

Environmental drivers of anuran calling phenology in a seasonal Neotropical ecosystem

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Abstract Temporal variation represents an important component in understanding the structure of ecological communities and species coexistence. We examined calling phenology of an assemblage of anurans in the Gran Chaco ecoregion of Bolivia by deploying automated recording devices to document nocturnally vocalizing amphibians nightly at seven ponds from 20 January 2011 until 31 October 2011. Using logistic regression, we modelled the relationships between temperature, rainfall and photoperiod with calling activity. There was a distinct seasonal effect with calling activity concentrated in the rainy season with no species detected during the dry season from June until the end of October. Calling activity was positively and significantly correlated with photoperiod in 9 of the 10 species analyzed, but there were distinct species-specific relationships associated with rainfall and temperature. All of these species utilize ephemeral ponds as breeding sites, which can account for their reliance on rainfall as an important driver in calling activity. Two prolonged breeders exhibited similar seasonal breeding patterns across the rainy season, but differed in their response to daily abiotic factors, which might be attributed to the constraints imposed by their reproductive mode. Explosive breeders needed several days of rain to elicit calling. Two pairs of congeners had distinct species-specific relationships between their calling activity and abiotic factors, even though the congeners shared the same reproductive mode, suggesting that the reproductive modes vary in the constraints imposed on calling activity. The patterns observed suggest that calling phenology of tropical anurans is determined by the interaction of exogenous factors (i.e. climatic variables) and endogenous factors (i.e. reproductive modes).

Key words: amphibian, Gran Chaco, photoperiod, reproductive mode, temporal community structure, weather.

INTRODUCTION

A central goal in ecology is to understand the factors that drive the variation in species phenologies, as they can provide insights to interactions and coexistence among species (Schoener 1974). An organism's phenology, that is the occurrence of vital cyclic activities within the year, is the product of abiotic and/or biotic factors, such as avoidance of predators or competitors, or tracking certain seasonal resources such as water, light or nutrients (Van Schaik *et al.* 1993; Bradshaw & Holzapfel 2007). However, the relative impact of these abiotic and biotic factors on an organism's phenology varies and is dependent on the appropriate timeframe (i.e. short-term *vs.* long-term). Activity cycles of ectothermic animals, such as amphibians, are strongly influenced by abiotic factors, principally temperature and rainfall, due to their permeable skin and aquatic reproduction (Duellman & Trueb 1994; Hartel *et al.* 2007). The timing of these events can have important consequences for the timing

of species interactions, and for those species with complex life cycles (e.g. amphibians), this can carry over to affect interactions occurring across multiple life stages and influence community composition at local scales (Parmesan 2007; Yang & Rudolf 2010; Todd *et al.* 2011).

Anuran communities exhibit latitudinal variation in the abiotic factors that drive reproductive activity, and within an assemblage, exhibit species-specific responses to these abiotic factors both in short-term (daily) and long-term (seasonal) periods (Aichinger 1987; Moreira & Barreto 1997; Oseen & Wassersug 2002; Kopp & Eterovick 2006; Saenz *et al.* 2006; Both *et al.* 2008; Canavero & Arim 2009; Canavero *et al.* 2009; Narins & Meenderink 2014). In their examination of geographic structure of community seasonality in amphibians, Canavero and Arim (2009) suggest that both latitude and diversity influence the nestedness and segregation of amphibians across time. Across regions, it is reported that anurans have longer reproductive periods in the wet tropics than those species occurring in tropical seasonal and temperate regions (Duellman & Trueb 1994). In temperate regions, temperature and rainfall, or their interaction,

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are the primary determinants of reproductive activity within the breeding season, but their relative influence varies by species (Bridges & Dorcas 2000; Oseen & Wassersug 2002; Saenz *et al.* 2006; Steen *et al.* 2013). In the tropics and subtropics, recent studies have suggested that photoperiod, rather than temperature and rainfall, is the most important predictor of anuran activity (Both *et al.* 2008; Canavero *et al.* 2008; Canavero & Arim 2009). However, even within the wet tropics, the roles of abiotic factors on anuran reproductive activity vary, ranging from not eliciting any response (Inger & Bacon 1968) to a non-random distribution of breeding activity across the rainy season, with abiotic factors such as rainfall being important drivers (Crump 1974; Gottsberger & Gruber 2004). Tropical anurans are also particularly diverse in their modes of reproduction (Duellman & Trueb 1994), with many species possessing complex oviposition behaviours such as terrestrial or arboreal oviposition, or depositing their eggs in foam nests (Magnusson & Hero 1991; Haddad & Prado 2005). These oviposition strategies are believed to have evolved as a means to reduce exposure of eggs and larvae to predators (Magnusson & Hero 1991). However, these reproductive modes also impose constraints, and species need to adjust their calling and breeding activity in accordance with their reproductive mode (Gottsberger & Gruber 2004).

Previous studies indicate multiple drivers influencing the calling activity of anurans across both daily and seasonal time periods. However, many of the studies conducted in tropical or subtropical regions have been conducted over coarse (i.e. monthly or weekly) time scales (e.g. Moreira & Barreto 1997; Both *et al.* 2008; Canavero & Arim 2009; Canavero *et al.* 2009). In this study, we utilized a fine-grain (i.e. daily timeframe) approach to quantify the abiotic correlates of calling activity in an assemblage of tropical anurans occurring in the Gran Chaco ecoregion of south-eastern Bolivia from the middle of the rainy season to the end of the dry season. We describe the pattern of calling phenology that arises from species-specific responses to abiotic factors, specifically we discuss the potential influence of life-history strategies (i.e. reproductive strategy (prolonged *vs.* explosive breeders) and reproductive mode) on the observed responses to these extrinsic factors.

