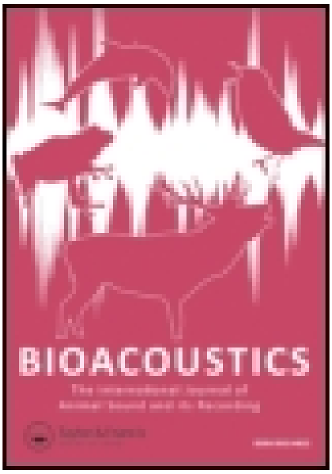

Bioacoustics: The International Journal of Animal Sound and its Recording
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tbio20

Patterns of daily and seasonal calling activity of a direct-developing frog of the subtropical Andean forests of Argentina

M.S. Akmentins[a], L.C. Pereyra[a], E.A. Sanabria[b] & M. Vaira[a]

[a] Centro de Investigaciones y Transferencia de Jujuy (CIT-JUJUY), CONICET, Universidad Nacional de Jujuy, Av. Bolivia 1711 (PC 4600), San Salvador de Jujuy, Argentina

[b] CONICET, Instituto de Ciencias Básicas, Facultad de Filosofía Humanidades y Artes, Universidad Nacional de San Juan, Av. José Ignacio de la Roza 230 (PC 5400), San Juan, Argentina
Published online: 07 Oct 2014.

Bioacoustics, 2014
http://dx.doi.org/10.1080/09524622.2014.965217

Taylor & Francis
Taylor & Francis Group

Patterns of daily and seasonal calling activity of a direct-developing frog of the subtropical Andean forests of Argentina

M.S. Akmentins[a]*, L.C. Pereyra[a], E.A. Sanabria[b] and M. Vaira[a]

[a]*Centro de Investigaciones y Transferencia de Jujuy (CIT-JUJUY), CONICET, Universidad Nacional de Jujuy, Av. Bolivia 1711 (PC 4600), San Salvador de Jujuy, Argentina;* [b]*CONICET, Instituto de Ciencias Básicas, Facultad de Filosofía Humanidades y Artes, Universidad Nacional de San Juan, Av. José Ignacio de la Roza 230 (PC 5400), San Juan, Argentina*

(*Received 16 March 2014; accepted 3 September 2014*)

Climate often regulates different aspects of the life cycle and activity of amphibians. Climatic seasonality may impose severe restrictions on breeding patterns of direct-developing terraranan frogs. We studied the influence of abiotic cues on calling activity of males of the direct-developing frog *Oreobates discoidalis* in the Yungas forests of north-western Argentina. Vocalization activity and daily emission pattern of the vocal repertoire were registered with a frog-logger, and climatic variables were registered with a data logger. We sampled two reproductive seasons from 2010 to 2011. We used ordinal logistic regression to evaluate the relationship between independent climatic variables and the intensity of calling activity. The calling season of males of *O. discoidalis* was triggered by the first rainfall of the aestival season. The species could be defined as crepuscular–nocturnal with a calling activity peak at dusk. Sporadic calling activity during day time was associated with conditions of high humidity and rainfall. Both the emission and the intensity of the advertisement call activity were influenced by time of the day, high levels of relative air humidity and presence of rainfall; air temperature was not a determinant factor in the calling activity of this frog species. Territorial calls were strongly associated with full chorus activity that could be associated with a mechanism of inter-male spacing.

Keywords: frog-logger; ordinal logistic regression; Terrarana; abiotic cues; territorial call; encounter call

Introduction

Climate directly affects many species via physiological constraints associated with species' tolerance and seasonal timing of activities such as growth and reproduction (Todd et al. 2011). Particularly, water availability and temperature regulate almost every aspect of the life cycle and activity of amphibians (Brattstrom 1979; Hillman et al. 2009). The rate of evaporative water loss affects daily and seasonal activity patterns of terrestrial anurans, hence reproductive activities such as male vocalization, oviposition and development of embryos are strongly influenced by rainfall and air humidity (Wells 2007).

Subtropical montane regions with strong climatic seasonality may impose severe restrictions on breeding patterns in direct-developing terraranan frogs, whose eggs are deposited in terrestrial habitats (Hedges et al. 2008). The Yungas' robber frog, *Oreobates discoidalis* (Peracca 1895), lives and breeds under the thick and wet understory of the Yungas Andean forests NW Argentina (Vaira 2002). *O. discoidalis* is the species with the

*Corresponding author. Email: msakmentins@conicet.gov.ar

southernmost distributional range of the megadiverse family Craugastoridae (Padial et al. 2008, 2014).

During the breeding season, males of *O. discoidalis* show a marked territorial behaviour and elaborated vocal repertoires (i.e. advertisement, territorial and encounter calls), used in agonistic interactions (Akmentins 2011). How often each vocalizations type is emitted by males during their daily cycle of vocal activity is still unknown. It might be expected that aggressive calls, associated with spacing between territorial males (Wells 1977), will be more frequently registered during advertisement call activity peaks.

