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Vocalization Behavior and Calling Phenology in Two Direct-developing Frogs of the genus *Oreobates* of Yungas Andean Forests in Northwest Argentina

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Abstract.—**Calling activity directly affects male mating success in anurans; thus, it is expected that the maximum calling effort would be allocated during the most favorable conditions to breed. We described the diel activity pattern and the calling phenology of two sympatric, allotopic, direct-developing frog species in a subtropical montane forest of northwestern Argentina: the Baritú's Robber Frog (*Oreobates barituensis*) and the Confused Robber Frog (*O. berdemenos*). We assessed the influence of abiotic environmental cues of temperature and air humidity at the microhabitat scale on the advertisement call emission of both species. We monitored the calling behavior at two nearby locations with passive acoustic monitoring surveys. We fitted Generalized Linear Mixed Models to determine the relationships between the calling activity and the abiotic environmental variables. We found remarkable interspecific differences in the calling behavior of these direct-developing frogs during the reproductive season. *Oreobates barituensis* showed a crepuscular/nocturnal activity without chorus formation in a non-continuous and short calling season, while *O. berdemenos* showed a broad diel vocalization pattern with chorusing behavior in an extended and continuous calling season. Environmental cues influenced advertisement call emission at the microhabitat scale; both species showed a negative relationship with temperature. Vocal activity of *O. berdemenos* also showed a negative relationship with air humidity and a positive relationship with time of the day. We emphasized the importance of considering calling effort as a population parameter in studies of anuran calling behavior.**

Key Words.—advertisement call; automated recording units; Brachycephaloidea; calling effort; environmental cues; passive acoustic monitoring; vocal behavior

Introduction

Advertisement calls are one of the most energy-demanding activities for anurans, with direct consequences on the mating success of males (Taigen and Wells 1985; Pough et al. 1992; Dyson et al. 2013). Therefore, it is expected that maximum calling effort, defined as the time and/or energy expended by a male frog in its calling behavior in a given time (Wells and Taigen 1986), would be carried out during optimal environmental conditions to breed (Lemckert and Mahony 2008). The combination of extrinsic (environmental), intrinsic (physiological), and social factors influencing the reproductive phenology in anurans (Wells 2007) could result in the divergence of diel vocalization patterns and the calling phenology in closely related frog species that occur in the same geographic area (Ospina et al. 2013; Bignotte-Giró et al. 2019).

The environmental cues temperature and humidity regulate almost all aspects of the life cycle of an amphibian (Hillman et al. 2009). The influence of these abiotic factors on the calling activity of anurans is commonly assessed at the species level or within anuran assemblages that occur in a reproductive habitat (Bolzan et al. 2019; Ulloa et al. 2019; Guerra et al. 2020a; Reeves and Conradie 2023). Moreover, these environmental conditions influence the calling activity patterns of anurans at the microhabitat scale (e.g., the reproductive habitat; Ziegler et al. 2016), but studies exploring the effect of abiotic cues in different microhabitats are scarce (Bonnefond et al. 2020).

Passive acoustic monitoring (PAM) is an efficient monitoring tool to study the vocal behavior of anuran species at different sites simultaneously and for extended periods (Dorcas et al. 2009; Hilje and Aide 2012; Pérez-Granados et al. 2020; Boullhesen et al. 2021). The bioacoustic records, coupled with environmental data, can help to elucidate the responses of calling activity to ecological cues in anurans (Sugai et al. 2019; Ulloa et al. 2019). By using automated recording units (ARUs), researchers can determine the hourly, daily, or seasonal variations in vocal behaviors and calling effort performed by anurans under natural conditions (Ospina et al. 2013; Jansen et al. 2016; Boullhesen et al. 2019; Guerra et al. 2020a; Ríos López and Villanueva-Rivera 2022). Therefore, bioacoustic records coupled with environmental data could represent crucial information to evaluate the behavioral responses of anurans to the effects of the global climate crisis, such as the extreme climatic events of severe droughts, false springs, late frost or snowfall, and severe weather (Jansen et al. 2009; Blaustein et al. 2010; Teixeira et al. 2019; Ulloa et al. 2019; Reeves and Conradie 2023).