METHODS

Study system

Our study was conducted in the semi-arid thorn forests of the Gran Chaco ecoregion of south-eastern Bolivia. The region has a warm, rainy season (November–March) and a cool, dry season (April–October). The surrounding forest in

this semi-arid region is predominately thorn forest; common tree species include *Schinopsis lorenzii* and *Aspidosperma quebracho-blanco* with cacti (e.g. *Opuntia* spp., *Cleistocactus baumannii* and *Eriocereus guelichii*) and bromeliads constituting the common understorey plants (Navarro & Maldonado 2002). Our study sites were located in one the most xeric regions of the Bolivian Chaco with annual rainfall and temperature averaging 513 mm and 24.6°C, respectively (Navarro & Maldonado 2002).

Anuran vocalization recordings

We collected audio recordings of nocturnally vocalizing amphibians at seven ponds within the vicinity of the Isoceño community of Yapiroa, one of approximately 25 indigenous communities occurring near the Parapeti River in the indigenous territory of Isoso, Provincia Cordillera, Departamento de Santa Cruz, Bolivia (19.60°S, 62.57°W; WGS 84). We used automated recording devices (SM2 + Song Meters: Wildlife Acoustics, Maynard, MA, USA), which allow for consistent sampling across extended periods of time (Bridges & Dorcas 2000), to record anuran vocalizations each night. Song Meters were attached to nearby trees within 2 m of the pond's edge (one per pond). The seven breeding ponds that were both artificial ($n = 5$) and natural ($n = 2$), and ranged in their hydroperiod from temporary ($n = 6$) to semi-permanent ($n = 1$). The Song Meters were deployed at the seven ponds from 20 January 2011 (mid-way through the rainy season) and recorded daily until 31 October 2011 (the end of the dry season). The scope of our study includes data collected from 20 January 2011 to 31 October 2011. Each Song Meter was set to record for 1 min at the start of each hour starting at 21.00 hours and ending at 01.00 hours, for a total of 5 min per night. The recordings were saved to secure digital cards, which were retrieved approximately every 2 weeks from each Song Meter. We listened to and transcribed the recordings and identified the vocalizations to species level and the number of calling individuals of each species were estimated. We followed the protocol of Saenz *et al.* (2006) when documenting the number of calling individuals per species per night; when the number of individuals per species calling was ≤ 4 , we felt that we could accurately count the total number of individuals calling; however, when > 4 individuals were calling, we assigned a value of 5, as it was impossible to determine the exact number of individuals. Thus, the nightly call intensity index of each species per pond could range from 0 (i.e. no individuals heard) to 25 (summed across five sampling minutes).

Abiotic factors

Previous studies have recognized that anuran calling activity varies across small spatial scales (Oseen & Wassersug 2002; Saenz *et al.* 2006) and similar studies have collected site-specific temperature and rainfall data. We relied on a centrally located weather station sited within the community of Yapiroa as the source for the temperature and rainfall data. The maximum distance between a Song Meter and the weather station was 2 km. The weather station consisted of a HOBO Data Logging Rain Gauge and a HOBO Pro v2

External Data Logger (Onset Computer Corporation, Pocasset, MA, USA). The temperature data logger was covered with an Onset Solar Radiation Shield to block its exposure to direct sunlight. Temperature was measured to the nearest 0.001°C and daily rainfall was measured to the nearest 0.1 mm. We computed the number of hours of daylight using Julian date and -19.6°S latitude for the study sites (Kirk 1994).

Statistical analyses

As in similar studies (e.g. Saenz *et al.* 2006), we observed several anuran species calling several days after a rain event. Therefore, we could not discern whether a species calling activity was an immediate response to precipitation or if it was the result of a lag or build up in precipitation. We used three different types of rainfall lag in our models. The first type was categorical (catlag) and simply indicated the occurrence of rainfall ranging from 1 to 5 days prior to the calling event. For example, catlag1 referenced rainfall 1 day prior to the calling event, catlag2 referenced rainfall 2 days prior to the calling event. The next lag type (rainlag) was the amount of daily rainfall that occurred from one to five nights prior to the calling event. For example, rainlag1 was the rainfall amount from 1 day prior, whereas rainlag2 was the amount of rainfall from 2 days prior to the calling event. The final lag variable type (cumulrain) examined the effects of the cumulative rainfall ranging from 1 to 5 days prior. For example, cumulrain2 equalled the total cumulative rainfall from 1 and 2 days prior to the calling event.

We used logistic regression with generalized estimating equations to test the relationship between the occurrence of daily anuran calling activity (0 = no calling and 1 = calling) and air temperature at 2100 h, daily rainfall, lags and accumulation in rainfall, and day length. Because ponds were repeatedly sampled, we used an autoregressive correlation structure. We began with a simple model including temperature and day length. We then added rainfall on the day of calling and variables reflecting lags and accumulation in rain-

fall (five models total). We used quasi-likelihood under the independence model criterion, adjusted for the number of parameters in the model (QICu) to compare models and considered the model with the lowest QICu to be the best model (Pan 2001).

RESULTS

We detected 14 species of anuran at our seven survey ponds (Appendix S1). These species did not exhibit much spatial partitioning in their use of calling sites as many species overlapped considerably (Appendix S1). Four species, *Dermatonotus muelleri*, *Leptodactylus elenae*, *Leptodactylus fuscus* and *Scinax fuscovarius*, were detected less than 10 days during the survey period (Appendix S2) and were excluded from analyses.

