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Author(s): Vinícius Matheus Caldart, Samanta Iop, Rodrigo Lingnau, and Sonia Zanini Cechin

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Calling Activity of a Stream-Breeding Frog from the Austral Neotropics: Temporal Patterns of Activity and the Role of Environmental Factors

Vinícius Matheus Caldart[1,3,4], Samanta Iop[1], Rodrigo Lingnau[2], and Sonia Zanini Cechin[1]

[1] Programa de Pós Graduação em Biodiversidade Animal, Centro de Ciências Naturais e Exatas, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil
[2] Universidade Tecnológica Federal do Paraná, Campus Francisco Beltrão, Paraná, Brazil

Abstract: Animal activity patterns can be influenced by selection pressures from local environmental conditions that might fluctuate at different temporal scales. Although studies with frog species and local populations can suggest how variation of environmental factors affects activity patterns, this topic has received little coverage for Neotropical diurnal frogs that inhabit streams, particularly for subtropical species. We described the temporal patterns of calling activity of Schmidt's Spinythumb Frogs (*Crossodactylus schmidti*) in southern Brazil and investigated the role of environmental factors on this activity. We recorded local environmental variables and monitored calling activity from October 2011 to September 2012, by counting the number of calling males and the number of emitted calls at hourly intervals throughout the day. Male frogs engaged in calling activity year-round, despite the local climatic seasonality. There was no seasonality in the number of calling males or in the number of calls; moreover, variation in photoperiod did not affect the duration of the calling activity throughout the year. *Crossodactylus schmidti* showed a predominantly diurnal calling activity, with a spike in the early morning followed by a gradual increase in activity during daytime hours, and a subsequent decrease in activity at dusk. Environmental factors had varying effects on calling activity: (1) monthly activity was positively associated with accumulated rainfall and air temperature; (2) early morning activity was greater when air temperatures were higher; and, (3) daytime calling activity was positively associated with light intensity. Whereas our results do not preclude the effect of other environmental factors in the calling behavior of male *C. schmidti,* accumulated rainfall, air temperature, and light intensity appear to be abiotic regulators of this activity at the analyzed temporal scales. We discuss the biological implications of these environmental factors in the calling activity and reproduction of *C. schmidti,* and compare the observed patterns with those of other taxa of diurnal stream-breeding frogs.

Key words: Air temperature; *Crossodactylus*; Daily activity; Hylodidae; Light intensity; Monthly activity; Rainfall

Selection imposed by environmental conditions is an important factor driving the evolution of activity patterns of many organisms, given that the conditions might fluctuate at different temporal scales in predictable or unpredictable ways (Aichinger 1987; Leynaud et al. 2008; Ospina et al. 2013). Seasonal variation in rainfall, photoperiod, and/or air temperature influences the activity patterns of many ectothermic species (e.g., Bertoluci 1998; Maciel et al. 2003; Canavero and Arim 2009; Rocha et al. 2014). In addition, a rapid change in a particular condition might also affect fitness-related activities of organisms (e.g., Jaeger et al. 1976; Navas 1996). In the context of mate choice, for instance, variable cloudy conditions might create a mosaic of light environments in the streams occupied by guppies (*Poecilia reticulata*), which affects visual assessment of male body color and brightness (Endler 1992). Although low light levels are not likely to impair visual sensitivity among nocturnal species (see Aho et al. 1993; Buchanan 1998; Cummings et al. 2008), variation in light levels might impair receiver perception and reduce signal efficacy in diurnally displaying frogs. For instance, at the light intensity levels typical of the early morning hours, the communication of Black-spotted Rock Frogs (*Staurois guttatus*) occurs primarily via acoustic signals, because low light putatively affects the efficacy of its visual displays (Grafe and Wanger 2007). Therefore, local environmental factors are expected to affect a species' temporal patterns of activity at different scales.

The activity patterns of anuran amphibians are commonly studied with regard to male calling activity (Wells 2007). Acoustic communication has a key role in the life-history of anurans, mediating social interactions (Wells 1977; Hutter et al. 2013), influencing risk of predation (Tuttle and Ryan 1981; Halfwerk et al. 2014) and parasitism (Bernal et al. 2006; Ferguson and Smith 2012), and being directly linked to breeding activity, and, ultimately, to reproductive success (Gerhardt 1991; Gerhardt and Huber 2002; Tárano and Herrera 2003). Anuran calling activity can be affected by intrinsic factors, such as ontogeny and circadian rhythm (Oishi et al. 2004), and by extrinsic factors, including environmental conditions (Wells 2007). A combination of intrinsic and extrinsic factors can influence the temporal reproductive strategy of a given species, the pattern of which can range from sporadic, explosive bouts of reproduction to prolonged or continuous breeding activity (Crump 1974; Wells 1977).