Although Brachycephaloidea is the most diverse Superfamily among amphibians, with more than 1,250 recognized species (Frost 2023), the calling behavior of its members is proportionally less studied than in other anuran groups (Guerra et al. 2020b; Rivera-Correa et al. 2021). These direct-developing frogs are attractive model organisms to study ecological behavioral traits because their specialized terrestrial reproductive mode depends primarily on environmental conditions such as humidity and temperature (Wells 2007; Hillman et al. 2009). Another striking feature of brachycephaloids is the diversity and complexity of their vocal behavior (Akmentins 2011; Lemes et al. 2012; Oliveira and Haddad 2017).

The Baritú's Robber Frog (*Oreobates barituensis*) and the Confused Robber Frog (*Oreobates berdemenos*) are two morphologically cryptic species at the southernmost distribution range of the megadiverse family Strabomantidae (Frost 2023). These ground-dwelling frogs occur in sympatry along their geographic distribution (Ferro et al. 2016). Nonetheless, these species can be considered allotopic because both occupy contrasting microhabitats within the Yungas Andean forests ecoregion of northwestern Argentina (Akmentins 2011); *O. barituensis* is found in open areas while *O. berdemenos* is found in leaf litter of forested areas. Despite the morphological similarities, both species are easily identifiable through the features of their advertisement call, with differences in temporal and spectral call parameters (Vaira and Ferrari 2008; Akmentins et al. 2022). These species share similar vocal repertoires, consisting of an advertisement call and two aggressive calls, a territorial call, and an encounter call employed in male-male territorial interactions (Akmentins 2011; Akmentins et al. 2022).

Although these two terrestrial frogs share similar morphological and behavioral characteristics, some degree of divergence in the temporality of the calling behavior can be expected, considering the contrasting microhabitats occupied by these species (Hauselberger and Alford 2005). This study aimed to compare the diel vocalization patterns and calling phenology of these two direct-developing frogs through PAM surveys in the Yungas Andean forests of northwestern Argentina. In addition, we aimed to relate the advertisement call emission to temperature and relative humidity at the microhabitat scale.

Materials and Methods

Study sites.—We monitored the calling activity of *Oreobates barituensis* and *O. berdemenos* in two locations separated by 3 km (airline) from each other in the subtropical Andean Cloud Forests of Jujuy province, Argentina. We selected the locations based on information from prior censuses indicating high densities of the target species, ensuring enough bioacoustics registries. The two study sites were in the phytogeographic stratum of the Upper Montane Forest of Yungas Andean forests (Grau and Brown 2000). We monitored *Oreobates barituensis* in Abra Honda (23°40'41.5"S; 64°55'37.2"W, 1,600 m elevation), which is an open area of mudstone cliffs dominated by grasses (*Lamphrothyrsus* sp.), surrounded by patches of Yungas Andean forests (Fig. 1). We monitored

Figure 1. The two study locations in the Yungas Andean forests of Calilegua mountains in Jujuy province, Argentina. Upper image: Abra Honda, where we recorded Baritú's Robber Frog (*Oreobates barituensis*. Lower image: Abra de Cañas, where we recorded Confused Robber Frog (*Oreobates berdemenos*. (Photographed by Mauricio Akmentins).

Oreobates berdemenos in Abra de Cañas (23°40’33.0”S; 64°53’52.3”W, 1,650 m elevation), which is a primary semi-deciduous forest area dominated by Myrtaceae tree species in the western limit of a protected area, the Parque Nacional Calilegua (Fig. 1).