Seasonal and daily call patterns

We observed variation in calling activity across the wet and dry seasons, as the majority of calling activity was concentrated in the rainy season between the months of January and the first week of April (Fig. 1, Table 1). However, we detected three species calling in the month of May after a large rainstorm: *Physalaemus biligonigerus*, *Pleurodema guayapae* and *Odontophrynus americanus*. No species was observed calling from June until the beginning of October (Fig. 1). At the start of the subsequent rainy season at the end of October we detected *L. fuscus* calling for the first and only time (Table 1).

We observed some variation in calling activity among species within the rainy season (Figs 1 and 2). While the number of individuals calling each night varied, *Leptodactylus bufonius* and *Phyllomedusa sauvagii* called

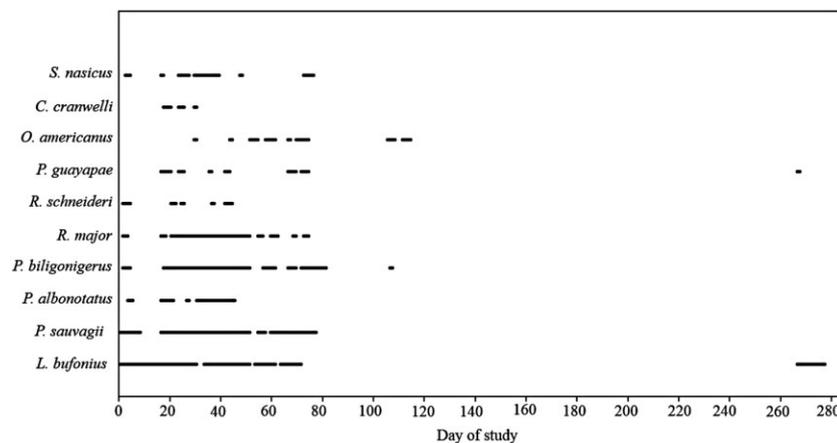


Fig. 1. The most frequent calling anuran species recorded over the 285-day study from 20 January 2011 to 31 October 2011 in the Bolivian Chaco. *Leptodactylus elenae*, *Leptodactylus fuscus*, *Dermatonotus muelleri* and *Scinax fuscovarius* were excluded because of small sample sizes. For species names, see Table 1.

Table 1. Calling activity and reproductive modes of 14 species of anurans in the Gran Chaco by month from 20 January 2011 to 31 October 2011

Family and species	RM	Month									
		January	February	March	April	May	June	July	August	September	October
Bufonidae											
<i>Rhinella major</i>	1	x	x	x	x						
<i>Rhinella schneideri</i>	1	x	x	x							
Ceratophryidae											
<i>Ceratophrys cranwelli</i>	1	x	x		x						
Hylidae											
<i>Phyllomedusa sauvagii</i>	3	x	x	x	x						
<i>Scinax fuscovarius</i>	1	x	x		x						
<i>Scinax nasicus</i>	1	x	x	x	x						
Leptodactylidae											
<i>Leptodactylus bufonius</i>	4	x	x	x	x						x
<i>Leptodactylus elenae</i>	4	x	x								
<i>Leptodactylus fuscus</i>	4										x
<i>Physalaemus albonotatus</i>	2	x	x	x	x	x					
<i>Pleurodema guayapae</i>	2	x	x	x	x	x					x
Microhylidae											
<i>Dermatonotus muelleri</i>	1		x								
Odontophryidae											
<i>Odontophrynus americanus</i>	1	x	x	x	x	x					x

The x symbol indicates that the species was observed calling in the month indicated. Blank cells represent no calling detected in that month for a given species. The species reproductive mode (RM) *sensu* Haddad and Prado (2005): 1 = Aquatic oviposition and exotrophic, aquatic tadpoles in lentic water (RM 1), 2 = Oviposition in floating foam nest and exotrophic, tadpoles in lentic water (RM 11), 3 = Oviposition on vegetation above water, exotrophic tadpoles drop into lentic water (RM 24), 4 = Oviposition and early larval stages in foam nest in subterranean nests, subsequent nest flooding, and exotrophic tadpoles in lentic water (RM 30)

nearly daily during the rainy season (Figs 1 and 2). *Physalaemus albonotatus*, *P. biligonigerus*, *Rhinella major* and *Scinax nasicus* were detected every month from January to April, but they called less frequently when compared with *L. bufonius* and *P. sauvagii* (Figs 1 and 2, Table 1). The calling activity for *Ceratophrys cranwelli* was concentrated towards the beginning of the sampling period (Figs 1 and 2). As previously mentioned, the calling activity of *L. bufonius* and *P. sauvagii* was fairly continuous throughout the rainy season, whereas the calling activity of *P. albonotatus*, *P. biligonigerus* and to a lesser extent *R. major* and *S. nasicus* were detected consistently for several days at a time (Figs 1 and 2). The calling activity of other species like *C. cranwelli*, *R. schneideri*, *O. americanus* and *P. guayapae* were detected over much shorter timeframes, often a single night (Figs 1 and 2). There was variation in the calling activity even among these species; *C. cranwelli* calling was concentrated at the beginning of the survey period, whereas the calling activity of other species such as *P. guayapae* and *O. americanus* occurred across a longer time period of the rainy season.

Abiotic correlates of calling activity

Because no species was recorded calling between June and early October, and only three species in late

October, we restricted data to 20 January 2011–27 June 2011 for the logistic regression analyses. The average temperature at 2100 h during the entire survey period (January–October) was 22.6°C (SD = 5.0°C, range = 9.4–31.2°C) (Fig. 3). The total rainfall recorded during the survey period was 466 mm and the highest amount of daily rainfall recorded was 67.4 mm (Fig. 3). The average temperature at 21h00 from 20 January 2011 to 27 June 2011 was 22.5°C (SD = 4.1°C, range = 9.4–30.1°C) (Fig. 3). The total rainfall recorded from 20 January 2011 to 27 June 2011 was 384 mm and the highest amount of daily rainfall recorded was 67.4 mm (Fig. 3).

