sizes (snout–vent length [SVL], given as $\bar{x}$ ± SD, minimum–maximum).

Perch height (cm)	*n*	SVL (mm)
61–70	1	16.54
51–60	1	16.75
41–50	13	17.63 ± 0.71, 16.93–19.04
31–40	19	17.72 ± 0.74, 16.73–19.05
21–30	23	17.72 ± 0.74, 16.02–19.60
11–20	7	17.41 ± 0.70, 16.70–18.33
1–10	8	17.56 ± 0.72, 16.67–18.60

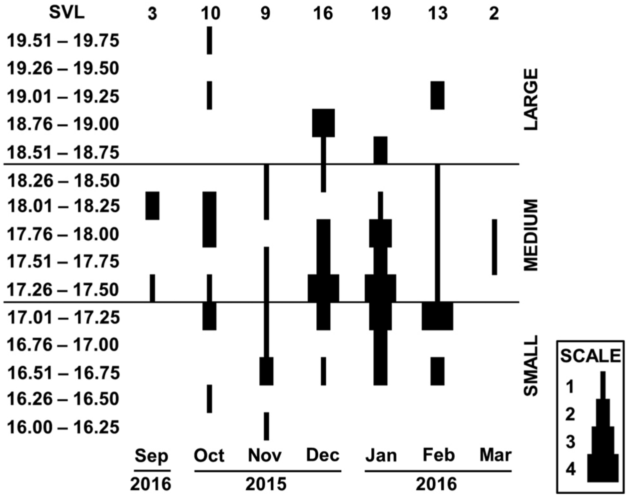

Figure 2. Distribution of snout–vent lengths (SVLs) of calling male *Dendropsophus sanborni* at Cantaclaro ranch, Itapé, Rio Claro, São Paulo, Brazil. The total number of males measured per month is indicated at the top of the figure. Bar width is proportional to the number of individuals for each size class indicated on the vertical axis (corresponding to the scale box). September 2016 is moved to the left side of the figure to facilitate the observation of the seasonal breeding pattern of the species.

Sixty-eight of the sampled calling males (about 94.4%) were using grass leaves positioned over the waterbody as calling perches, while only four (5.6%) were using grass leaves but positioned over the ground (Table 2). Of the 72 males captured, 55 (76.4%) were on perches of intermediate height (21–50 cm). We did not find any statistically significant variation in perch height among mean calling male size ($F = 0.8383$; $P = 0.5448$; df = 6), indicating that there is also no spatial organization or spatial structuring throughout the breeding season based on male size.

DISCUSSION

Seasonal reproductive activity

The breeding season of *Dendropsophus sanborni* in the region of Rio Claro, São Paulo, Brazil, has a duration of

7 months, beginning in September and ending in March, with a peak in January, and thus can be classified as prolonged (sensu Wells, 1977; Wells, 2010). Toledo et al. (2003) recorded the same period of activity for *D. sanborni* in another locality in the municipality of Rio Claro. Although it seems *D. sanborni* always exhibits a prolonged reproductive pattern, its period of reproductive activity can vary among different areas of its occurrence. For example, Santos et al. (2008) reported reproductive activity for *D. sanborni* from August to May in the municipality of Santa Maria, state of Rio Grande do Sul, South Brazil, with sporadic vocalizations during hotter nights in July. Near Santa Maria, Ximenez and Tozetti (2015) recorded reproductive activity between August and March. Our study indicates that the length of the breeding season is associated with abiotic factors, such as rainfall, air and water temperatures, and relative air humidity. Thus, the variation observed in the length of the breeding season of *D. sanborni* among locations most likely follows variation related to the distinctive characteristics of each locality, particularly variation associated with climate and microhabitat.