Study species.—*Oreobates barituensis* is listed as Near Threatened in the International Union for Conservation of Nature (IUCN) Red Lists (IUCN 2022), as their populations are decreasing. Adult males average a snout-vent length (SVL) of 30.7 ± 1.4 (standard deviation) mm and a mean weight of 2.2 ± 0.3 g (n = 101; unpubl. data). Like other representatives of the genus *Oreobates*, this species has a rupicolous (found only in rocky environments) habit associated with sedimentary rock outcrops in open areas of Yungas Andean forests, commonly associated with human disturbances or landslides processes. Males call over the bare ground in open areas of mudstone cliffs (Akmentins 2011; Goldberg et al. 2012). The advertisement call of this species is a short trill composed of five to six notes with a dominant frequency of about 3.2 kHz (Vaira and Ferrari 2008).

Oreobates berdemenos is listed as Vulnerable in the IUCN Red Lists (IUCN 2022), based on its decreasing population trend and their restricted extent of occurrence. Adult males average SVL of 28.1 ± 6.9 mm and a mean weight of 2.1 ± 0.3 g (n = 106; unpubl. data). This species is a typical leaf litter-dwelling strabomantid frog found in the thick and wet understory of primary and secondary Yungas Andean forests. Males call from the ground perched on leaf litter or rocks covered with moss (Akmentins 2011; Akmentins et al. 2022). The advertisement call of this species is a long trill composed of 10 to 16 notes with a dominant frequency of about 1.9 kHz (Akmentins et al. 2022).

Passive acoustic monitoring.—We deployed two automated recording units (ARUs), one Song Meter SM2 and one Song Meter SM4 (Wildlife Acoustics Inc., Maynard, Massachusetts, USA), to record the calling activity of males of *O. barituensis* and *O. berdemenos* from 1 October 2017 to 31 January 2018 in coincidence with the reproductive season span of the targeted species (Vaira 2002; Akmentins et al. 2015). We attached the ARUs to trees 1.5 m above the ground and protected them from rain and solar radiation with a metallic roof. We programmed the ARUs to record 1 min every hour in a stereo channel and stored the recordings as a WAV format file (sample frequency = 16 KHz, 16-bit resolution, and 16 dB microphone gain). We analyzed the acoustic recordings in the laboratory using Raven Pro© 1.5 software (Cornell Lab of Ornithology, Ithaca, New York, USA). For each 1-min interval recording, we quantified the intensity of the advertisement call activity of the *Oreobates* species according to the numerical classification scheme proposed by Bridges and Dorcas (2000) as follows: 0 = no vocalization; 1 = only one male vocalizing; 2 = multiple males vocalizing, although it is possible to distinguish individuals calls; 3 = multiple males vocalizing overlapping their advertisement calls in full chorus, with no possibility to distinguish individuals calls (see Fig. 2 for examples). We installed a data logger HOBO® MX2301 (ONSET Computer, Bourne, Massachusetts, USA) beneath the cover of each ARU to measure air temperature and relative air humidity, programmed to record the environmental variables at hourly intervals.