Environmental factors can affect different species in different ways within a given community (Ospina et al. 2013). For anuran communities from the Neotropics, the role of environmental factors on the temporal patterns of calling activity is relatively well-known (e.g., Zina et al. 2007; Both et al. 2008; Van Sluys et al. 2012). The calling activity of tropical anuran communities is generally affected by variation in air temperature and rainfall (Zina et al. 2007; Van Sluys et al. 2012), whereas similar activity among subtropical communities is mainly affected by variation in air temperature and photoperiod (Both et al. 2008; Canavero et al. 2008; Canavero and Arim 2009). Although these are recurrent patterns observed at the community level, there are several species of explosive-breeders in subtropical

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[3] Present Address: Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, no. 321, Cidade Universitária, 05508-900 São Paulo, SP, Brazil.
[4] Correspondence: e-mail, viniciuscaldart@yahoo.com.br

habitats whose calling activity is also influenced by rainfall (e.g., Vaira 2005; Caldart et al. 2013a). Much less is known about the effects of environmental factors on the calling activity of Neotropical diurnal frogs that inhabit streams, and our understanding of the temporal patterns of activity for this group of frogs is poor.

There are 46 species currently recognized in Family Hylodidae (Frost 2015), most of which occur in tropical areas of the Brazilian Atlantic Rainforest (e.g., Almeida-Gomes et al. 2007a). In contrast, only a few species have a subtropical distribution reaching the southernmost portion of Brazil (Caldart et al. 2013b; Lingnau et al. 2013). To date, only two studies have investigated the effects of environmental factors on calling activity of two species of tropical hylodids (Hatano et al. 2002; Almeida-Gomes et al. 2007b), whereas there have been no investigations of the effects of similar factors in a subtropical species. Studies with individual species and local populations can provide valuable information on how variation of local environmental conditions might affect the evolution of activity patterns at different temporal scales (Wells 2007). Hence, investigating the temporal patterns of calling activity and the role of environmental factors in a subtropical species of hylodid allows for comparisons across a widely distributed anuran taxon of the Atlantic Rainforest.

Here, we investigated the temporal patterns of calling activity of the Neotropical stream-breeding frog, *Crossodactylus schmidti*. This species has a distribution associated with the Misiones Nucleus of the seasonally dry tropical forests, including isolated patches of habitat and transitional areas (sensu Iop et al. 2011) in Argentina, Paraguay, and southern Brazil (Frost 2015). It inhabits rocky streams in which males preferentially use exposed rocks (see Supplemental Material, Fig. S1) to emit advertisement calls, aggressive calls, and visual signals (Caldart et al. 2011, 2014). We addressed the following questions: (1) how is male calling activity distributed along daily and monthly scales; and, (2) what are the roles of environmental variables in regulating calling activity at both temporal scales? We expected that (A) the daytime calling activity would be affected by light intensity, because an increase in light intensity could provide a better discrimination of the sender's signals to intended receivers (i.e., enhanced signal-to-noise ratio, see Endler 1992, 1993); and (B) the monthly calling activity would be affected by variation in air temperature and photoperiod, because these variables are often related to the calling activity of subtropical frogs (Both et al. 2008; Canavero et al. 2008; Canavero and Arim 2009).

MATERIALS AND METHODS

Study Site and Data Acquisition

Our study was conducted at the Turvo State Park (27°14′34.08″S, 53°57′13.74″W; in all cases, datum = WGS84; 376 m above sea level), located in the municipality of Derrubadas, in the northwest region of the state of Rio Grande do Sul, Brazil. The park is considered one of the last large remnants of mesophytic semideciduous forest (sensu Oliveira-Filho et al. 2006) in southern Brazil, covering an area of 17,491.4 ha (SEMA 2005) adjacent to the border of the Uruguay River and near the Argentinean forests of the Moconá Provincial Park and the Yabotí International Biosphere Reserve. The local climate is characterized as subtropical, subhumid with a dry summer, with an annual rainfall of 1787 mm, a mean annual temperature of 18.8°C, and a mean temperature of the coldest month of 13.3°C (Maluf 2000).

We investigated the temporal patterns of calling activity of a *C. schmidti* population using acoustic monitoring within fixed points (Rand and Drewry 2001), in a 150-m section of a first order stream (27°14′36.56″S, 53°57′14.30″W) in which we had detected an abundant presence of *C. schmidti* (Iop et al. 2011). We established three fixed sites for acoustic monitoring (Rand and Drewry 2001) in this section of the stream, each separated by at least 40 m to avoid acoustic interference. From October 2011 to September 2012, 2 d per mo and at hourly intervals during the daytime (0500 to 1900 h), and for a period of 10 min at each site, the first author counted the number of calling males and the number of advertisement and aggressive calls emitted by all males. The procedure was always employed at the stream margin, and only included individuals calling within a radius of approximately 5 m around each site. The observer could acoustically distinguish each calling male within the defined perimeter, because there is little overlap in the calls of nearby males (Caldart et al. 2011) and call recognition is improved by listening at the margin as opposed to at the stream bed.