The aim of this study was to determine the influence of abiotic cues on seasonal and daily patterns of calling activity of males of *O. discoidalis* in the Yungas forests of north-western Argentina, and to determine the dial emission patterns of the different types of calls (i.e. advertisement, territorial and encounter call) of the vocal repertories of this species.

Materials and methods

Study site

We conducted the field work in the locality of Jaire (24°01′8.7″S, 65°23′28.1″W, datum World Geodetic System (WGS) 84; 1703 m asl), Jujuy province, north-western Argentina. The study area is an upland mosaic of patches of well-preserved Yungas forest with patches of second-growth forests. Combined data on rainfall and air temperature show a highly seasonal climate pattern for the area, with a mean annual temperature of 17.5°C and mean annual precipitation of 1100 mm. The climate presents a marked seasonality, with a rainy period during the warmer months from October to May, and a dry season during the coldest months from June to September (Figure 1).

Data collection

We collected data during two sampling periods, the first from September 2010 to February 2011 and the second from September 2011 to February 2012.

We used an automated recording device or ‘frog-logger’ in order to determine: (1) the influence of abiotic cues on the vocalization activity of males of *O. discoidalis* and (2) the daily emission pattern of the different call types of the vocal repertoire of this species. The frog-logger was constructed following Peterson and Dorcas (1994), with a type I tapes (TDK© A90, TDK Corporation, Tokyo, Japan). The frog-logger was housed in a watertight plastic box and the external microphone was covered using a plastic cone and attached to a tree 1.5 m above the ground. Coupled with the recording device we deployed a data logger (HOBO® U10-003 Temp/RH Data Logger Onset Co., Cape Code, MA, USA) for the recording of both air temperature and relative humidity (RH).

Before the deployment of the frog-logger device, we visited the study area on a weekly basis (or more than one time per week in the case of precipitation occurrence) at the beginning of September in each sampling season (Vaira 2002). Each time we conducted aural transect surveys during daytime (between 17:00 and 18:00 h) and night (between 21:00 and 22:00 h) to detect vocal activity (Zimmerman 1994). When we detected calling activity (considered as the start date of the breeding season), we deployed the frog-logger. We considered vocalization activity ceased after 7 consecutive days without registered vocalizations on tapes (the last day with registered vocalizations was considered the end of calling season). After the withdrawal of the frog-logger, we continued visiting the study area (on a weekly basis) until March to confirm that frogs had not resumed calling activity.