We observed that the beginning and end of the breeding season of *Dendropsophus sanborni* coincide with the beginning and end of the rainy season, respectively (as defined by Koeppen; see Zaine and Perinotto, 1996). The seasonal distribution of anuran species activity can be influenced by several interrelated factors that are subject to daily, monthly, and annual variation (such as maximum and minimum temperatures, rainfall, and hydroperiod; e.g., Kopp and Eterovick, 2006; Hartel et al., 2007; Gally and Zina, 2013; Akmentins et al., 2015; Hurme, 2015; Luna-Gómez et al., 2017; Leivas et al., 2018). Thus, interactions of these factors may be responsible for variation in the reproductive periods of anurans. For *D. sanborni,* we observed that in addition to rainfall, other climatic traits influenced reproductive activity, including those for the region obtained from the meteorological station (mean minimum air temperature, minimum monthly air temperature, and maximum monthly air temperature), as well as those we measured directly during the nights of our field visits (air temperature, water temperature, and relative air humidity). The colder and drier season clearly limited the activity of the species, whereas the hotter and rainier season provided abiotic conditions favorable for breeding activity (see Wells, 1977; Shahriza et al., 2010; Van Sluys and Guido-Castro, 2011; Waldez et al., 2011; Schalk and Saenz, 2016).

Temporal and spatial social structure

Larger calling males were not detected at the beginning of the species' breeding season, at the end, nor in November, and variation in body size in the chorus over months was not statistically significant. The absence of larger males at the beginning and the end of the season is most likely due to still unideal climatic conditions for reproduction. Our results demonstrated statistically that males of all sizes (large, medium, and small) called throughout the entire rainy season, suggesting that a single, marked moment for breeding recruitment of younger (smaller) males and a temporally ordered social spatial structure based on body size do not occur in *Dendropsophus sanborni* reproduction.

Males of *Dendropsophus sanborni* called on perches 1–70 cm in height and exhibited preference for intermediate heights, which might represent a trade-off between propagation of vocalizations and exposure to sound-oriented predators (see Zuk and Kolluru, 1998; Amézquita and Hödl, 2004; Jacobs and Bastian, 2017). However, variation in body size of calling males among perch heights was not statistically significant, indicating that the vertical spatial organization of males is not based on body size. Further, the majority of males were observed using the same type of vegetation as calling sites, demonstrating that the use of calling sites is not based on size either. Overall, the microhabitats most preferred by males for calling sites likely reflect the best habitat characteristics and the most appropriate conditions for the reproductive mode of the species (e.g., perch height, perch type, water and soil distances; see Haddad and Prado, 2005; Dias et al., 2014; Cunha and Napoli, 2016; Mageski et al., 2016). *Dendropsophus sanborni* has a reproductive mode characterized by floating oviposition in aquatic vegetation, using lentic or lotic and permanent or temporary waterbodies (Cardoso, 1981; Haddad and Prado, 2005; Both et al., 2008), traits that are clearly linked to the microhabitats used by males as calling sites as recorded in the present study.

Dendropsophus sanborni males have been reported in the literature to be territorial, with intrasexual disputes primarily with the emission of advertisement calls and secondly with physical aggression (see Cardoso, 1981; Martins and Jim, 2003). According to Cardoso (1981), *D. sanborni* exhibits intense competition, with calling males spaced by short distances in the chorus and with frequent physical fights. Although we did not measure the distances among males, we also did not observe physical combat during the breeding season. Our data indicate that competition for territories was not intense and also that calling males did not resort to fights. Physical combat is generally avoided and used only as a last option during territorial disputes, since fights are energetically costly (and deviate energy from reproduction) and cause physical wear, injuries, and increased exposure to predators (Robertson, 1986; Giasson and Haddad, 2006; Bastos et al., 2011; Morais et al., 2012; Pereira and Maneyro, 2016; Oitaven et al., 2017).

Our recaptures of marked calling males agree with the literature and indicate some degree of site fidelity, but they provide only minimal support (since recaptures were very rare) for the hypothesis that males occupy the same territories throughout the breeding season. Also, our three recaptured calling males encompassed all of our size classes (small, medium, and large), suggesting that endurance of calling males is not associated with body size in *D. sanborni,* but it is also difficult to make any strong statement about the relationship between endurance and body size with few recaptures.

Our low recapture rate also suggests a high frequency of replacement of calling males throughout the rainy season, thereby significantly changing the composition of the chorus monthly. Given that our study was carried out in a 90-m transect along a slow-flowing stream, and that connections with other areas suitable for reproduction of *Dendropsophus sanborni* are present, a high rate of male replacement could be explained by migration and dispersion events, with the males that we sampled actually representing a subpopulation of *D. sanborni*. According to Pellet et al. (2007) and Wagner et al. (2011), superpopulations may be common for anurans, with individuals moving among subpopulations. Migration, dispersion, and time of permanence in each subpopulation are usually affected by competition, availability of breeding resources, and quality of microhabitats. Alternatively, our replacement hypothesis is supported by the fact that males of prolonged breeding anurans do not necessarily remain reproductively active for an entire breeding season (Grafe and Meuche, 2005; Castellano et al., 2009). Finally, other ecological mechanisms such as predation might also have acted as a selector of males, affecting the social structure of *D. sanborni* (see Ryan et al., 1982; Benard, 2007).