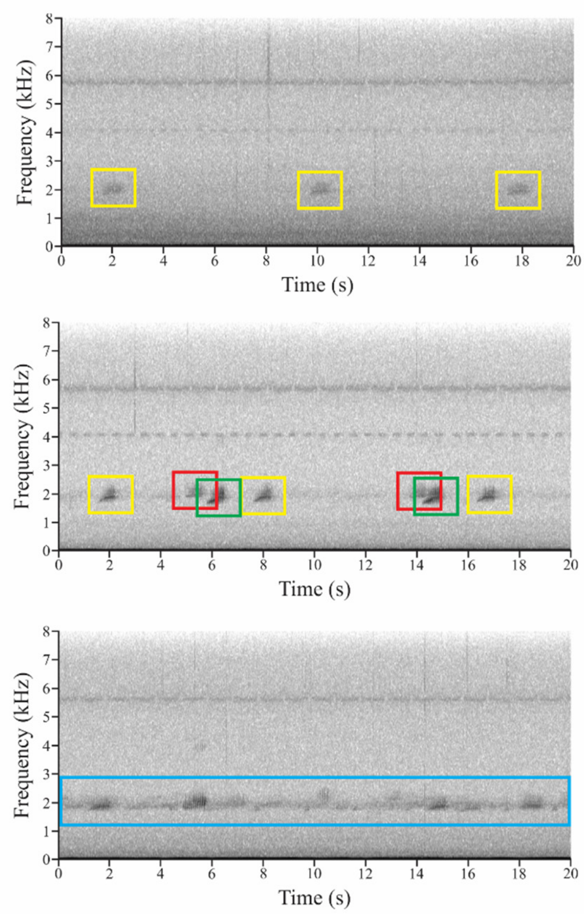

Figure 2. Three spectrograms showing a 20-s frame of 1 min recording of the calling activity of Confused Robber Frog (*Oreobates berdemenos*) obtained with an automated recording unit in Abra de Cañas, Jujuy province, Argentina. Examples of the classification scheme used for ranking the intensity of advertisement calling activity: activity level 1 = one male calling (upper spectrogram); activity level 2 = three males calling with the possibility of recognizing individual calls (middle spectrogram); activity level 3 = full chorus (lower spectrogram). Yellow, green, and red squares indicate calls of one individual. Light blue lines indicate full chorus calling activity.

Statistical analyses.—We characterized and compared the recorded abiotic environmental variables, air temperature and percentage of relative humidity, in the surveyed locations by reporting the daily mean ± standard deviation. Because we repeatedly measured the variables on both locations over time, observations closer to each other in time could exhibit a higher correlation than observations farther apart in time. We used Linear Mixed Effect Models, with a first-order autoregressive correlation structure to compare air temperature and relative air humidity between locations (West et al. 2022). We evaluated model assumptions, and corroborated that all assumptions were met. We assessed and compared patterns of hourly calling activity between both species with circular plots, excluding days without calling activity, following Pereyra et al. (2016). We classified diurnal calling activity registries between 0600 to 1900 and nocturnal calling activity registries between 2000 to 0500 following Akmentins et al. (2015). We also estimated the daily calling effort of each species, calculated as the proportion of the number of hours with vocal activity over 24 h following Boullhesen et al. (2019).

We used Generalized Linear Mixed Models (GLMM) assuming binomial distribution and a logit-link function to relate the presence (1) or absence (0) of calling activity of *O. barituensis* and *O. beredemenos* with abiotic environmental variables, such as the time of day of each 1-min bioacoustic record, relative air humidity (%), and air temperature (°C) as fixed effects. We treated the dates of bioacoustics registries as a random effect. We did not include variables with a strong correlation (Spearman's Rank Correlation ≥ 0.7) in the same model (Fielding and Haworth 1995). We tested all possible combinations of variables in the global model, including the null model. We used Akaike's Information Criterion corrected for small samples (AIC_c) to select the best model given the data; the model with the lowest AIC_c value was considered the best supported by the data (Burnham and Anderson 2002). When this procedure selected several models, we dealt with model uncertainty by conducting a model averaging over all models (Burnham and Anderson 2002), computing averaged estimate parameters (β) and its unconditional standard error (estimate precision, hereafter SE). We evaluated the magnitude of the effect of each parameter through AIC_c weights (w*i*) and 95% confidence intervals, concluding that the effect of a parameter was significant when the confidence interval excluded zero (Mazerolle 2006). We implemented model fitting and selection with the lme4 (Bates et al. 2015) and MuMIn (Barton 2009) packages, respectively, in R version 4.0.3 (R Development Core Team 2020).

Results

Abra Honda, the locality of *O. barituensis*, showed a broad daily range in the measured environmental variables (Fig. 3), with a mean daily air temperature of 20.5° ± 5.6° C and a mean daily relative air humidity of 80 ± 19% (from 24 November 2017 to 21 January 2018). Abra de Cañas, the locality of *O. berdemenos*, presented relatively stable weather conditions (Fig. 5), with slight variation along the day compared to Abra