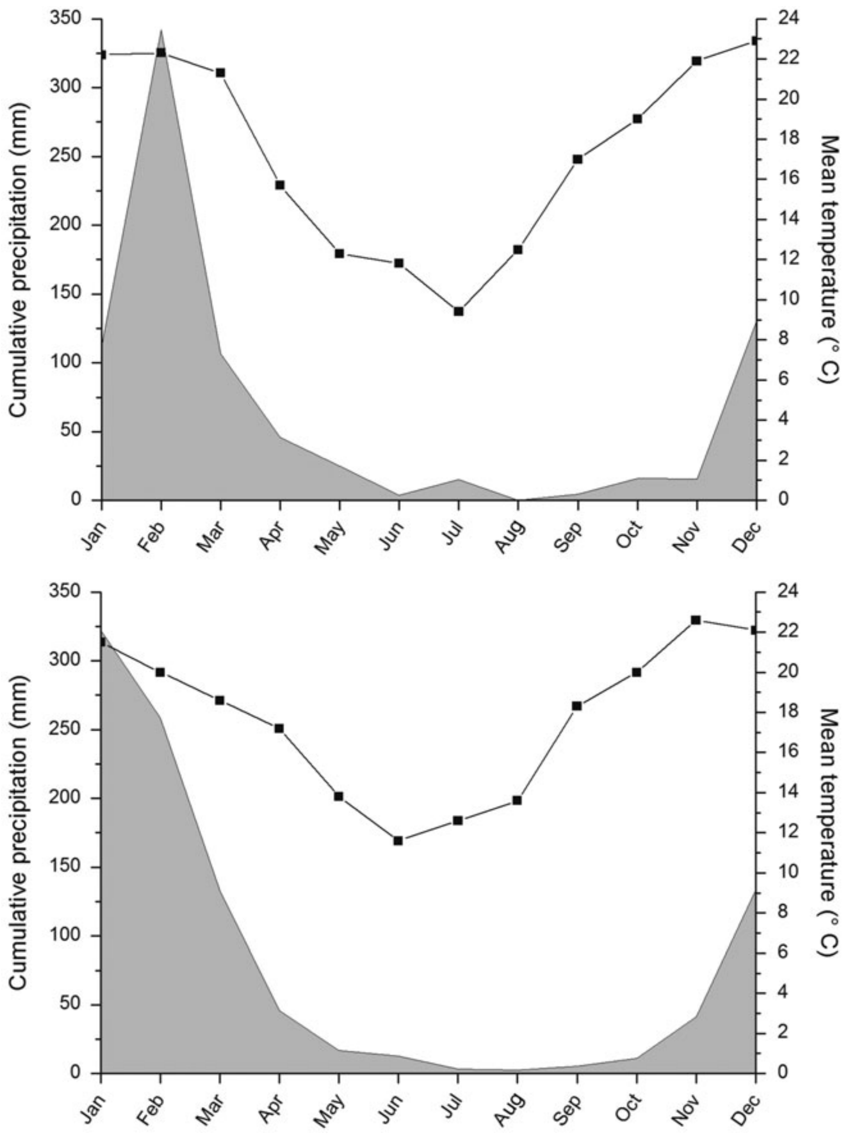

Figure 1. Monthly mean air temperature (line) and cumulative rainfall (bars) at San Salvador de Jujuy, NW Argentina (18 km from the study area). Data are from 2010 (top) and 2011 (below).

The frog-logger recorded for 1 min every hour. Tapes were changed once every $3\frac{1}{2}$ days. Recordings were later digitized and analysed. For each 1-min interval recording, we identified the type of emitted vocalization (advertisement call, territorial call and encounter call), following Akmentins (2011). The intensity of the advertisement call activity was quantified according to the numerical classification scheme used by Bridges and Dorcas (2000) as follows: 0 = no vocalization; 1 = only one male vocalizing; 2 = multiple males vocalizing, but not a full chorus and 3 = many males vocalizing in a full chorus.

To calculate the average calling intensity, full chorus frequency, territorial call frequency and territorial call frequency in each day hour, we only used days with 24 h of continuous registries and with at least one 1-min period with registered calling activity. We also noted the presence/absence of rainfall by hearing the sound of raindrops on the plastic hood of microphone (only heavy and moderate rainfall was detected with this method). The data logger was programmed to simultaneously register with frog-logger records the weather variables at hourly intervals.

Statistical analysis

We used ordinal logistic regression (OLR) with a logit-link function to evaluate the relation between independent variables and intensity of calling activity of *O. discoidalis*. This statistical method was selected because the response variable 'intensity of vocal activity' is an ordinal variable with four levels ordered sequentially. The OLR assumes that relations between the explanatory variables and the dependent ordinal variable are independent of the categories presented by the ordinal variable, and therefore changes in explanatory variables cause the same change in the ratio of cumulative probability of all categories. This assumption was verified through the test of parallel lines (Hosmer and Lemeshow 2000; Agresti 2007). The goodness of fit of the logistic model was assessed using Wald's χ^2 test. Critical *P*-value to determine statistical significance was set to <0.05. Independent variables were time of the record (*h*), relative ambient humidity (%RH), air temperature (°C) and presence/absence of rainfall at the time of calling records. To ensure the independence of predictor variables, we calculated Pearson correlation coefficients for all pairwise combinations of independent variables. We considered $r \leq 0.70$ a suitable criterion for omitting a variable (Fielding and Haworth 1995; Tabachnick and Fidell 2006).

Results

We obtained a total of 924 1-min interval records from the two sampling periods. Of which 587 registries were from the first breeding season, beginning on 8 December 2010 and extended until 4 January 2011 (a span of 27 days). During the second breeding season, beginning on 21 November 2011 and extended until 9 December 2011 (span of 19 days), we obtained 337 1-min intervals registries.

Advertisement call activity showed a peak of calling intensity at sunset between 20:00 and 21:00 h, the calling activity continued through the night and decreased after dawn (Figure 2).

Daytime advertisement call activity (between 06:00 and 19:00 h) was about 30% of the total calling records (80 of 273 of advertisement call registries in both seasons). Diurnal vocal activity was related to high RH (95.6 ± 7.0%), and the presence of rainfall in half of these registries.

We graphically examined the relation between the number of daily amount of 1-min registries with advertisement call activity and environmental conditions (daily amount of 1-min registries with rainfall and daily means of temperature and RH) during the 2010 breeding season (Figure 3). At the beginning of the breeding season, from 9 to 26 December 2010, advertisement call activity was coupled with rainfall. Subsequent to this date, the vocalization activity dropped suddenly despite rainfall presence and high average values of air humidity remaining close to saturation values (100% RH).