It is well documented that body size is an important trait for sexual selection and for defining territory (see Robertson, 1986; Wells, 2010; Dittrich et al., 2018), but our study did not show any spatial organization based on this trait. Usually, larger males are more successful in physical combat, and thus are more able to occupy better locations during best periods of the breeding season (Berec, 2017; Clause, 2017; Dias et al., 2017; Ospina-L. et al., 2017). Endurance favors those who remain reproductively active for longer periods of time and larger males may also spend more time as components of breeding choruses and, consequently, increase their reproductive successes (Halliday and Tejedo, 1995; Friedl and Klump, 2005; Sullivan and Kwiatkowski, 2007; Castellano et al., 2009; Keogh et al., 2012; Basto-Riascos et al., 2017; Ospina-L. et al., 2017). de Sá et al. (2014) observed size-organized temporal and spatial social structure for calling males, along with breeding recruitment of younger males, in *Boana albopunctata* (Spix, 1924) studied at the same locality as the present study. These authors observed that larger males of *B. albopunctata* initiated reproductive activity when resources were still scarce and, as months passed, larger males gradually ceased their activity, thus providing space for smaller males to breed. Therefore, for *Dendropsophus sanborni* we expected to observe that larger males would occupy better positions in time and space during the breeding season and would possess territories for longer periods of time, engage in combat, and occupy perches as calling sites mostly over the water and at intermediate heights. We also expected some recruitment of younger individuals towards the end of the breeding season. Together, these reproductive characteristics would indicate strong territorial behavior among males with size-driven advantages; however, we observed the opposite in *D. sanborni.*

While our first hypothesis, that the seasonal dynamics of *Dendropsophus sanborni* are conditioned by abiotic factors, was supported, our second hypothesis, that calling males are organized spatially and temporally based on body size, was unexpectedly refuted. We know that social organization in anurans is, in general, dependent on a combination of endogenous and exogenous factors (Sullivan and Kwiatkowski, 2007; López et al., 2011; Llusia et al., 2013; Steen et al., 2013). For example, McCaffery and Lips (2013) observed that the availability of breeding sites for *Espadarana prosoblepon* (Boettger, 1892) limited population abundance, whereas Kluge (1981), studying reproductive resources in *Boana rosenbergi* (Boulenger, 1898), observed that population abundance influenced male territorial behavior. Given these findings, we believe that the non-size-determined spatiotemporal structure and absence of strong territoriality observed for calling males of *D. sanborni* in our study are likely a consequence of the relatively small size of individuals of the species combined with the high abundance of vegetation used as calling sites in the studied area. We were most likely watching a scenario of low intrasexual competition among calling males. Alternatively, studies have indicated that for some lek-breeding anurans there are no reproductive advantages for larger males and that their reproductive strategies favor traits and behaviors other than body size and physical combat (Kluge, 1981; Gerhardt et al., 1987; Pröhl, 2003; Smith and Roberts, 2003; Friedl and Klump, 2005; Martin et al., 2011; Jacobs et al., 2016; Zhu et al., 2016). Therefore, we encourage future studies on *D. sanborni* to make more frequent observations per month, and directly in the field, in order to better understand the territoriality of calling males. Such efforts should focus on better detecting frequencies of physical combat, time spent by males in the chorus, potential migrations and dispersions, as well as the relationships between these behaviors and body size. Furthermore, studies including neighboring subpopulations might also help to better understand the relationship between spatiotemporal social organization and body size of calling males of *D. sanborni*.