To investigate the occurrence of nocturnal activity, the same procedure was employed from November 2011 to January 2012, 1 d per mo and at hourly intervals during the night (2000 to 0400 h). The nocturnal calling activity of *Hylodes* and *Crossodactylus* species is typically sporadic (Hatano et al. 2002; Almeida-Gomes et al. 2007b); likewise, a pilot study carried out by us indicated sporadic nocturnal calling activity in *C. schmidti*. Thus, we restricted our evaluation of nocturnal calling activity in *C. schmidti* to an interval comprising the spring and summer months—the period of greatest anuran activity in southern Brazil. During each diurnal and nocturnal count we measured the following variables at the sites with a THAL-300 (Instruterm®) device: air temperature, water temperature, air humidity, and light intensity. Subsequently, for each day of monitoring, we obtained the duration of the photoperiod (in minutes) from the interactive yearbook of the Observatório Nacional Brasileiro (2014), and the accumulated amount of rainfall for 7 d and 15 d prior to each sampling, sourced from the database of the Instituto Nacional De Meteorologia (2014) for the nearest weather station in Rio Grande do Sul, which was located 56 km from the study area.

Statistical Analysis

The mean and maximum number of calling males were positively correlated at all temporal scales (monthly activity, $r = 0.82$, $P = 0.001$; daily activity, $r = 0.76$, $P = 0.001$), as were the number of emitted calls (monthly activity, $r = 0.90$, $P < 0.001$; daily activity, $r = 0.73$, $P = 0.002$); therefore, we used the mean values of activity to describe the temporal patterns of calling with the respective measures of data variation. Calling activity was expressed as two dependent variables: the mean number of calling males per hourly and monthly intervals, and the mean number of calls emitted per hourly and monthly intervals (e.g., Heyer et al. 1994; Hatano et al. 2002; Almeida-Gomes et al. 2007b). Because the three monitoring sites were acoustically independent from each other, we summed the number of calling males and the number of calls at the three sites for each hour interval. Because we conducted two diurnal monitoring periods each month with the same population, we used only the maximum abundance of calling males and the maximum number of calls registered for each hour interval in order to obtain our dependent variables used for analysis, thus avoiding pseudoreplication.

To evaluate the effect of the environmental variables on daily and monthly calling activity, we used Generalized Regression Models (Nelder and Wedderburn 1972; McCullagh and Nelder 1983) with forward stepwise model building (Zar 1999) in Statistica software (v10; Statsoft 2011). To investigate the variables affecting monthly calling activity, we built a model for each dependent variable, including the following uncorrelated predictor variables: mean air temperature, mean air humidity, mean light intensity, photoperiod, 7 d of accumulated rainfall, and 15 d of accumulated rainfall. We found that minimum, mean, and maximum air temperatures were correlated ($r > 0.55$, $P < 0.05$ in all cases), and thus we included only mean air temperature in the models because it provides a better representation of air temperature variation along both daily and monthly scales. Moreover, we included both air temperature and photoperiod in monthly models because these variables were not correlated in our data set ($r = 0.4$, $P > 0.05$).

To investigate variables affecting daily calling activity, we built a model for each dependent variable for the early morning activity (0500 to 0600 h) and for the remaining daytime activity (0700 to 1900 h), including the following uncorrelated predictor variables: mean air temperature, mean air humidity, and mean light intensity. This division of the daily activity was necessary because a whole daytime interval model (0500 to 1900 h) did not detect any relationship between the predictor variables and the number of calling males or calls (i.e., no variable was retained in the models; $P > 0.05$ in all cases), most likely because the early daily activity of *C. schmidti* (0500 to 600 h) and values for predictor variables such as light intensity for those hours differed greatly from those obtained for the rest of day. Water temperature was not used in any model because this variable was strongly correlated with air temperature ($r > 0.8$, $P < 0.001$ in all cases), and air humidity was excluded from models of early morning activity because of a strong correlation with air temperature within those hours ($r > 0.9$, $P < 0.001$ in all cases). Using a linear regression between the duration of photoperiod (minutes) and the duration of the calling activity (the interval between the first and the last call recorded for the daily interval; minutes), we also determined whether photoperiod affected the duration of the calling activity throughout the year. All variables were log-transformed for statistical standardization, with the exception of air humidity, which was arcsine-transformed.