The lowest temperature at which vocalization activity was recorded was 6.9°C (full chorus activity at 23:00 h on 12 December 2010, 94.7% RH and presence of rainfall). The highest temperature at which vocalization activity was recorded was 22.6°C, on this

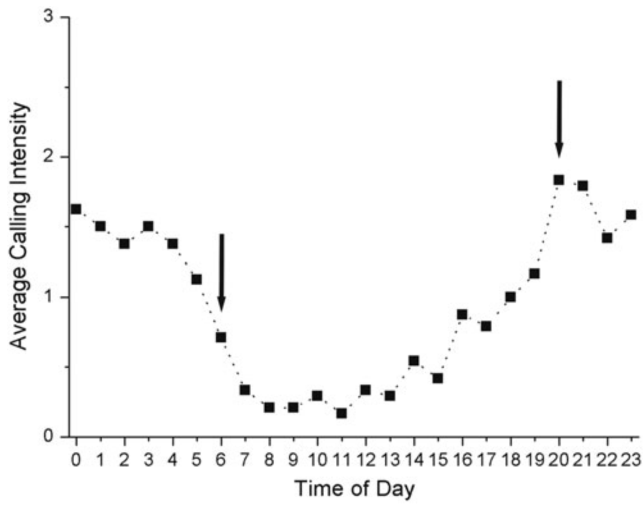

Figure 2. Daily calling patterns of males of *O. discoidalis*. Mean calling activity was calculated by averaging the recorded calling activity levels for each day hour over all days with 24 h of continuous registry and at least 1 h with call activity. Black arrows indicate dawn and dusk.

occasion territorial calls of an isolated male were registered (19:00 h on 12 November 2010, 83.8% RH). Temperatures below or above the range of registered vocalization temperatures are very infrequent: only six registries were below 6.9°C, corresponding to 0.5% of the entire hourly registries; records above 23°C represent only the 6.7% of the hourly registries (Figure 4). The minimum percentage of relative air humidity at which vocalization activity was recorded was 74% RH; on this occasion, sporadic advertisement calls of several males were registered (20:00 h on 25 November 2011, 18.9°C). In both calling seasons, relative air humidity registered during calling activity of the frogs was restricted to the higher percentages compared with the entire range of hourly registries (Figure 4).

Because correlation coefficients ranged well below the suggested cut-off, all explanatory variables were included in the OLR analysis. The test indicated no significant difference for the corresponding regression coefficients across the response categories ($\chi^2 = 13.109$; df = 8; $P = 0.12$), suggesting that the model assumption of parallel lines was not violated in the model. The overall fit of the model was significant ($\chi^2 = 155.27$; df = 4; $P < 0.001$), so we can assume that there is a relation between the dependent variable and the independent variables. Based on the observed significance levels of the resulting OLR model, relative air humidity, rainfall and time of the day (later in the day) were positively related to the intensity of vocal activity (Table 1). Air temperature was not related significantly to the vocalization activity of *O. discoidalis* (Table 1).

Territorial calls were heard most often at night and sporadically with daylight showing a similar daily pattern to the full chorus activity (Figure 5), with a strong correlation (Spearman's rank correlation = 0.88; $P < 0.001$). Territorial calls were frequent and without a clear pattern of variation during the calling season.

The encounter calls were difficult to distinguish from ambient noise, particularly during heavy rainfall or full chorus activity. These calls were less frequent than territorial calls and did not show a noticeable circadian pattern: they seem to be heard regardless of the time of the day (Figure 5). The relation between frequency of occurrence of the