ACKNOWLEDGMENTS

We thank Maria José O. Campos and Luiz Marcelo de Carvalho for allowing us to use Cantaclaro ranch as a study site. We are grateful to Andrea Rösel de Lourenço, Antônio B.A. Fontanella, Jefferson P. Felipuci, Juliana P. Jurgilas, Andréa F.C. Mesquita, Camila L. Cavalheiro, Giuliana Garcia, Fernanda M.G. de Oliveira, Letícia A.C. da Silva, João Arthur B.S. de Souza, and Verônica Knorre for assistance in the field. We are also grateful to Mayara M. dos Santos, two anonymous reviewers, and the editor of SAJH, Taran Grant, for comments and suggestions in the first version of the manuscript. We thank Erik Wild for improving our use of written English. We also thank CEAPLA/IGCE for climatological data. FPS and CFBH are grateful to São Paulo Research Foundation (FAPESP) for the grants #2014/24972-4 and #2013/50741-7, respectively. CFBH is also grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a research fellowship. The Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio)/Instituto Brasileiro de Meio Ambiente dos Recursos Naturais Renováveis (IBAMA) provided the collecting license (47515-5). All procedures followed protocols authorized and approved by the ethics committee on animal use (Comissão de Ética no Uso de Animal, CEUA; № 03/2016, Protocol 9597/15) of the Instituto de Biociências, Universidade Estadual Paulista (UNESP).

REFERENCES

Akmentins M.S., Pereyra L.C., Sanabria E.A., Vaira M. 2015. Patterns of daily and seasonal calling activity of a direct-developing frog of the subtropical Andean forests of Argentina. *Bioacoustics* 24:89–99. DOI

Akopyan M., Kaiser K., Vega A., Savant N.G., Owen C.Y., Dudgeon S.R., Robertson J.M. 2018. Melodic males and flashy females: geographic variation in male and female reproductive behavior in red-eyed treefrogs (*Agalychnis callidryas*). *Ethology* 124:54–64. DOI

Amézquita A., Hödl W. 2004. How, when, and where to perform visual displays: the case of the Amazonian frog *Hyla parviceps*. *Herpetologica* 60:420–429. DOI

Basto-Riascos M.C., López-Caro J., Vargas-Salinas F. 2017. Reproductive ecology of the glass frog *Espadarana prosoblepon* (Anura: Centrolenidae) in an urban forest of the Central Andes of Colombia. *Journal of Natural History* 51:2535–2550. DOI

Bastos R.P., Alcantara M.B., Morais A.R., Lingnau R., Signorelli L. 2011. Vocal behaviour and conspecific call response in *Scinax centralis*. *The Herpetological Journal* 21:43–50.

Benard M.F. 2007. Predators and mates: conflicting selection on the size of male pacific treefrogs (*Pseudacris regilla*). *Journal of Herpetology* 41:317–320. DOI

Berec M. 2017. Where is my place? Quick chorus structure assembly in the European tree frog. *Acta Herpetologica* 12:109–112. DOI

Boettger O. 1892. Katalog Der Batrachier-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt. Gebrüder Knauer, Frankfurt am Main.

Both C., Kaefer I.L., Santos T.G., Cechin S.T.Z. 2008. An austral anuran assemblage in the Neotropics: seasonal occurrence correlated with photoperiod. *Journal of Natural History* 42:205–222. DOI

Boulenger G.A. 1898. An account of the reptiles and batrachians collected by Mr. W.F.H. Rosenberg in western Ecuador. *Proceedings of the Zoological Society of London* 66:107–128. DOI

Botto V., Castellano S. 2016. Attendance, but not performance, predicts good genes in a lek-breeding treefrog. *Behavioral Ecology* 27:1141–1148. DOI

Brunetti A.E., Taboada C.A., Faivovich J. 2014. The reproductive biology of *Hypsiboas punctatus* (Anura: Hylidae): male territoriality and the possible role of different signals during female choice. *Salamandra* 50:215–224. DOI

Caldart V.M., Iop S., Lingnau R., Cechin S.Z. 2016. Calling activity of a stream-breeding frog from the austral Neotropics: temporal patterns of activity and the role of environmental factors. *Herpetologica* 72:90–97. DOI

Castellano S., Zanollo V., Marconi V., Berto G. 2009. The mechanisms of sexual selection in a lek-breeding anuran, *Hyla intermedia*. *Animal Behaviour* 77:213–224. DOI

Cardoso A.J. 1981. Organização Espacial e Temporal na Reprodução e Vida Larvária em uma Comunidade de Hilídeos no Sudeste do Brasil (Amphibia, Anura). M.Sc. dissertation, Universidade Estadual de Campinas, Brazil.