The logistic regression models revealed significant associations between the abiotic variables and calling activity, with each species exhibiting a distinct relationship, but some general trends were also observed (Table 2). With the exception of *O. americanus*, the calling activities of all species were significantly and positively correlated with photoperiod. As another general trend, the majority of species calling were significantly and positively associated with the amount of rainfall on the night of the calling event; the only exceptions were *R. schneideri*, *P. albonotatus* (no association) and *L. bufonius* (significant negative association) (Table 2).

The calling activity of *Phyllomedusa sauvagii* and *Scinax nasicus* were significantly and positively

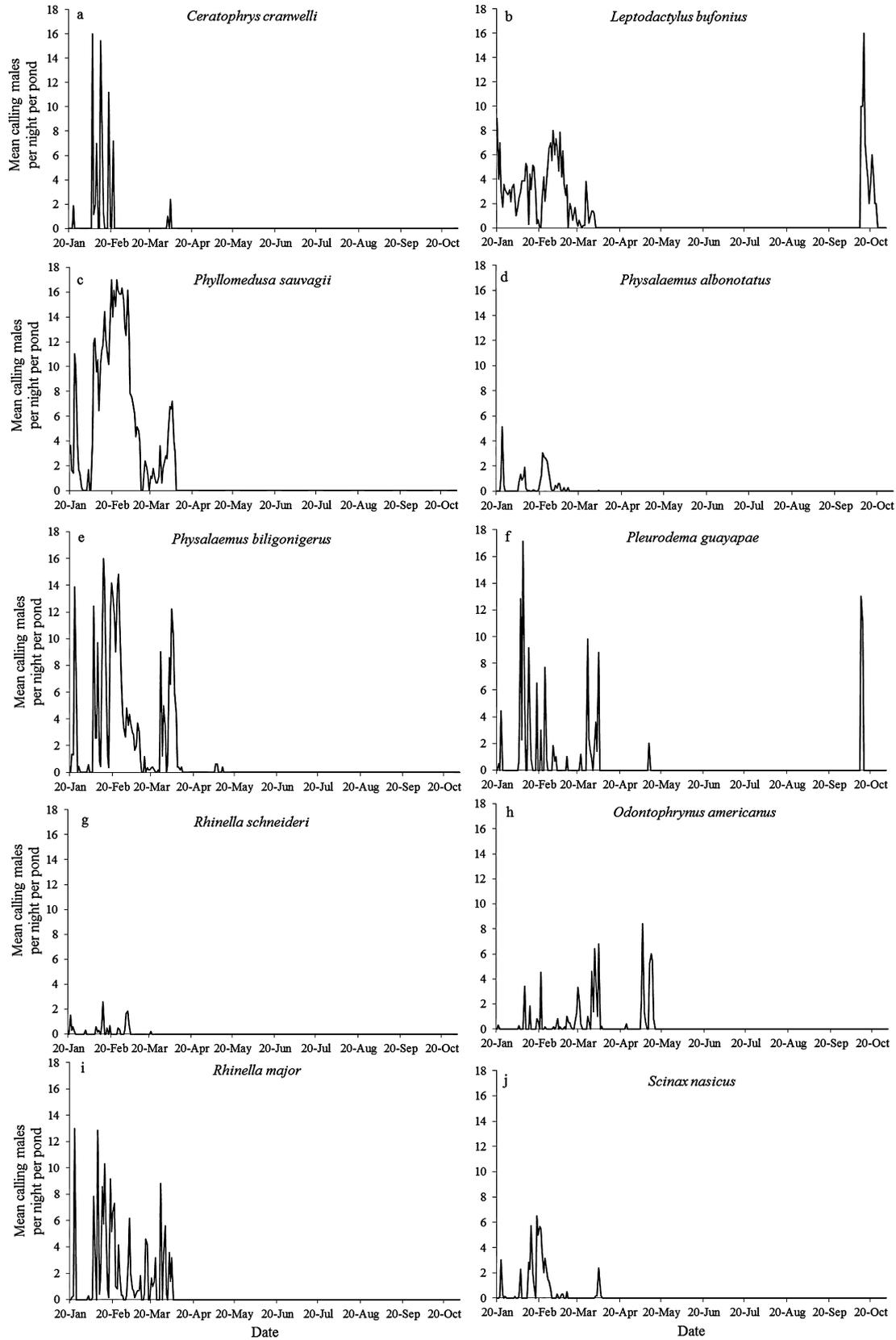


Fig. 2. Call intensity scores for 10 species of anurans each night at seven ponds from 20 January 2011 to 31 October 2011: (a) *Ceratophrys cranwelli*, (b) *Leptodactylus bufonius*, (c) *Phyllomedusa sauvagii*, (d) *Physalaemus albonotatus*, (e) *Physalaemus biligonigerus*, (f) *Pleurodema guayapae*, (g) *Rhinella schneideri*, (h) *Odontophrynus americanus*, (i) *Rhinella major* and (j) *Scinax nasicus*. Ponds were located within the vicinity of the Isoceño community of Yapiroa, Cordillera Province, Santa Cruz Department, Bolivia.