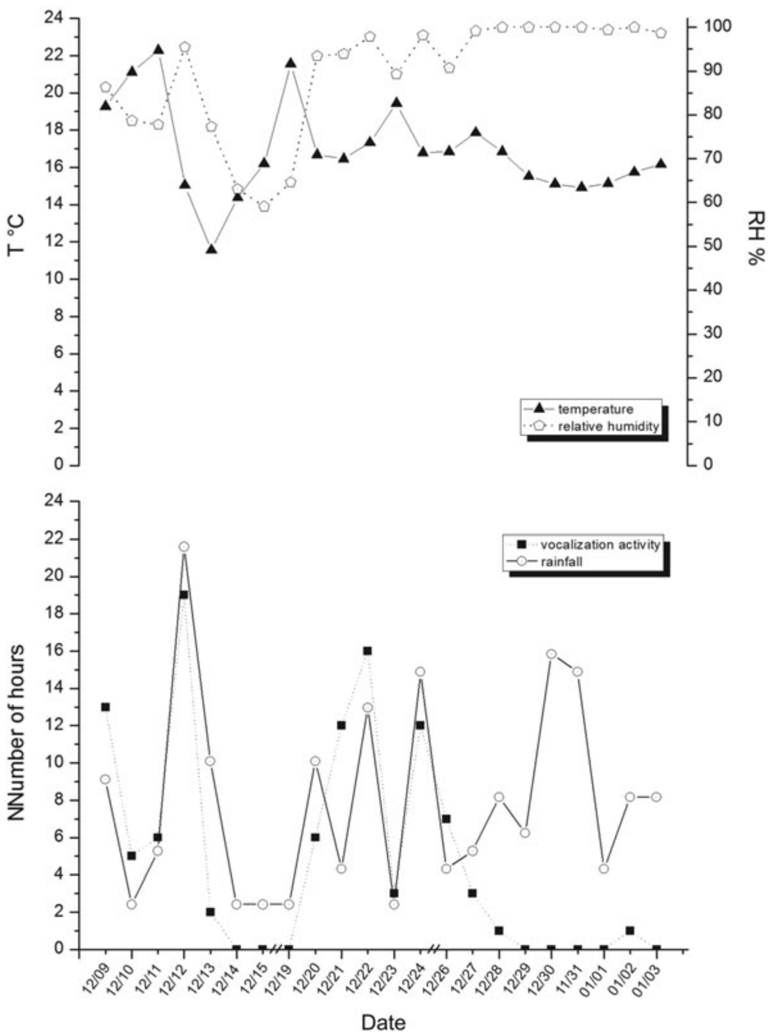

Figure 3. Vocalization activity and climatic data of first reproductive season of *O. discoidalis* (2010). Top: daily average of air temperature (°C) and relative air humidity (RH%). Bottom: number of hours at which calling activity was recorded and number of hours with rainfall each day. We only considered days with 24 h of continuous recordings.

encounter calls and full chorus activity was not statistically significant (Spearman's rank correlation = 0.31; $P = 0.14$), but was related to frequency of occurrence of territorial calls (Spearman's rank correlation = 0.55; $P = 0.005$). These results should be taken with caution as they could be biased due to an incomplete registry.

Discussion

The calling activity of Yungas' robber frog *O. discoidalis* in the study area was relatively short and largely restricted to the onset of summer and the rainy season. Most anuran species of Yungas forests are pond breeders and show a more prolonged calling season until the end of summer (Vaira 2002).

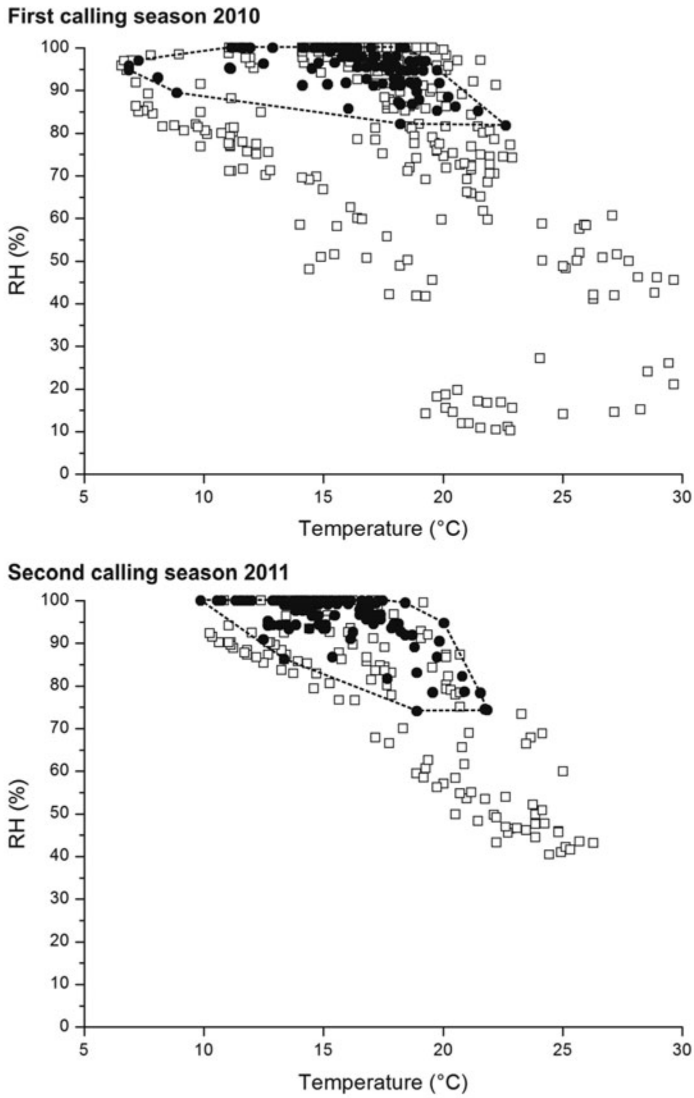

Figure 4. Registries of air temperature (°C) and relative air humidity (RH%) at the study site of both calling seasons (2010–2011) during the 1-min records with advertisement calling activity of males of *O. discoidalis* (black circles), and hourly registries of air temperature and RH without calling activity (white squares). Minimum convex polygons (black dashed lines) include all registries associated with vocalization activity.