To assess the occurrence or absence of seasonality in calling activity, we performed a circular statistical analysis (Zar 1999) of the distribution of the calling activity throughout the year in Oriana software (v4; Kovach 2011). Each month was converted in angles of 30° and the number of active males and calls were assumed as frequencies for each angle. We estimated the mean vector (μ, representing the interval at which the most calling activity occurs), the circular standard deviation (SD) of the mean vector, and the length of mean vector (r, a measure of data dispersion, varying from 0 to 1). We use the Rayleigh Test of Uniformity (Zar 1999) to calculate the probability of the null hypothesis that calling activity is uniformly distributed throughout the year; a significant result of the Rayleigh Test ($P < 0.05$) indicates that the data are not uniformly distributed and there is a significant mean direction. Descriptive statistics are given as means ± 1 SD, calculated from data pooled per hourly and monthly intervals.

Results

Male *C. schmidti* were active throughout the year, with the mean number of calling males varying from 2 ± 2 (range = 0–3) in July, to 5 ± 2 (range = 0–9) in October, November, and March (Fig. 1A). The mean number of emitted calls varied from 3 ± 2 (range = 0–7) in July, to 21 ± 17 (range = 2–65) in March (Fig. 1B). Although there was a reduction in calling activity in the coldest months, there was no seasonality in the number of calling males ($\mu = 329.12 \pm 122.03°$, $r = 0.10$; Rayleigh Test = 0.47, $P = 0.63$; Fig. 2A), or in the number of calls emitted ($\mu = 339.10 \pm 117.78°$, $r = 0.12$; Rayleigh Test = 2.41, $P = 0.09$; Fig. 2B). Similarly, variation in photoperiod did not affect the duration of the calling activity throughout the year ($R^2_{\mathrm{adj}} = 0.06$, $P = 0.46$).

The calling activity of *C. schmidti* was predominantly diurnal (Fig. 2C–D), with a peak in the early morning occurring both in the number of calling males (mean = 6 ± 2 at 0500 h, range = 0–8; Fig. 2C) and in the number of calls (mean = 26 ± 21 at 0600 h, range = 1–65; Fig. 2D). This spike in activity was followed by a gradual increase in activity during the daytime hours, and a subsequent decrease in activity at dusk (Fig. 1C–D). Nocturnal calling activity was relatively low (Fig. 2C–D), with a small number of calling males (mean = 1 ± 1, range = 0–4) and few calls (mean = 1 ± 2, range = 0–17).

Air temperatures ranged from 23.9° to 30.8°C in the warmest month (January), and from 13.4° to 23.6°C in the coldest month (July). Generally, environmental factors influenced the calling activity of *C. schmidti,* although the effects varied across our models (Table 1). The number of calling males per month increased with accumulated rainfall only, whereas the number of calls emitted per month increased with both accumulated rainfall and air temperature (see Supplemental Material, Figs. S2–S5). We observed that water flow in the study stream varied on account of changes in rainfall amounts throughout the year (minimum of 5.7 mm in May, maximum of 171.3 mm in October), and that males ceased calling activity during heavy precipitation.

Both the number of calling males and number of emitted calls increased with air temperature (Supplemental Material, Figs. S6–S8) during the early morning (0500 to 0600 h), whereas during the day (0700 to 1900 h) both number of calling males and emitted calls increased with light intensity (Supplemental Material, Figs. S9–S11). Males called within the following ranges of values of the environmental variables: 15 d accumulated rainfall = 5.7 mm (May) to 171.3 mm (October); air temperature = 13.4°C (0700 h, in July) to 30.8°C (1200 h, in January); and, light intensity = 0 lux (1900 to 0500 h) to 1317 lux (usually at 1300 h).

Discussion

We have described a continuous pattern of calling activity for *C. schmidti* from subtropical Brazil, and showed that