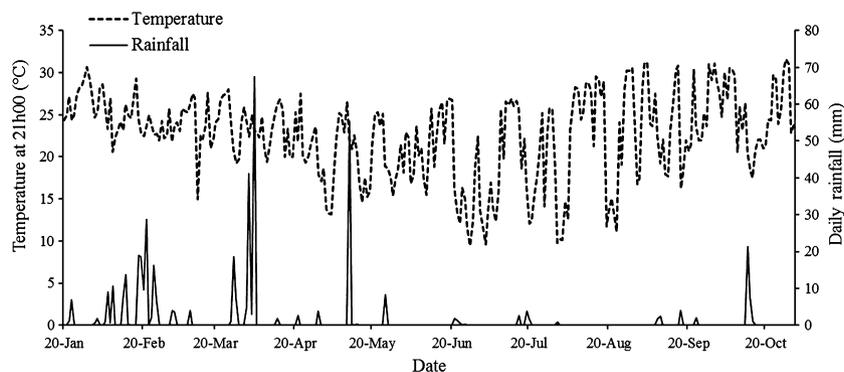


Fig. 3. Daily rainfall (mm; solid line) and air temperature at 2100 h (°C; dashed line) collected from a centrally located weather station in the Isoceño community of Yapiroa, Cordillera Province, Santa Cruz Department, Bolivia from 20 January 2011 to 31 October 2011. Total accumulated rainfall during the survey period was 466 mm.

correlated with photoperiod, rainfall on the night of the calling event, and lags in the amount or occurrence of rainfall (Table 2). Calling activity varied slightly between the two species of *Physalaemus*; although each species exhibited similar responses to rainfall and photoperiod, they differed in their response to temperature: *P. albonotatus* calling was significantly negatively associated with temperature, whereas *P. biligonigerus* exhibited no relationship (Table 2). Similarly, the other pair of congeners, the two *Rhinella* species, differed in their calling activity. The main differences being that on the night of calling, *R. major* activity was positively correlated with rainfall and temperature, whereas *R. schneideri* exhibited no relationship with rainfall, and a significant negative association with temperature (Table 2). *Ceratophrys cranwelli* and *P. guayapae* exhibited the same associations between calling activity and abiotic variables (Table 2). Calling activity in *O. americanus* was positively associated with amount of rainfall on the night of the calling event, but negatively associated with cumulative amount of rainfall after 4 days (Table 2).

DISCUSSION

Usually generalized as being explosive breeders (Duellman 1999), our study demonstrates that anurans of the Gran Chaco ecoregion span the spectrum of breeding activity of prolonged and explosive breeders (Wells 1977). There was no single abiotic

factor that was the dominant driver in calling activity in any of the 10 species analyzed; rather, we observed that at least two abiotic factors (rainfall and photoperiod) were influencing the calling activity in Chacoan anurans. Similar studies in tropical and subtropical regions found that anurans exhibited a range of responses to climatic factors, ranging from rainfall being the most important variable associated with calling activity to no association between anuran reproductive activity and rainfall and/or temperature (Inger & Bacon 1968; Crump 1974; Gottsberger & Gruber 2004; Kopp & Eterovick 2006). However, some recent studies have identified photoperiod as the predominant driver in reproductive activity in the tropics and subtropics (Both *et al.* 2008; Canavero & Arim 2009). In our study, we found that photoperiod was an important driver of calling activity in 9 of the 10 species analyzed (*O. americanus* being the exception) in addition to rainfall and/or temperature. Our study design could account for the fact that photoperiod was not the only abiotic variable driving calling activity in the Chaco frog assemblages as compared with similar seasonal tropical and subtropical assemblages; sites in those studies were surveyed monthly as compared with nightly monitoring as in our study (Both *et al.* 2008; Canavero & Arim 2009). In some instances, the abiotic variables used varied in the time period over which they were collected; rainfall and temperature were monthly averages, whereas photoperiod was calculated from the day of the survey (Canavero & Arim 2009). We have shown that in most instances, amount of rainfall on the night of the calling

Table 2. Results of the best-fit logistic regression models for ten species of anurans in the Bolivian Gran Chaco