Cayuela H., Léna J.P., Lengagne T., Kaufmann B., Mondy N., Konecny L.,… Joly P. 2017a. Relatedness predicts male mating success in a pond-breeding amphibian. *Animal Behaviour* 130:251–261. DOI

Cayuela H., Lengagne T., Joly P., Léna J.P. 2017b. Females trade off the uncertainty of breeding resource suitability with male quality during mate choice in an anuran. *Animal Behaviour* 123:179–185. DOI

Clause J.K. 2017. When it counts, size does matter: complex territoriality in *Oophaga pumilio* (Schmidt, 1857). *Mesoamerican Herpetology* 4:255–262.

Crump M.L. 1974. Reproductive strategies in a tropical anuran community. *Miscellaneous Publication of the Museum of Natural History of University of Kansas* 61:1–68.

Cunha M.S., Napoli M.F. 2016. Calling site selection by the bromeliad-dwelling treefrog *Phyllodytes melanomystax* (Amphibia: Anura: Hylidae) in a coastal sand dune habitat. *Studies on Neotropical Fauna and Environment* 51:144–151. DOI

de Sá F.P., Zina J., Haddad C.F.B. 2014. Reproductive dynamics of the Neotropical treefrog *Hypsiboas albopunctatus* (Anura, Hylidae). *Journal of Herpetology* 48:181–185. DOI

de Sá F.P., Zina J., Haddad C.F.B. 2016. Sophisticated communication in the Brazilian torrent frog *Hylodes japi*. *PloS One* 11:e0145444. DOI

Dias T.M., Maragno F.P., Prado C.P., Cechin S.Z. 2014. Reproductive site selection in the leaf-frog *Phyllomedusa azurea* Cope, 1862 (Anura: Hylidae) in altered areas of the Brazilian Cerrado. *Journal of Natural History* 48:2689–2699. DOI

Dias T.M., Santos T.G., Maragno F.P., Oliveira V.F., Lima C., Cechin S.Z. 2017. Breeding biology, territoriality, and reproductive site use by *Phyllomedusa iheringii* (Anura: Phyllomedusidae) from the South American Pampa in Brazil. *Salamandra* 53:257–266.

Dittrich C., Rodríguez A., Segev O., Drakulić S., Feldhaar H., Vences M., Rödel M.O. 2018. Temporal migration patterns and mating tactics influence size-assortative mating in *Rana temporaria*. *Behavioral Ecology* 29:418–428. DOI

Friedl T.W., Klump G.M. 2005. Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. *Animal Behaviour* 70:1141–1154. DOI

Gally M.C., Zina J. 2013. Reproductive behaviour of *Physalaemus kroyeri* (Anura: Leiuperidae) in the municipality of Jequié, state of Bahia. *Journal of Natural History* 47:1627–1644. DOI

Gerhardt H.C., Daniel R.E., Perrill S.A., Schramm S. 1987. Mating behaviour and male mating success in the green treefrog. *Animal Behaviour* 35:1490–1503. DOI

Giasson L.O.M., Haddad C.F.B. 2006. Social interactions in *Hypsiboas albomarginatus* (Anura: Hylidae) and the significance of acoustic and visual signals. *Journal of Herpetology* 40:171–180. DOI

Grafe T.U., Meuche I. 2005. Chorus tenure and estimates of population size of male European tree frogs *Hyla arborea:* implications for conservation. *Amphibia-Reptilia* 26:437–444. DOI

Gutiérrez G., Lüddecke H. 2002. Mating pattern and hatching success in a population of the Andean frog *Hyla labialis*. *Amphibia-Reptilia* 23:281–292. DOI

Haddad C.F.B., Prado C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience* 55:207–217. DOI

Haddad C.F.B., Toledo L.F., Prado C.P.A. 2008. Anfíbios da Mata Atlântica: Guia dos Anfíbios Anuros da Mata Atlântica. Neotropica LTDA, São Paulo.

Halliday T., Tejedo M. 1995. Intrasexual selection and alternative mating behaviour. Pp. 419–468, in Heatwole H., Sullivan B.K. (Eds.), Amphibian Biology, Vol. 2: Social Behaviour. Surrey Beatty, Chipping Norton.