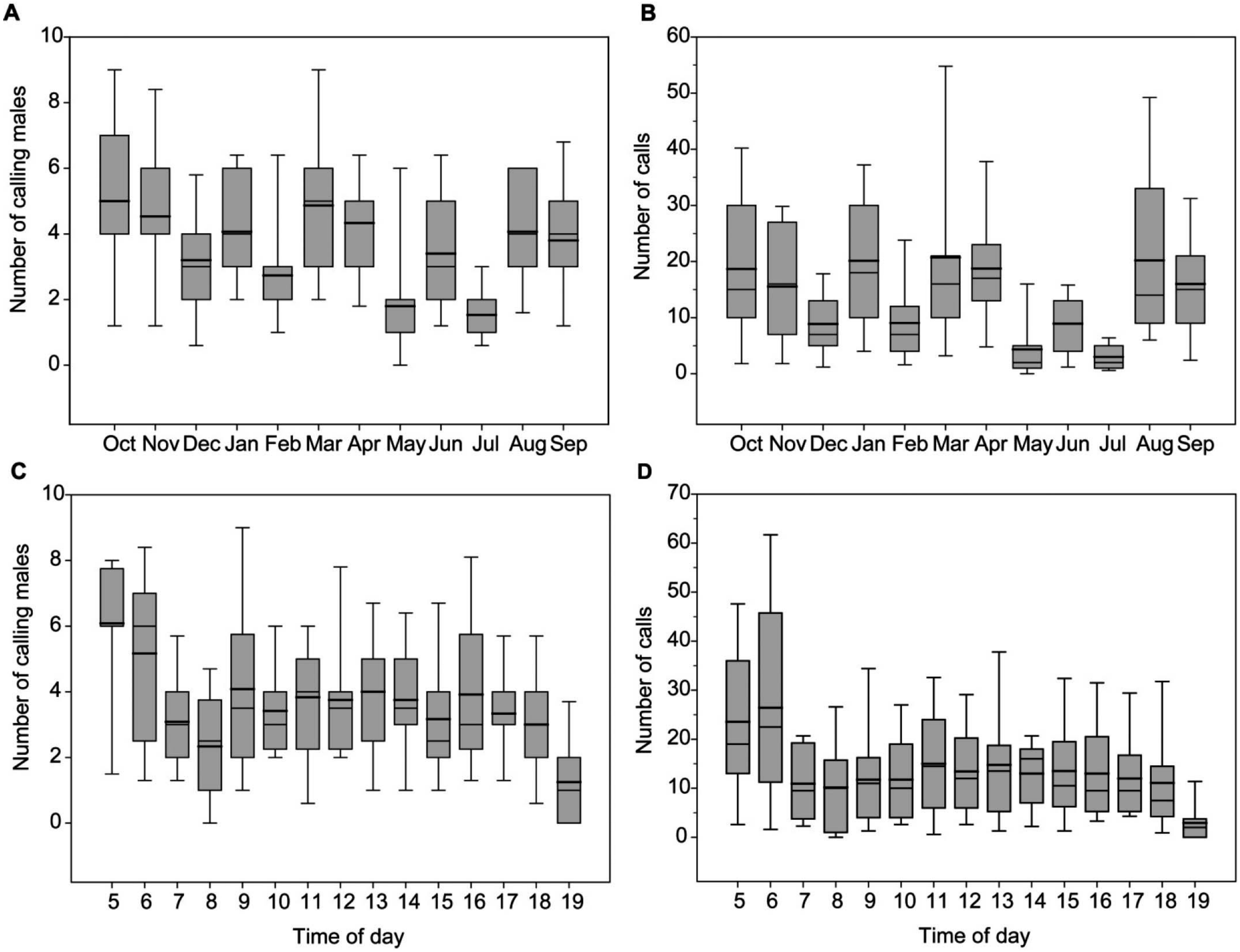

FIG. 1.—Temporal variation in the calling activity of Schmidt's Spinythumb Frogs (*Crossodactylus schmidti*) in southern Brazil, as measured along two time scales. (A) Number of calling males at monthly intervals; (B) number of calls recorded at monthly intervals; (C) number of calling males at hourly intervals; (D) number of calls recorded at hourly intervals. Plots show mean (thick solid line) and median (thin solid line), interquartile range (shaded box) and 10th and 90th percentiles (whiskers).

environmental factors exert varying effects on patterns of monthly and daily calling activity. At a monthly scale, accumulated rainfall and air temperature both positively affected the number of calls, whereas only the accumulated rainfall affected the number of calling males. The daily calling activity of *C. schmidti* was positively affected by air temperature in the early morning hours and by light intensity during the rest of the day. Although *C. schmidti* had predominant diurnal calling activity, a few males irregularly and sporadically called during the night, as has been reported for Rio Grande Tree Toads (*Hylodes meridionalis*) in southern Brazil (Lingnau et al. 2013).

We did not observe any seasonality in the calling activity of *C. schmidti,* and there were no effects of photoperiod in the number of calling males, number of calls, or in the duration of calling activity throughout the year. Instead, males of *C. schmidti* were active year-round, a contrasting pattern to that of many frog species from the austral Neotropics (i.e., calling activity correlated with the longer photoperiods and higher temperatures; Both et al. 2008; Canavero et al. 2008; Canavero and Arim 2009; Kaefer et al. 2009). The monthly activity of *C. schmidti* also differs from that of some confamilial species occurring in southeastern Brazil. For example, male *Hylodes phyllodes* do not call in the months of the dry season with the shortest photoperiods (Hatano et al. 2002). Furthermore, the duration of the calling activity of *H. phyllodes* and *Crossodactylus gaudichaudii* throughout the year is affected by the variation in photoperiod (Hatano et al. 2002; Almeida-Gomes et al. 2007b), whereas we did not detect such a relationship for *C. schmidti*. The continuous pattern of calling activity that we have described for *C. schmidti* provides further support for the contention that rates of male and female gametogenesis are relatively constant in the study area; the regular occurrence of free-swimming tadpoles in streams (VMC, personal observation) is also suggestive of this pattern.