Species	Variable	Estimate	SE	LCL95 – UCL95	Z	P
<i>Rhinella major</i>	Intercept	-18.8	1.19		-15.8	<0.0001
	Temperature	0.06	0.01	-21.1 to -16.4	5.02	<0.0001
	Photoperiod	1.26	0.11	0.04 to 0.09	11.93	<0.0001
	Rainfall	0.04	0.01	1.05 to 1.46	5.3	<0.0001
	Catlag1	0.98	0.2	0.03 to 0.06	4.99	<0.0001
	Catlag2	0.07	0.16	0.6 to 1.37	0.44	0.6603
	Catlag3	-0.19	0.15	-0.24 to 0.38	-1.25	0.2104
	Catlag4	0.31	0.13	-0.49 to 0.11	2.33	0.0199
<i>Rhinella schneideri</i>	Intercept	-31.0	2.96	-36.8 to -25.2	-10.5	<0.0001
	Temperature	-0.18	0.04	-0.27 to -0.1	-4.2	<0.0001
	Photoperiod	2.66	0.29	2.1 to 3.22	9.27	<0.0001
	Rainfall	-0.04	0.03	-0.1 to 0.02	-1.31	0.191
	Catlag1	0.92	0.28	0.38 to 1.47	3.3	0.001
	Catlag2	-0.72	0.29	-1.28 to -0.16	-2.53	0.0115
	Catlag3	-0.78	0.51	-1.78 to 0.22	-1.52	0.1274
	Catlag4	-0.5	0.41	-1.31 to 0.31	-1.21	0.225
<i>Ceratophrys cranwelli</i>	Intercept	-83.6	16.2	-115.3 to -51.9	-5.16	<0.0001
	Temperature	-0.34	0.13	-0.59 to -0.1	-2.73	0.0064
	Photoperiod	6.91	1.41	4.15 to 9.66	4.91	<0.0001
	Rainfall	0.19	0.05	0.09 to 0.29	3.72	0.0002
	Catlag1	1.34	0.3	0.76 to 1.93	4.54	<0.0001
	Catlag2	0.24	0.32	-0.38 to 0.87	0.77	0.44
	Catlag3	-1.53	0.31	-2.13 to -0.93	-5	<0.0001
	Catlag4	2.05	0.34	1.38 to 2.73	5.96	<0.0001
<i>Phyllomedusa sauvagii</i>	Intercept	-29.3	3.14	-35.5 to -23.1	-9.33	<0.0001
	Temperature	0.01	0.02	-0.02 to 0.04	0.59	0.5558
	Photoperiod	2.3	0.26	1.8 to 2.8	8.99	<0.0001
	Rainfall	0.02	0	0.01 to 0.03	4.88	<0.0001
	Rainlag1	0.04	0.01	0.02 to 0.06	3.59	0.0003
	Rainlag2	0.03	0.01	0.02 to 0.04	4.29	<0.0001
	Rainlag3	0.03	0.01	0.01 to 0.05	3.7	0.0002
	Rainlag4	0.01	0	0 to 0.01	1.37	0.1716
<i>Scinax nasicus</i>	Intercept	-33.6	4.98	-43.4 to -23.8	-6.75	<0.0001
	Temperature	-0.06	0.05	-0.17 to 0.05	-1.06	0.2906
	Photoperiod	2.57	0.43	1.73 to 3.41	6	<0.0001
	Rainfall	0.05	0.01	0.03 to 0.07	5.36	<0.0001
	Rainlag1	0.06	0.01	0.03 to 0.09	4.15	<0.0001
	Rainlag2	0.03	0.01	0 to 0.06	2.18	0.0295
	Rainlag3	0.02	0.01	0 to 0.04	1.75	0.0796
	Rainlag4	0.03	0	0.03 to 0.04	7.38	<0.0001
<i>Leptodactylus bufonius</i>	Intercept	-40.0	5.01	-49.8 to -30.2	-7.98	<0.0001
	Temperature	0.1	0.04	0.03 to 0.17	2.94	0.0033
	Photoperiod	3.06	0.38	2.32 to 3.8	8.09	<0.0001
	Rainfall	-0.07	0.02	-0.1 to -0.04	-4.33	<0.0001
	Catlag1	0.12	0.23	-0.33 to 0.56	0.52	0.6036
	Catlag2	0.08	0.2	-0.31 to 0.48	0.4	0.6871
	Catlag3	0.31	0.21	-0.11 to 0.72	1.44	0.149
	Catlag4	0.03	0.2	-0.37 to 0.42	0.14	0.8859
Catlag5	0.64	0.08	0.49 to 0.8	8.29	<0.0001	

Table 2. *Continued*

Species	Variable	Estimate	SE	LCL95 – UCL95	Z	P
<i>Physalaemus albonotatus</i>	Intercept	-25.5	3.23	-31.9 to -19.2	-7.91	<0.0001
	Temperature	-0.11	0.02	-0.15 to -0.08	-6.17	<0.0001
	Photoperiod	1.99	0.26	1.47 to 2.5	7.56	<0.0001
	Rainfall	0	0.01	-0.02 to 0.03	0.16	0.8761
	Catlag1	0.61	0.36	-0.1 to 1.31	1.69	0.0907
	Catlag2	1.33	0.23	0.88 to 1.78	5.78	<0.0001
	Catlag3	0.26	0.15	-0.03 to 0.55	1.75	0.08
	Catlag4	0.51	0.24	0.03 to 0.98	2.08	0.0376
<i>Physalaemus biligonigerus</i>	Intercept	-18.0	2.37	-22.6 to -13.3	-7.57	<0.0001
	Temperature	-0.01	0.02	-0.06 to 0.03	-0.51	0.6069
	Photoperiod	1.32	0.23	0.86 to 1.77	5.67	<0.0001
	Rainfall	0.04	0.01	0.02 to 0.06	3.26	0.0011
	Catlag1	1.3	0.17	0.97 to 1.64	7.62	<0.0001
	Catlag2	0.68	0.13	0.42 to 0.94	5.05	<0.0001
	Catlag3	-0.08	0.11	-0.3 to 0.14	-0.71	0.4797
	Catlag4	0.84	0.1	0.64 to 1.04	8.17	<0.0001
<i>Pleurodema guayanae</i>	Intercept	-24.4	4.76	-33.7 to -15.1	-5.13	<0.0001
	Temperature	-0.15	0.07	-0.29 to -0.02	-2.29	0.0223
	Photoperiod	2.02	0.51	1.01 to 3.02	3.92	<0.0001
	Rainfall	0.09	0.02	0.06 to 0.12	5.7	<0.0001
	Catlag1	1.19	0.19	0.82 to 1.56	6.35	<0.0001
	Catlag2	0.11	0.47	-0.81 to 1.04	0.23	0.8146
	Catlag3	-0.89	0.19	-1.27 to -0.51	-4.62	<0.0001
	Catlag4	1.31	0.19	0.95 to 1.67	7.06	<0.0001
<i>Odontophrynus americanus</i>	Intercept	-3.91	2.88	-9.55 to 1.73	-1.36	0.174
	Temperature	0.05	0.03	-0.01 to 0.11	1.58	0.1146
	Photoperiod	-0.03	0.32	-0.66 to 0.61	-0.08	0.9377
	Rainfall	0.07	0.01	0.05 to 0.09	7.35	<0.0001
	Cumulrain2	0.03	0.02	-0.01 to 0.08	1.54	0.1234
	Cumulrain3	0.02	0.02	-0.01 to 0.06	1.23	0.2189
	Cumulrain4	-0.03	0.01	-0.05 to -0.01	-3.2	0.0014
	Cumulrain5	0.01	0.01	0 to 0.02	1.45	0.146