Hartel T., Sas I., Pernetta A.P., Geltsch I.C. 2007. The reproductive dynamics of temperate amphibians: a review. *North-Western Journal of Zoology* 3:127–145.

Heyer R., McDiarmid R.W., Donnelly M.A., Hayek L.A.C., Foster M. 2001. Medición y Monitoreo de la Diversidad Biológica: Métodos Estandarizados para Anfíbios. Universidad de la Patagonia San Juan Bosco, Chubut.

Höglund J., Alatalo R.V. 2014. Leks. Princeton University Press, Princeton.

Hurme K.J. 2015. Reproductive and spatial ecology of *Leptodactylus insularum* (Anura, Leptodactylidae) in Panama. *Journal of Herpetology* 49:36–45. DOI

Jacobs D.S., Bastian A. 2016. Predator–Prey Interactions: Co-evolution between Bats and Their Prey. Springer International Publishing, Cham. DOI

Jacobs L.E., Vega A., Dudgeon S., Kaiser K., Robertson J.M. 2016. Local not vocal: assortative female choice in divergent populations of red-eyed treefrogs, *Agalychnis callidryas* (Hylidae: Phyllomedusinae). *Biological Journal of the Linnean Society* 120:171–178. DOI

Jaquiéry J., Broquet T., Aguilar C., Evanno G., Perrin N. 2010. Good genes drive female choice for mating partners in the lek-breeding European. *Evolution* 64:108–115. DOI

Keogh J.S., Noble D.W.A., Wilson E.E., Whiting M.J. 2012. Activity predicts male reproductive success in a polygynous lizard. *PLoS One* 7:e38856. DOI

Kluge A.G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 160:1–170.

Kopp K., Eterovick P.C. 2006. Factors influencing spatial and temporal structure of frog assemblages at ponds in southeastern Brazil. *Journal of Natural History* 40:29–31. DOI

Laird K.L., Clements P., Hunter K.L., Taylor R.C. 2016. Multimodal signaling improves mating success in the green tree frog (*Hyla cinerea*), but may not help small males. *Behavioral Ecology and Sociobiology* 70:1517–1525. DOI

Leivas P.T., Mayer T.B., Fávaro L.F. 2018. The reproductive biology of *Dendropsophus minutus* (Amphibia: Anura) in South of Brazil. *Herpetology Notes* 11:395–403.

Llusia D., Márquez R., Beltrán J.F., Moreira C., do Amaral J.P. 2013. Environmental and social determinants of anuran lekking behavior: intraspecific variation in populations at thermal extremes. *Behavioral Ecology and Sociobiology* 67:493–511. DOI

López J.A., Scarabotti P.A., Ghirardi R. 2011. Seasonal patterns of abundance and recruitment in an amphibian assemblage from the Paraná River floodplain. *Interciencia* 36:538–544.

Luna-Gómez M.I., García A., Santos-Barrera G. 2017. Spatial and temporal distribution and microhabitat use of aquatic breeding amphibians (Anura) in a seasonally dry tropical forest in Chamela, Mexico. *Revista de Biología Tropical* 65:1082–1094. DOI

Mageski M.M., Ferreira R.B., Beard K.H., Costa L.C., Jesus P.R., Medeiros C.C., Ferreira P.D. 2016. Bromeliad selection by *Phyllodytes luteolus* (Anura, Hylidae): the influence of plant structure and water quality factors. *Journal of Herpetology* 50:108–112. DOI

Martin C., Guy L., Taylor R.C. 2011. Male position relative to foam nests influences female mate choice in the Túngara frog, *Physalaemus pustulosus*. *Journal of Herpetology* 45:178–180. DOI

Martins I.A., Jim J. 2003. Bioacoustic analysis of advertisement call in *Hyla nana* and *Hyla sanborni* (Anura, Hylidae) in Botucatu, São Paulo, Brazil. *Brazilian Journal of Biology* 63:507–516. DOI

Martof B.S. 1953. Territoriality in the green frog, *Rana clamitans*. *Ecology* 34:165–174. DOI

McCaffery R., Lips K. 2013. Survival and abundance in males of the glass frog *Espadarana prosoblepon* in central Panama. *Journal of Herpetology* 47:162–168. DOI

Méndez-Narváez J., Amézquita A. 2014. Physical combat in the poison-arrow frog, Kokoé-pá (*Oophaga histrionica*) from Arusi, Choco, Colombia. *Herpetology Notes* 7:1–2.