The daily cycle of vocalization of these leaf litter dwelling frogs could be defined as crepuscular–nocturnal, with calling activity peaks at dusk. Nocturnal calling activity is a common feature in terraranan frogs, with a vocalization activity peak at dusk and also a less intense peak at dawn (Drewry and Rand 1983; Lüddecke et al. 2000; Duellman and Lehr 2009; Hilje and Aide 2012; Ospina et al. 2013).

Emission of advertisement call and intensity of the activity (e.g. full choruses) were highly influenced by the time of the day and environmental conditions of high relative air humidity and/or presence of rainfall. The influence of abiotic cues such as relative air

Table 1. OLR results of the influence of abiotic cues on calling activity of males of *O. discoidalis*.

	Estimate	Std. error	Wald	Df	*P*
Threshold					
[Activity = 0]	6.34	1.19	28.01	1	< 0.001
[Activity = 1]	6.71	1.20	31.30	1	< 0.001
[Activity = 2]	7.35	1.20	37.38	1	< 0.001
Time of registry	0.04	0.01	11.71	1	< 0.001
Ambient temperature (°C)	0.01	0.03	0.08	1	0.77
RH%	0.06	0.01	38.92	1	< 0.001
Precipit. = 0	− 0.98	0.17	35.18	1	< 0.001
Precipit. = 1	0	–	–	0	–

Notes: Intensity of the advertisement call activity: 0 = no vocalization; 1 = only one male vocalizing; 2 = multiple males vocalizing, but not full chorus formation; 3 = many males vocalizing in a full chorus. Precipit. = 0 (without rainfall); precipit. = 1 (with rainfall).

humidity on calling activity in anurans is strongly dependent on the reproductive mode, time of activity (diurnal/nocturnal), temporal pattern of reproduction (explosive breeders/ prolonged breeders), habitat (terrestrial/arboreal/aquatic), mating system, among other characteristics of each species (see Oseen and Wassersug 2002). In the particular case of terrestrial frogs, high air humidity levels avoid desiccation during calling activity (Woolbright 1985; Fogarty and Vilella 2001; Hauselberger and Alford 2005). In contrast to the negative effect in calling activity of arboreal species of Terrarana (Ospina et al. 2013), rainfall seems to be a trigger of calling activity in ground-dwelling species (Navas 1996; Van Sluys et al. 2012).

Occasionally, males of *O. discoidalis* were active during daylight. Diurnal vocal activity in direct-developing frogs could be considered as an opportunistic behaviour associated with particular conditions of high humidity and/or rainfall presence (Navas 1996; Van Sluys et al. 2012).

Surprisingly, air temperature was not a significant predictor of calling activity for *O. discoidalis*. The range of temperatures of vocal activity of this direct-developing frog was almost equal to the daily range of ambient temperatures; higher temperatures than 23°C were infrequent and occur during daytime, when males were mainly inactive. Temperature plays an important role limiting the vocalization activity of terraranan species that inhabit upland localities or tropical regions (Navas 1996; Van Sluys et al. 2012). *O. discoidalis* inhabits a middle altitudinal range (from 900 to 1900 m asl) of the subtropical Andean Yungas forests, consequently males are not exposed to thermal extremes during their daily vocalization period.

Territorial calls recorded in males of *O. discoidalis* were described as a long-distance territorial interaction, proposed as associated with the defence of males' vocalization sites (Akmentins 2011). In this study, we registered these calls most often at the beginning of the night and strongly associated with full chorus activity peaks. This association reinforces the idea that these types of aggressive calls act as a mechanism of inter-male spacing (Wells and Schwartz 2007). Moreover, the unclear daily pattern in the emission of encounter calls might be partially attributed to the lower frequency of these vocalizations compared with the dominant frequency of advertisement and territorial calls (Akmentins 2011), so that frog-loggers may not register these calls due to the ambient noise.

Direct-developing frog species are independent of water bodies for reproduction, but they have a strong dependence on water/moisture availability in their habitat (Gonzales-Voyer et al. 2011). Understanding the interactions between abiotic cues and calling