The probability of each species calling was modelled with the following variables: 2100 h air temperature, photoperiod, amount of rainfall on the night of the calling event, a lag referencing the occurrence of rainfall ranging from 1 to 5 days prior (catlagX, where X corresponds to the number of days prior to calling), a lag indicating the amount of rainfall occurring from 1 to 5 days prior to the calling event (rainlagX, where X corresponds to the number of days prior to calling) and/or a lag in cumulative rainfall that occurred from 1 to 5 days prior to the calling date (cumulrainX, where X corresponds to the number of days prior to calling). LCL95 = 95% lower confidence level, UCL95 = 95% upper confidence level.

event, lags in rainfall and/or daily temperature (along with photoperiod) were important drivers in calling activity for all of the anuran species. As our study highlights, we stress the importance of using abiotic data collected across similar timeframes when attempting to elucidate the factors driving calling phenology in tropical anurans.

The permanency of breeding sites utilized by anurans may also influence their response to abiotic factors. Rainfall tends not to influence calling activity of anurans that utilize semi-permanent breeding ponds, whereas anurans that rely on temporary breeding sites depend on rainfall for the establishment and continued persistence of ponds and to stimulate

calling activity (Saenz *et al.* 2006; Steen *et al.* 2013). In the nearby Chiquitano region of Bolivia, rainfall is an important driver of calling activity as several species of anurans that utilized temporary ponds (Schulze *et al.* 2009). All of the Chacoan anurans detected in this study utilize ephemeral ponds as breeding sites, which likely explains their significant and positive associations with nightly rainfall or lags in rainfall on previous nights, highlighting that rainfall is an important driver in their calling activity.

There was interspecific variation in the responses to these abiotic factors, and even those species that exhibited similar seasonal activity patterns or those with similar reproductive modes appeared to be responding

to different abiotic factors (Gottsberger & Gruber 2004). Two species, *Leptodactylus bufonius* and *Phyllomedusa sauvagii*, had nearly the same pattern in seasonal calling activity; they were prolonged breeders (Wells 1977) across the entire rainy period. The physiology of these two species may provide insights as to their consistent, continuous reproductive activity; *L. bufonius* is one of the few Chacoan anurans with prolonged spermatogenesis occurring almost across the entire year (Ceï 1949a). *Phyllomedusa sauvagii* is well-known for its ability to limit its water loss with the waxy secretion that it produces and coats across its skin (Shoemaker *et al.* 1972), thus allowing these frogs to remain active even during the driest periods. Even though these species were similar in their seasonal activity patterns, differences occurred in their daily calling patterns, particularly in their response to rainfall. Calling activity of *L. bufonius* was negatively associated with daily rainfall, whereas *P. sauvagii* showed a positive response. In addition, the calling activity of both species was positively associated with lags in rainfall, but calling in *P. sauvagii* was positively associated with the amount of rainfall from the previous nights, whereas *L. bufonius* called when rain occurred the previous nights, although the amount of rainfall was not important. The difference in the reproductive mode of these two species may provide some explanation to the observed differences in call patterns. Prior to calling, an *L. bufonius* male excavates an underground nest chamber where it breeds with a female and the nest is later capped with mud (Ceï 1949b; Reading & Jofré 2003). Once the nest is sealed, the tadpoles can persist for over 40 days or until heavy rainfall floods the nest allowing the tadpoles to enter a nearby pond (Philibosian *et al.* 1974; Ceï 1980; Reading & Jofré 2003). Thus, the condition of the mud and the reproductive mode of this species may constrain its daily breeding activity. During nights of heavy rainfall, *L. bufonius* may not be able to construct or maintain the integrity of the nest chamber as it could collapse in on itself and cover recently oviposited eggs with mud; however, the occurrence of rainfall on previous nights may leave the mud still malleable, thereby allowing the male to construct the nest chamber. Newly sealed nests are also vulnerable to predation if the nest breaks apart too soon; Reading and Jofré (2003) observed that newly sealed *L. bufonius* nests that were quickly inundated with water broke down and the egg masses were preyed upon by heterospecific tadpoles. *Phyllomedusa sauvagii* is unique in this assemblage in that it is the only species in the system that oviposits on vegetation overhanging ponds (Perotti 1997). As Gottsberger and Gruber (2004) observed in other species of *Phyllomedusa* that possess the same reproductive mode, calling activity in *P. sauvagii* coincides with high amounts of rainfall occurring across several days, and after the ponds have filled with water.

This ensures that the chance of the eggs desiccating is low as they develop and that when they finally hatch, the tadpoles will drop into a well-established pond that has little risk of drying (Gottsberger & Gruber 2004). A similar pattern was also observed in the Chiquitano dry forest of Bolivia, where *Phyllomedusa boliviana* exhibited prolonged calling activity over an artificial pond (Schulze *et al.* 2009).