On a monthly scale, the positive effect of accumulated rainfall on the number of calling *C. schmidti* might be related to specific requirements associated with the reproductive mode (Mode 3, sensu Haddad and Prado 2005). Males of *Crossodactylus* and *Hylodes* usually call from rocks and, during courtship, excavate pebbles from the margins of

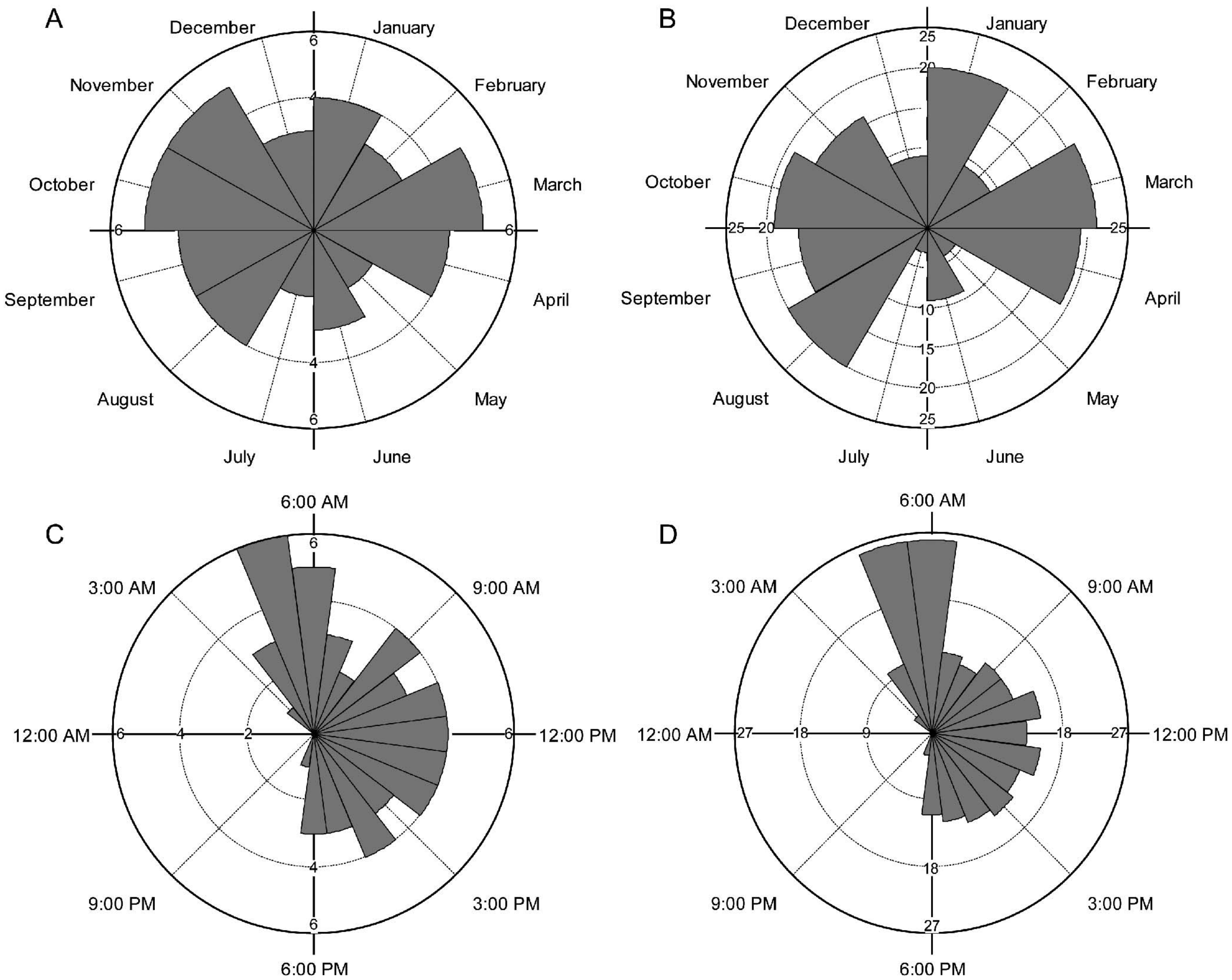

FIG. 2.—Polar graphs depicting the calling activity of Schmidt's Spinythumb Frogs (*Crossodactylus schmidti*) in southern Brazil, as measured along two time scales. (A) Mean number of calling males recorded at monthly intervals; (B) mean number of calls recorded at monthly intervals; (C) mean number of calling males recorded at hourly intervals; (D) mean number of calls recorded at hourly intervals. Data of daily activity (C, D) are based on 12 observations made from 0500 to 1900 h, and three observations made from 2000 to 0400 h.