Morais A.R., Batista V.G., Gambale P.G., Signorelli L., Bastos R.P. 2012. Acoustic communication in a Neotropical frog (*Dendropsophus minutus*): vocal repertoire, variability and individual discrimination. *The Herpetological Journal* 22:249–257.

Müller H., Liedtke H.C., Menegon M., Beck J., Ballesteros-Mejia L., Nagel P., Loader S.P. 2013. Forests as promoters of terrestrial life-history strategies in east African amphibians. *Biology Letters* 9:20121146. DOI

O'Brien D.M., Keogh J.S., Silla A.J., Byrne P.G. 2018. The unexpected genetic mating system of the red-backed toadlet (*Pseudophryne coriacea*): a species with prolonged terrestrial breeding and cryptic reproductive behaviour. *Molecular Ecology* 27:3001–3015. DOI

Oitaven L.P.C., Santos J.R.O., Silva A.O., Gamballe P.G., Moura G.J.B. 2017. Description of vocalizations and analysis of variation intra and inter-individual of *Pristimantis ramagii* (Boulenger, 1888) in an upland swamp, Northeast Brazil. *Herpetology Notes* 10:197–203.

Ospina-L. A.M., Rios-Soto J.A., Vargas-Salinas F. 2017. Size, endurance, or parental care performance? Male–male competition, female choice, and non-random mating pattern in the glassfrog *Centrolene savagei*. *Copeia* 105:575–583. DOI

Pellet J., Helfer V., Yannic G. 2007. Estimating population size in the European tree frog (*Hyla arborea*) using individual recognition and chorus counts. *Amphibia-Reptilia* 28:287–294. DOI

Pereira G., Maneyro R. 2016. Use of reproductive microhabitat by *Melanophryniscus montevidensis* (Anura: Bufonidae) from Uruguay. *Zoological Science* 33:337–344. DOI

Plenderleith T.L., Stratford D., Lollback G.W., Chapple D.G., Reina R.D., Hero J.M. 2018. Calling phenology of a diverse amphibian assemblage in response to meteorological conditions. *International Journal of Biometeorology* 62:873–882. DOI

Pröhl H. 2003. Variation in male calling behaviour and relation to male mating success in the strawberry poison frog (*Dendrobates pumilio*). *Ethology* 109:273–290. DOI

Rafinesque C.S. 1815. Analyse de Nature, ou Tableau de l'Universe et des Corps Organisés. Jean Barravecchia, Palermo. DOI

Robertson J.G.M. 1986. Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. *Animal Behaviour* 34:763–772. DOI

Rosa G.M., Andreone F. 2012. Fighting for a leaf: agonistic behaviour in Malagasy frogs of the genus *Guibemantis* (Anura Mantellidae). *Ethology Ecology & Evolution* 24:198–204. DOI

Roff D.A. 2015. The evolution of mate choice: a dialogue between theory and experiment. *Annals of the New York Academy of Sciences* 1360:1–15. DOI

Ryan M.J., Tuttle M.D., Rand A.S. 1982. Bat predation and sexual advertisement in a Neotropical anuran. *The American Naturalist* 119:136–139. DOI

Saenz D., Fitzgerald L.A., Baum K.A., Conner R.N. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetological Monographs* 20:64–82. DOI

Santos A.A.S. 2007. BioEstat, Version 5.3. Available from: https://www.mamiraua.org.br/downloads/programas.

Santos T.G., Kopp K., Spies M.R., Trevisan R., Cechin S.Z. 2008. Distribuição temporal e espacial de anuros em área de Pampa, Santa Maria, RS. *Iheringia: Série Zoologia* 98:244–253. DOI

Schalk C.M., Saenz D. 2016. Environmental drivers of anuran calling phenology in a seasonal Neotropical ecosystem. *Austral Ecology* 41:16–27. DOI

Schmidt K.P. 1944. New frogs from Misiones and Uruguay. *Field Museum of Natural History Publication. Zoological Series* 29:153–160. DOI

Shahriza S., Ibrahim H.J., Anuar M.S.S. 2010. The correlation between total rainfall and breeding parameters of white-lipped frog, *Rana labialis* (Anura: Ranidae) in Kedah, Malaysia. *Tropical Natural History* 10:131–139.