The patterns of calling activity of *C. cranwelli*, *O. americanus*, *P. guayapae* and *S. nasicus* are indicative of explosive breeders (*sensu* Wells 1977); although they were detected nearly every month in the rainy period, they called only over short periods (i.e. one to several days). *Ceratophrys cranwelli*, *O. americanus* and *S. nasicus* oviposit their eggs directly in the water (Ceï 1980; Perotti 1997), whereas *P. guayapae* constructs a flattened foam nest, but its eggs are often exposed even while in the foam nest and vulnerable to predators (Schalk 2012; Valetti *et al.* 2014). Many tadpoles in the tropics have omnivorous or carnivorous feeding habits and are known to prey upon eggs and tadpoles of heterospecifics (Heyer *et al.* 1975; Magnusson & Hero 1991; Altig *et al.* 2007; Schalk *et al.* 2014). Given that the eggs of *C. cranwelli*, *O. americanus*, *P. guayapae* and *S. nasicus* are exposed and vulnerable to predators (Magnusson & Hero 1991), these species may breed over short periods as a means to limit exposure of their eggs to heterospecific tadpoles and other potential predators (e.g. invertebrates (CMS, unpubl. data) or killifishes (Montaña *et al.* 2012)) as the pond is colonized by predators over time. While the calling activity of these explosive breeders was positively correlated with daily rainfall, all four species were positively correlated to lags in rainfall, particularly with the day before calling occurred. Explosive breeders tend to utilize ephemeral sites, to which they often need to migrate as the ponds are formed (Wells 1977; Saenz *et al.* 2006). The highly fossorial species can remain inactive for long periods (Ceï 1980; Valetti *et al.* 2014), and therefore, they likely need several days of rain to stimulate their emergence and migration to their breeding sites. Similarly, the hylid *S. nasicus* needs to migrate from their arboreal refugia to their breeding sites, which may explain a similar pattern in its calling activity.

In the lowland tropical forest of French Guiana, Gottsberger and Gruber (2004) observed a temporal partitioning of species breeding and calling activity in accordance to their reproductive mode. If reproductive mode imposes constraints on breeding activity in all anurans, then we would expect to see an emerging pattern where species with the same reproductive mode exhibit a similar response to the abiotic factors, as was observed in Gottsberger and Gruber (2004). However, in our study, congeners with the same reproductive modes exhibited different responses to the abiotic factors in their daily calling activity. The two

pairs of congeners occurring in this system (*R. major*/*R. schneideri* and *P. albonotatus*/*P. biligonigerus*), did not partition themselves spatially in their use of calling sites, nor temporally as they overlapped in their calling activity across the latter half of the rainy season. The reproductive modes of some species impose stronger constraints on the reproductive activity as compared with others (Gottsberger & Gruber 2004). Both species of *Physalaemus* and *Rhinella* breed only when a pond has already formed; *Physalaemus* species create floating foam nests that contain eggs, while both species of *Rhinella* oviposit directly in the water. Thus a pond needs to be newly formed or already established for breeding to commence as compared with *L. bufonius* for example (Cei 1949b). The reproductive modes of *Rhinella* spp. and *Physalaemus* spp. may not impose strong constraints on when these species are able to breed once a pond is formed, which may allow them to exhibit different responses to the abiotic factor and partition calling activity over short time periods, reducing their overlap. Studies have shown that in other communities, species partition themselves acoustically, spatially and temporally as a means to reduce competition (Crump 1974; Hödl 1977; Duellman & Pyles 1983). It is unclear as to why these species exhibit the temporal partitioning observed. Reproductive character displacement, that is the accentuation of differences in courtship behaviour in sympatric populations relative to differences in allopatric populations may provide a mechanism underlying the observed pattern (Brown & Wilson 1956). In anurans, most studies of reproductive character displacement typically focus on differences in mating calls or female mate choice in allopatric and sympatric populations of frogs (Blair 1974; Gerhardt 1994). However, other aspects associated with courtship behaviour, such as the selection of calling sites could be explored in this framework; the observed pattern may be the result as a means to reduce competition for calling sites. Höbel and Gerhardt (2003) observed that males of the green tree frog (*Hyla cinerea*) called from higher perch sites when syntopic with the congener *Hyla gratiosa*. In the Chaco, each congeneric pair utilizes the same type of calling site at the breeding ponds; *Rhinella schneideri* and *R. major* call from the edges of ponds (Cei 1980; Schalk & Morales 2012), whereas *P. albonotatus* and *P. biligonigerus* call from the water's surface and among emergent vegetation (Cei 1980; Schalk 2010). Given that there is high overlap in the types of calling sites used by each congeneric pair, suitable calling sites may be limited around breeding ponds. Thus, these populations may diverge in the environmental conditions that drive calling activity, allowing the males to segregate temporally and gain access to calling sites that may be otherwise unavailable. To further explore these mechanisms, the calling activity of allopatric popula-

tions of each of the congeneric pair of these species would need to be compared with the syntopic pattern observed in this study. In addition, these patterns highlight that those studies that group and generalize species breeding activity by their reproductive mode (e.g., Gottsberger & Gruber 2004) may not be able to detect the subtle, species-specific differences in breeding activity, especially across short (i.e. daily) timeframes.

This study highlights the importance of weather on regulating the timing of reproductive phenology in this assemblage of tropical anurans. Our understanding of how exogenous (i.e. climatic variables) and endogenous factors (i.e. reproductive modes) interact to influence the temporal partitioning of these species can provide insights on the structure of larval assemblages and the interactions occurring within the breeding ponds (Todd *et al.* 2011). Amphibians exhibit the strongest response to climate warming scenarios by an earlier onset of breeding phenology (Parmesan 2007), thus our results could have implications to understanding potential climate change scenarios and the mistimed species interactions that occur as a result (Yang & Rudolf 2010; Todd *et al.* 2011; Saenz *et al.* 2013). Although extreme weather events (e.g., drought) can negatively affect amphibian reproductive activity (Jansen *et al.* 2009), our study suggests that even subtle changes in environmental factors, such as an increase in the intermittent period between rainfall, may impact the calling phenology of tropical anurans.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Occurrence of calling males across seven surveyed ponds.

Appendix S2. Call intensity scores for the four rare species of anurans each night.