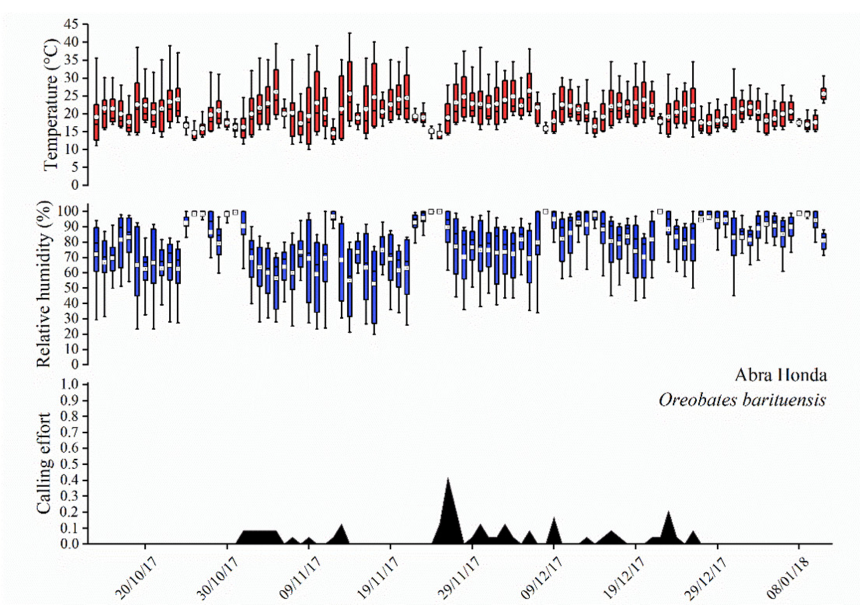

Figure 3. Daily air temperature, relative air humidity, and calling effort phenology of Baritú's Robber Frog (*Oreobates barituensis*) registered in Abra Honda, Jujuy province, Argentina. Boxplots show the mean value (circle/square), 25 and 75 percentiles, and daily range. Calling effort was calculated as the proportion of daily hours with vocal activity over 24 h. Date format at bottom is day/month/year.

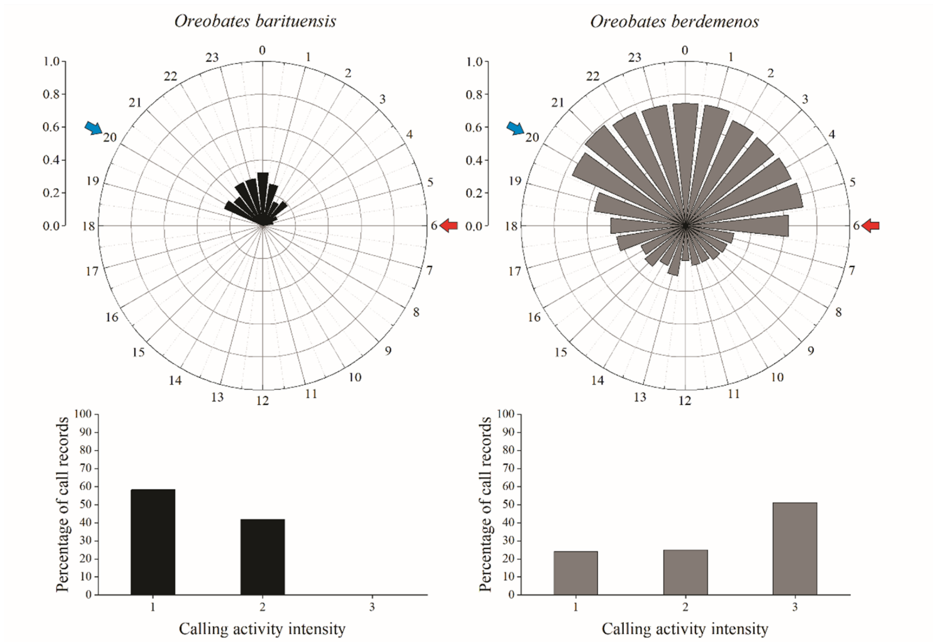

Figure 4. The daily pattern of calling activity and advertisement call intensity of the direct-developing frogs Baritú's Robber Frog (*Oreobates barituensis*, left) and Confused Robber Frog (*Oreobates berdemenos*, right) registered during the entire calling season (October 2017 to January 2018) of both species in two locations in the Yungas Andean forests of northwestern Argentina. Calling activity was calculated as the proportion of number of hourly registries over the total number of days with registries of vocal activity. Advertisement call intensity was classified following the numerical classification scheme proposed by Bridges and Dorcas (2000). Red arrow indicates dawn; blue arrow indicates dusk.