Smith M.J., Roberts J.D. 2003. Call structure may affect male mating success in the quacking frog *Crinia georgiana* (Anura: Myobatrachidae). *Behavioral Ecology and Sociobiology* 53:221–226. DOI

Sousa J.G., Ávila R. 2015. Body size, reproduction and feeding ecology of *Pleurodema diplolister* (Amphibia: Anura: Leiuperidae) from Caatinga, Pernambuco state, Northeastern Brazil. *Acta Herpetologica* 10:129–134. DOI

Spix J.B.v. 1824. Animalia nova sive species novae Testudinum et Ranarum, quas in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspicius Maximiliani Josephi I Bavariae Regis. F.S. Hübschmanni, Monachii. DOI

Steen D.A., McClure C.J.W., Graham S.P. 2013. Relative influence of weather and season on anuran calling activity. *Canadian Journal of Zoology* 91:462–467. DOI

Sullivan B.K., Kwiatkowski M.A. 2007. Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. *Functional Ecology* 21:666–675. DOI

Toledo L.F., Zina J., Haddad C.F.B. 2003. Distribuição espacial e temporal de uma comunidade de anfíbios anuros do município de Rio Claro, São Paulo, Brasil. *Holos Environment* 3:136–149. DOI

Turin R.A.F., Nali R.C., Prado C.P.A. 2018. Intraspecific call variation in a Neotropical gladiator frog with a complex advertisement call. *Amphibia-Reptilia* 39:31–39. DOI

Van Sluys M., Guido-Castro P. 2011. Influence of temperature and photoperiod on the activity of *Melanophryniscus moreirae* (Miranda-Ribeiro 1920) (Anura: Bufonidae) on the Itatiaia Plateau, southeastern Brazil. *South American Journal of Herpetology* 6:43–48. DOI

Vilaça T.R.A., Silva J.R.D.S., Solé M. 2011. Vocalization and territorial behaviour of *Phyllomedusa nordestina* Caramaschi, 2006 (Anura: Hylidae) from southern Bahia, Brazil. *Journal of Natural History* 45:1823–1834. DOI

Waldez F., Menin M., Rojas-Ahumada D.P., Lima A.P. 2011. Population structure and reproductive pattern of *Pristimantis* aff. *fenestratus* (Anura: Strabomantidae) in two non-flooded forests of Central Amazonia, Brazil. *South American Journal of Herpetology* 6:119–126. DOI

Wagner N., Pellet J., Lötters S., Schmidt B.R., Schmitt T. 2011. The superpopulation approach for estimating the population size of 'prolonged' breeding amphibians: examples from Europe. *Amphibia-Reptilia* 32:323–332. DOI

Wells K.D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25:666–693. DOI

Wells K.D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. *Animal Behaviour* 26:1051–1054. DOI

Wells K.D. 2010. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago.

Ximenez S.S., Tozetti A.M. 2015. Seasonality in anuran activity and calling season in a Brazilian subtemperate wetland. *Zoological Studies* 54:47. DOI

Yu J., Chen C., Jin L., Zhao L., Liao W. 2016. No evidence for significant effect of body size and age on male mating success in the spot-legged treefrog. *Asian Herpetological Research* 7:41–45. DOI

Zaine M.F., Perinotto J.A.J. 1996. Patrimônios Naturais e História Geológica da Região de Rio Claro, SP. Câmara Municipal de Rio Claro, Rio Claro.

Zar J.H. 1999. Biostatistical Analysis. Prentice Hall International Inc., New Jersey.

Zheng Y., Deng D., Li S., Fu J. 2010. Aspects of the breeding biology of the Omei mustache toad (*Leptobrachium boringii*): polygamy and paternal care. *Amphibia-Reptilia* 31:183–194. DOI

Zhu B., Wang J., Zhao L., Sun Z., Brauth S.E., Tang Y., Cui J. 2016. Bigger is not always better: females prefer males of mean body size in *Philautus odontotarsus*. *PloS One* 11:e0149879. DOI

Zuk M., Kolluru G.R. 1998. Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology* 73:415–438. DOI