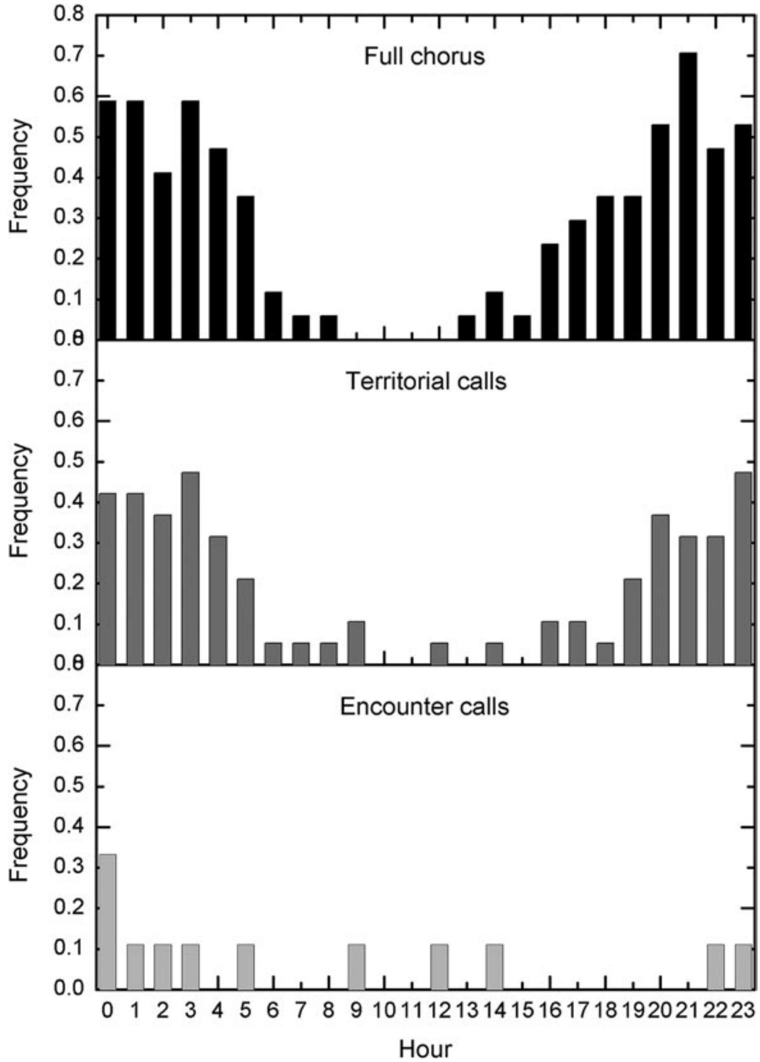

Figure 5. Frequency of occurrence of full chorus activity (top), frequency of occurrence of territorial calls (centre) and frequency of occurrence of encounter calls (below) during the daily cycle of vocal activity of males of *O. discoidalis*. Frequencies were calculated with the number registries at each day hour over all days with 24 h of continuous registries and at least 1 h with call activity.

activity at different temporal scales (e.g. monthly, daily and hourly) of terrestrial breeding frogs that inhabit in forested areas is essential when conducting biodiversity inventories. Terraranans frogs are usually underestimated in amphibians' biodiversity inventories, mainly because of their cryptic life habits and because they do not use water bodies for reproduction (Duellman and Lehr 2009).

Future scenarios of climate change predict more 'tropical' conditions for the subtropical Yungas forest of NW Argentina, with an increment in temperature and precipitation (Gonzáles et al. 2008). Long-term monitoring of reproductive phenology with a combination of automated recording systems and data loggers for climatic conditions could help to detect possible shifts in the breeding behaviour of Yungas forests' amphibians in response to changes in the climatic conditions (Todd et al. 2011; Ospina et al. 2013; While and Uller 2014).

Acknowledgements

The authors thank Cátedra de Agroclimatología FCA-UNJu for the climate data of Augusto M. Romain weather station. The authors are also grateful to the anonymous reviewers for comments that greatly improved the manuscript.

Funding

This research was partially supported by a Secter-UNJu [grant number D-084] and PICTO-UNJu [grant number 153].

References

Agresti A. 2007. An introduction to categorical data analysis. 2nd ed. New York, NY: Wiley.

Akmentins MS. 2011. Vocal repertoire of two species of *Oreobates* Jiménez de la Espada, 1872 (Anura: Strabomantidae) of the Yungas Andean forest, NW Argentina. J Nat Hist 45(29–30):1789–1799.

Brattstrom BH. 1979. Amphibian temperature regulation studies in the field and laboratory. Am Zool 19(1):345–356.

Bridges AS, Dorcas ME. 2000. Temporal variation in anuran calling behavior implications for surveys and monitoring programs. Copeia. (2):587–592.

Drewry GE, Rand AS. 1983. Characteristics of an Acoustic Community: Puerto Rican frogs of the genus *Eleutherodactylus*. Copeia. (4):941–953.

Duellman WE, Lehr E. 2009. Terrestrial-breeding frogs (Strabomantidae) in Peru. Münster: Natur- und Tier-Verlag, Naturwissenschaft.

Fielding AH, Haworth PF. 1995. Testing the generality of bird habitat models. Conserv Biol 9(6):1466–1481.