submerged rocks to construct an underwater chamber where oviposition occurs (Weygoldt and Silva 1992; Haddad and Giaretta 1999; de Sá et al. 2015). Episodes of heavy rainfall change the streambed profile (Lake 2000), potentially displacing rocks used as calling sites and the sediment that males dig to construct oviposition sites. Furthermore, heavy rainfall might impair acoustic signals because of the increased background noise (Brumm and Slabbekoorn 2005). Early larval stages of *Crossodactylus* and *Hylodes* appear to be restricted to the underwater chambers, because only free-swimming tadpoles older than Stage 25 (sensu Gosner 1960) were observed and collected in captivity (Weygoldt and Silva 1992) and in nature (de Sá et al. 2015; Silva-Soares et al. 2015; VMC, personal observation). Therefore, we argue that the effect of rainfall on calling activity might impose some pressure on males' selection and maintenance of fitness-related resources (e.g., calling and oviposition sites) whose availability varies in a temporal and spatial context (see Silva and Giaretta 2008). The degree to which variation in rainfall affects the availability, selection, and maintenance of these resources—and therefore, reproductive success—should be investigated further in *Hylodes* and *Crossodactylus*.

The positive relationship between air temperature and the number of *C. schmidti* calls per month was expected, because this variable is well-known to influence anuran calling performance (Lingnau and Bastos 2007; Wells 2007). Mean air temperature at our study site was correlated with minimum air temperature ($r = 0.8$, $P < 0.001$); thus, either parameter should exhibit a similar relationship to the number of calls recorded per month in *C. schmidti.* Air temperature also affected the monthly activity of *H. phyllodes* in southeastern Brazil (Hatano et al. 2002).

The spike in activity of *C. schmidti* in the early morning hours (0500 to 0600 h) is consistent with the pattern reported for other hylodid species occurring in Brazil (Hatano et al. 2002; Almeida-Gomes et al. 2007b) and for ecologically similar species in Asia (Grafe and Wanger 2007; Preininger et al. 2013). The early morning spike in *C. schmidti* calling activity was more pronounced than has

TABLE 1.—Results of the generalized regression model analysis of the effects of environmental factors on the temporal calling activity of the frog *Crossodactylus schmidti* in southern Brazil. Values set in boldface indicate statistical significance of the listed factor, which was retained in the final models.

	Dependent variable									
	Number of calling males					Number of calls				
Model	β	F	df	P	R^2_{adj}	β	F	df	P	R^2_{adj}
Monthly activity		14.90	1,10	**0.003**	**0.56**		14.12	2,9	**0.002**	**0.70**
15 d accumulated rainfall	0.77	14.90		**0.003**		0.59	12.36		**0.007**	
7 d accumulated rainfall	–0.02	0.00		0.97		0.15	0.25		0.63	
Air temperature	0.38	4.83		0.06		0.52	9.67		**0.013**	
Air humidity	–0.07	0.11		0.75		–0.11	0.36		0.57	
Light intensity	0.22	0.91		0.37		0.18	0.65		0.45	
Photoperiod	0.33	3.17		0.11		0.16	0.80		0.40	
Early morning activity (0500 to 0600 h)		17.73	1,22	**<0.001**	**0.42**		23.04	1,22	**<0.0001**	**0.49**
Air temperature	0.67	17.73		**<0.001**		0.72	23.04		**<0.0001**	
Light intensity	–0.17	1.21		0.28		–0.16	1.11		0.30	
Daytime activity (0700 to 1900 h)		25.63	1,11	**<0.001**	**0.67**		31.32	1,11	**<0.001**	**0.72**
Light intensity	0.84	25.63		**<0.001**		0.86	31.32		**<0.001**	
Air temperature	0.00	0.00		0.99		–0.05	0.08		0.79	
Air humidity	0.24	0.62		0.46		0.20	0.57		0.47	
Whole day activity (0500 to 1900 h)[a]			0,14		0			0,14		0
Air temperature	–0.03	0.01		0.92		–0.08	0.09		0.77	
Air humidity	–0.37	2.06		0.18		–0.39	2.32		0.15	
Light intensity	0.06	0.05		0.83		0.04	0.02		0.89	