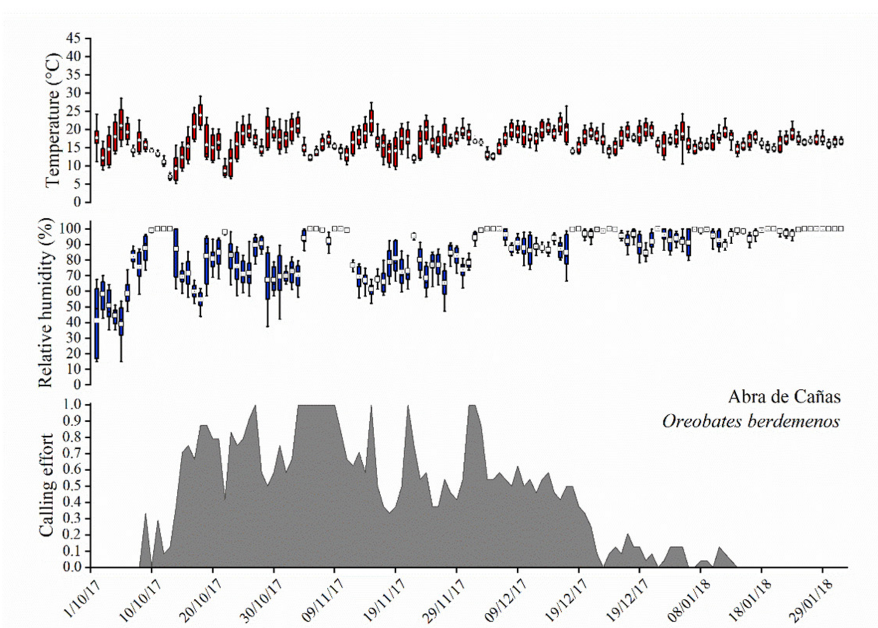

Figure 5. Daily air temperature, relative air humidity, and calling effort phenology of Confused Robber Frog (O*reobates berdemenos*) registered in the locality of Abra de Cañas (Parque Nacional Calilegua), Jujuy province, Argentina. Boxplots showed the mean value (circle/square), 25 and 75 percentiles, and daily range. Calling effort was calculated as the proportion of daily hours with vocal activity over 24 h. Date format at bottom is day/month/year.

Table 1. Set of supported Akaike's Information Criterion models (ΔAIC_c < 2) for the calling activity of Baritú's Robber Frog (*Oreobates barituensis*) and Confused Robber Frog (*Oreobates berdemenos*) with their respective support (AIC_cweight). Variables in the model are Hour = time of the day of each 1-min bioacoustic record, Temp = air temperature (°C), and RH = relative humidity (%). The abbreviation df = degrees of freedom.

Model	df	AIC_c	ΔAIC_c	AIC_c weight
Oreobates barituensis				
Hour + Temp	4	496.6	0	0.67
Temp	3	498	1.41	0.33
1 (Null model)	2	530.8	34.16	0
Oreobates berdemenos				
Hour + RH + Temp	5	24,010.5	0	1
1 (Null model)	2	2,485.2	74.75	0

Honda (Fig. 3). Mean daily air temperature from 1 November 2017 to 31 January 2018 was 16.7° ± 3.4° C, and the mean daily relative air humidity was 86.5 ± 15.7%. Abra Honda presented a significantly higher mean temperature (Estimate = 3.48°, standard error = 0.13, t = 26.26, phi = 0.90, P < 0.01) and a lower percentage of air humidity (Estimate = -8.07%, standard error = 0.55, t = -14.56, phi = 0.94, P < 0.01) than Abra de Cañas.