Fogarty JH, Vilella FJ. 2001. Evaluating methodologies to survey *Eleutherodactylus* frogs in Montane forests of Puerto Rico. Wildlife Soc Bull 29(3):948–955.

González AA, Sarmiento F, Minetti JL. 2008. Cambios Globales en el Noroeste Argentino (21°–32°S) con Referencias a la Provincia más Pequeña de Argentina [Global Changes in Northwest Argentina (21°–32°S) with reference to the Smallest Province of Argentina]. Pirineos 163:51–62.

Gonzalez-Voyer A, Padial JM, Castroviejo-Fisher J, De la Riva I, Vilà C. 2011. Correlates of species richness in the largest neotropical amphibian radiation. J Evol Biol 24:931–942.

Hauselberger KF, Alford RA. 2005. Effects of season and weather on calling in the Australian Microhylid frogs *Austrochaperina robusta* and *Cophixalus ornatus*. Herpetologica 61(4):349–363.

Hedges SB, Duellman WE, Heinicke MP. 2008. New world direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. Zootaxa 1737:1–182.

Hilje B, Aide TM. 2012. Calling activity of the common tink frog (*Diasporus diastema*) (Eleutherodactylidae) in secondary forests of the Caribbean of Costa Rica. Trop Conserv Sci 5(1):25–37.

Hillman SS, Withers PC, Drewes RC, Hillyard SD. 2009. Ecological and environmental physiology of amphibians. New York, NY: Oxford University Press.

Hosmer DW, Lemeshow S. 2000. Applied logistic regression. 2nd ed. New York, NY: Wiley.

Lüddecke H, Amézquita A, Bernal X, Guzmán F. 2000. Partitioning of vocal activity in a neotropical highland-frog community. Stud Neotrop Fauna Environ 35(3):185–194.

Navas CA. 1996. The effect of temperature on the vocal activity of tropical anurans: a comparison of high and low-elevation species. J Herpetol 30(4):488–497.

Oseen KL, Wassersug RJ. 2002. Environmental factors influencing calling in Sympatric Anurans. Oecologia 133(4):616–625.

Ospina OE, Villanueva-Rivera LJ, Corrada-Bravo CJ, Aide TM. 2013. Variable response of anuran calling activity to daily precipitation and temperature: implications for climate change. Ecosphere 4(4):1–12.

Padial JM, Chaparro JC, De la Riva I. 2008. Systematics of *Oreobates* and the *Eleutherodactylus discoidalis* species group (Anura) based on two mtDNA genes and external morphology. Zool J Linn Soc 152:737–773.

Padial JM, Grant T, Frost D. 2014. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. Zootaxa 3825(1):1–132.

Peracca MG. 1895. Viaggio del Dr. Borelli nella Rep. Argentina e nel Paraguay. Rettili e Anfibi [Journey of Dr. Borelli in the Czech, Argentina, and Paraguay. Reptiles and Amphibians]. Bollettino dei Musei di Zoologia e Anatomia Comparata della R. Universita di Torino 10:1–32.

Peterson CR, Dorcas ME. 1994. Automated data acquisition. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LA, Foster MS, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Washington, DC: Smithsonian Institution Press.

Tabachnick BG, Fidell LS. 2006. Using multivariate statistics. 5th ed. Needham Heights, MA: Allyn & Bacon.

Todd BD, Scott DE, Pechmann JHK, Gibbons JW. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proc Roy Soc B Biol Sci 278(1715):2191–2197.

Vaira M. 2002. Anurans of a subtropical montane forest in northwestern Argentina: ecological survey and a proposed list of species of conservation concern. Biodivers Conserv 11:1047–1062.

Van Sluys M, Marra RV, Boquimpani-Freitas L, Rocha CFD. 2012. Environmental factors affecting calling behavior of sympatric frog species at an Atlantic Rain Forest Area, southeastern Brazil. J Herpetol 46(1):41–46.

Wells KW. 1977. The social behaviour of Anuran amphibians. Anim Behav 25:666–693.

Wells KW. 2007. The ecology and behavior of amphibians. Chicago, IL: The University of Chicago Press.

Wells KW, Schwartz JJ. 2007. The behavioral ecology of Anuran communication. In: Narins PM, Feng AS, Fay RR, Popper AN, editors. Hearing and sound communication in amphibians. New York, NY: Springer.

While GM, Uller T. 2014. Quo vadis amphibia? Global warming and breeding phenology in frogs, toads and salamanders. Ecography 37(10):921–929.

Woolbright LL. 1985. Patterns of nocturnal movement and calling activity by the tropical frog *Eleutherodactylus coquii*. Herpetologica 41(1):1–9.

Zimmerman BL. 1994. Audio strip transects. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LA, Foster MS, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Washington, DC: Smithsonian Institution Press; p. 92–97.