[a] Model with no effects of environmental factors (see explanation in the statistical analysis section).

been recorded for other species, and occurred consistently regardless of month. A possible explanation for this pattern is that reduced atmospheric turbulence at dawn favors acoustic-signal transmission over long ranges (i.e., acoustic transmission hypothesis; Henwood and Fabrick 1979), although studies with birds have revealed that signaling at dawn is more advantageous in open habitats than in forests (Wiley and Richards 1978; Dabelsteen and Mathevon 2002; Brown and Handford 2003). Studies on fine-scale temporal variation in the degradation of acoustic signals of diurnal stream-breeding frogs are needed to further test this hypothesis. Specifically, other factors that could explain the early morning spike in activity, such as circadian rhythms (Oishi et al. 2004) or social cues (Dabelsteen and Mathevon 2002), should be considered.

In the remaining daylight hours (0700 to 1900 h), both the number of calling *C. schmidti,* and the number of calls produced, were positively correlated with light intensity at the calling sites. One hypothesis for this relationship is that increased luminosity favors the discrimination of visual signals by intended receivers (Endler 1992, 1993). Diurnally displaying frogs that couple call production with visual signals should limit their displays when low light levels reduce visual signal efficacy. Similar patterns have been reported for males of *C. gaudichaudii* (Almeida-Gomes et al. 2007b) and *H. phyllodes* (Hatano et al. 2002), and males of the Black-spotted Rock Frogs (*Staurois guttatus*) shift their signaling modality from primarily acoustic to primarily visual as light levels increase in calling sites throughout the day (Grafe and Wanger 2007).

We have provided novel information on the temporal patterns of calling activity for a subtropical hylodid, *Crossodactylus schmidti* (Schmidt's Spinythumb Frogs). The patterns, and the influence of environmental factors on those patterns, are consistent with those representing several species of diurnal stream-breeding frogs (i.e., continuous activity, peak in the early morning, and effects of rainfall, light intensity, and air temperature), and contrast with those of most nocturnal frog species from the austral Neotropics (i.e., absence of calling seasonality and no effects of photoperiod vs. seasonal activity correlated with the longer photoperiods and higher temperatures). Moreover, the biological explanations we discussed regarding the temporal patterns of activity, and the effects that environmental factors can have on those patterns, provide a number of directions for further investigation with diurnal stream-breeding frogs.

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RESUMO: Os padrões de atividade animal podem ser influenciados por pressões seletivas de condições ambientais locais que podem flutuar em diferentes escalas temporais. Embora estudos com espécies de anuros e populações locais podem sugerir como a variação de fatores ambientais afeta os padrões de atividade, este assunto tem recebido pouca cobertura para anuros diurnos neotropicais que habitam riachos, particularmente para espécies subtropicais. Nós descrevemos os padrões temporais da atividade de vocalização de uma rã diurna de riacho (Schmidt's Spinythumb Frogs, *Crossodactylus schmidti*) no sul do Brasil e investigamos o papel dos fatores ambientais sobre esta atividade. Nós registramos variáveis ambientais locais e monitoramos a atividade de vocalização entre outubro de 2011 e setembro de 2012, através da contagem do número de machos em atividade de canto e do número de cantos emitidos em intervalos de uma hora ao longo do dia. Os machos estiveram em atividade de vocalização durante todo o ano, apesar da típica sazonalidade climática local. Não houve sazonalidade no número de machos ativos ou no número de cantos emitidos; além disso, a variação no fotoperíodo não afetou a duração da atividade de vocalização ao longo do ano. *Crossodactylus schmidti* apresentou uma atividade de canto predominantemente diurna, com um pico no início da manhã seguido de um aumento gradual da atividade durante o dia, e uma subsequente diminuição da atividade ao anoitecer. Os fatores ambientais tiveram efeitos variáveis sobre a atividade de vocalização: (1) a atividade mensal foi positivamente associada à precipitação acumulada e à temperatura do ar; (2) a atividade do início da manhã foi maior quando as temperaturas do ar eram mais altas; e, (3) a atividade diurna foi positivamente associada com a intensidade luminosa. Apesar dos nossos resultados não excluírem o efeito de outros fatores ambientais no comportamento de vocalização dos machos de *C. schmidti*, a precipitação acumulada, a temperatura do ar e intensidade luminosa parecem ser reguladores abióticos da atividade de vocalização nas escalas temporais analisadas. Nós discutimos as implicações biológicas destes fatores ambientais sobre a atividade de canto e reprodução de *C. schmidti*, e comparamos os padrões observados com os de outros táxons de rãs diurnas de riachos.

Supplemental Material

Supplemental material associated with this article can be found online at http://dx.doi.org/10.1655/Herpetologica-D-15-00029.S1.

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