The calling season of *O. barituensis* started on 26 November 2017 and ended on 4 January 2018, resulting in 67 1-min advertisement call records. Calling effort was non-continuous, with two main periods of calling activity across the entire calling season (Fig. 3). The pattern of diel calling activity was considered nocturnal and was concentered between 2000 to 0300 (Fig. 4). Full choruses were not registered for this species; only rank 2 calling activity (multiple males vocalizing spaced) was recorded, representing nearly 42% of the total call registries (Fig. 4).

Air temperature and relative air humidity at Abra Honda were strongly correlated (Pearson's r = 0.85); therefore, we did not consider models containing both variables for *O. barituensis*. We selected two models based on the AIC_c values (Table 1), which included the variables time of the day and air temperature. Air temperature was negatively related to the emission of advertisement call. Time of day presented a positive relationship, but because the 95% Confidence Interval contained zero, we considered this effect not significant (Table 2).

The calling season of *O. berdemenos* started on 9 October 2017 and ended on 13 January 2018, yielding 1,141 1-min advertisement call records during the calling season. Daily calling effort of *O. berdemenos* males was relatively intense, with five peaks of continuous calling activity during the 24 h of the day. The most extended peaks of activity occurred over seven consecutive days (Fig. 5). The diel calling activity pattern was mainly nocturnal and was concentered between 2000 to 0500. Diurnal calling activity, however, was also frequent with increased intensity at dawn and dusk (Fig. 4). Full choruses were the most common calling activity intensity, representing 51.1% of total call registries (Fig. 4).

We included all independent variables in the models for *O. berdemenos* because correlation coefficients ranged well below the suggested cutoff. We selected one model based on the AIC_c values (Table 1). Air temperature and relative humidity presented a negative effect on the calling activity of *O. berdemenos*, whereas time of day showed a positive effect (Table 2).

Discussion

We observed a substantial divergence in the calling behavior and diel activity patterns of two closely related direct-developing frog species using PAM survey throughout the entire calling season. *Oreobates barituensis* and *O. berdemenos* shared similar vocal repertoires (Akmentins 2011; Akmentins et al. 2022), but their calling behavior seemed to be conditioned differently by the environmental abiotic cues at the microhabitat scale. The first noticeable behavioral

Table 2. Model averaged estimates and unconditional standard error (SE) of the variables included in the sets of candidate Akaike's Information Criterion models (with ΔAIC < 2) of calling activity of males of Baritú's Robber Frog (*Oreobates barituensis*) and Confused Robber Frog (*Oreobates berdemenos*) related to environmental variables and location. Parameter weight (w_i) and its 95% Confidence Interval (95% CI) are also included. Variables in the model are Hour = time of the day of each 1-min bioacoustic record, Temp = air temperature (° C), and RH = relative humidity (%). Parameters with significant effects are in bold.

Model	*Oreobates barituensis*				*Oreobates berdemenos*			
	Estimate	SE	w_i	(95% CI)	Estimate	SE	w_i	(95% CI)
Intercept	0.67	0.88		(-1.05, 2.41)	7.26	1.51		(4.28, 10.34)
RH		–		–	**-0.04**	**0.01**	**0.97**	**(-0.06, -0.01)**
Temp	**-0.26**	**0.05**	**0.76**	**(-0.36, -0.16)**	**-0.28**	**0.04**	**1**	**(-0.36, -0.32)**
Hour	0.03	0.02	0.61	(-0.01, 0.07)	**0.02**	**0.01**	**0.74**	**(0.001, 0.03)**

difference between these frogs can be observed in their chorusing behavior; *O. barituensis* presented a sporadic and spaced vocal activity without full chorus formation as was reported for other strabomantid frogs (Granados-Pérez and Ramírez-Pinilla 2020). This finding is confirmed by nearly 15 y of fieldwork in all known populations of *O. barituensis*, where full choruses have never been heard by the four authors. By contrast, *O. berdemenos* presented an intense and relatively continuous chorusing behavior.

Our study also showed that *O. barituensis* is strictly nocturnal, while *O. berdemenos* is mainly nocturnal with considerable vocal activity during the daylight hours. Similar contrasting diel activity patterns of advertisement call emission were reported in sympatric species of the genus *Eleutherodactylus* in Cuba (Bignotte-Giró et al. 2019). The extended calling activity observed in *O. berdemenos* was previously interpreted as an opportunistic behavior associated with highly humid/rainy weather conditions (Akmentins et al. 2015), but further studies are needed to elucidate whether this reproductive strategy of extended diel calling activity is an attempt to increase their mating success despite the metabolic costs (McCauley et al. 2000; Siegler et al. 2016).

The combination of sporadic vocalization, lack of chorusing behavior, and nocturnal diel activity pattern observed in *O. barituensis* was reflected in a strikingly lower calling effort during the reproductive season than the one recorded for *O. berdemenos*. Males of *O. barituensis* call exposed on bare soil in open areas (Akmentins 2011), probably increasing their exposure to potential predators. Therefore, males of this species could be adjusting their calling behavior to more sporadic activity, avoiding large and loud choruses to minimize the predation risk in concordance with several species of anurans that employ a similar strategy (Tuttle and Ryan 1981; Lemes et al. 2012; Trillo et al. 2013: Legett et al. 2020). The restricted calling activity of *O. barituensis* could also be related to a water-conservative behavior because spaced and less intense calling activity could decrease the desiccation risk faced by anuran males when vocalizing in open habitats (Heatwole et al. 1969; Pough et al. 1983). These scenarios were the opposite for *O. berdemenos* because males call under closed canopies, which provide calling males better cover, presumably reducing predation and desiccation risks.

Another difference between these *Oreobates* frogs was the extension of their calling season; *O. barituensis* presented a relatively short and irregular calling season lasting nearly two months, while *O. berdemenos* presented a long and continuous calling season that lasted four months. Vaira et al. (2002) reported an extreme inter-annual variation extension of the calling seasons for *O. berdemenos* in Parque Nacional Calilegua (where one of our study sites was placed), lasting from three to five consecutive months. Given the evolving climate crisis, studying the calling phenology of direct-developing frogs through multi-annual PAM surveys could help to elucidate if changes in their interannual calling period are a response to extreme climatic events (Jansen et al. 2009; Rocha Usuga et al. 2017).

The decrease in calling activity with the increase in air temperature was a common response for both frog species, which is expected considering that air temperature is consistently noted as one of the main drivers of calling activity among terrestrial breeding anurans (Pengilley 1971; Navas 1996; Van Sluys et al. 2012; Oliveira and Haddad 2017; Ríos López and Villanueva-Rivera 2022). The negative relationship between the calling activity of *O. berdemenos* and air relative humidity has also been registered in other anuran species (Hatano et al. 2002; Steelman and Dorcas 2010). Male *O. berdemenos* seemed to stop calling when the weather conditions became too wet as the rainy season became established (Akmentins et al. 2015), which could be linked to water saturation of leaf-litter on the forest floor, a condition that can be unfavorable considering that this species lays eggs on the ground (Salica et al. 2023). The influence of time of the day on calling activity was previously reported for *O. berdemenos* and other direct-developing frogs, with an increase of calling activity at dawn and the first night hours (Akmentins et al. 2015; Oliveira and Haddad 2017).

Recommendations.—The use of PAM surveys in studies of the vocal behavior of Neotropical anurans allows the simultaneous registry of calling activity in multiple locations and for broader time lapses, becoming a valuable tool to collect and manage large amounts of information (Brooke et al. 2000; Hilje and Aide 2012; Akmentins et al. 2015; Boullhesen et al. 2021). We highlight the importance of considering the calling effort not only as an individual feature but also as a relevant population parameter when studying anuran calling behavior. By monitoring the calling effort performed by males throughout the entire calling season, it is possible to identify more accurately the calling periods and to improve the searching efforts of anuran populations in inventory and monitoring programs (Lemckert and Mahony 2008; Dutilleux and Curé 2020; Ríos López and Villanueva-Rivera 2022).

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