



Calling behaviour of *Elachistocleis matogrosso* (Anura, Microhylidae) is associated with habitat temperature and rainfall

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ABSTRACT

Anuran calling behaviour is determined by environmental, endogenous, and social factors. The effect of these factors usually differs among and within species. We used acoustic monitoring to evaluate the effects of environmental predictors on the daily occurrence and call production of *Elachistocleis matogrosso* (Microhylidae) in the north-eastern Brazilian Pantanal. We monitored the calling behaviour of the species over a complete annual cycle at four acoustic monitoring stations. Daily occurrence was positively associated with high minimum air temperature at all sites, and was also related to days with high abundant rainfall at two sites. This result suggests that the minimum temperature acts as the main trigger initiating calling activity in this species. In contrast, call production was positively related to rainfall and accumulated rainfall over the previous three days, with no effect of air temperature. This observation could be related to a high abundance of calling males after some rainy periods, when more water bodies are available for reproduction. Our findings reveal the importance of performing studies at different spatial-temporal and calling scales because the effects of environmental predictors on anuran calling behaviour may differ among sites, and this factor is also important when analysing daily occurrence or call production.

ARTICLE HISTORY

Received 26 May 2019
Accepted 16 August 2019

KEYWORDS

Anuran; automated recorder; Brazil; communication; Pantanal; signal recognition software

Introduction

Due to strong declines in a large number of anuran species over the past two decades (Stuart et al. 2004; Scheele et al. 2019), efforts dedicated to anuran conservation and monitoring programmes have increased in recent years (Navas et al. 2016). Data collected using standardised protocols are useful for estimating population trends, evaluating which factors explain declining estimates, and developing adequate protection management

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 Supplemental data for this article can be accessed <https://doi.org/10.1080/09524622.2019.1658642>.

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practices for wildlife conservation (Dorcas et al. 2009). Anuran monitoring is based on auditory cues, since vocalising is the predominant form of communication among anurans and because of anurans' cryptic and mainly nocturnal behaviour (Wells 1977; Guerra et al. 2018). The calling behaviour of anurans mainly occurs during the breeding season, and calls are primarily used to attract females but also act as territorial and distress signals (Toledo et al. 2015). Temporal and environmental factors can influence the calling activity of anurans (Oseen and Wassersug 2002; Saenz et al. 2006), which may have an impact on their detection probability and the number of calls and individuals detected during anuran surveys (Navas 1996). Temporal and environmental factors may lead to biased estimates of occupancy (Mazerolle et al. 2007), community composition (De Solla et al. 2006), or population (Royle 2004), among other issues. Therefore, there is a need to conduct anuran surveys when the detection probability is highest to maximise the cost effectiveness of monitoring programmes (Dorcas et al. 2009).

As ectotherms, anurans obtain body heat exclusively from the environment (Narins 2001), and thus calling and hearing are temperature-dependent (Van Dijk et al. 1990; Navas 1996). At the same time, the act of calling is costly in terms of the expenditures of energy and time (Ryan et al. 1981) and may increase the risk of predation for calling males (Duellman and Trueb 1994; Kotiaho 2001). Thus, males typically use environmental and/or social cues to determine the best times for display (Brooke et al. 2000) and hence maximise the potential benefits while minimizing associated costs (Wong et al. 2004). Indeed, several monitoring programmes (e.g. the North American Amphibian Monitoring Program) recommend that volunteers should perform surveys within certain temperature and temporal parameters (Bridges and Dorcas 2000; Dorcas et al. 2009).

Temperature and rainfall are the primary factors that influence the life cycle and calling activity of anurans (e.g. Navas 1996; Almeida-Gomes et al. 2007; Van Sluys et al. 2012). These factors are usually positively related to anuran calling activity (Navas 1996; Brooke et al. 2000), but some studies have detected a negative relationship (Milne et al. 2013; Ospina et al. 2013). The calling activity of anurans can also be triggered by other environmental predictors, such as humidity, light intensity or wind. Specifically, anuran calling activity usually increases with the increase in environmental humidity (Bellis 1962; Almeida-Gomes et al. 2007), while moonlight (Johnson and Batie 2001; Buchanan 2006) and wind usually negatively influence such behaviour (Saenz et al. 2006; Steelman and Dorcas 2010).

Although anuran calling and reproductive activity are influenced by exogenous factors, there are also clear relationships with endogenous factors (Lofts 1974). Like most vertebrates, vocal activity and reproduction in anurans are strongly regulated by hormones (Yamaguchi and Kelley 2002; Arch and Narins 2009), but they are also related to the photoperiod (Both et al. 2008). Indeed, the relative importance and effects of environmental variables in triggering the calling activity of anurans differ among species according to their reproductive strategy (Plenderleith et al. 2018), location of calling sites (Gottsberger and Gruber 2004) and body size (Van Sluys et al. 2012), among other factors. The effects of environmental variables on anuran vocal activity differ even between sympatric species or species of the same genus (Oseen and Wassersug 2002; Van Sluys et al. 2012). Likewise, the calling activity of a species may vary among different populations due to microscale variations in physical conditions and/or differences in anuran density (Brooke et al. 2000). Therefore, concurrent analyses of multiple variables over large spatial and temporal scales are necessary to increase our knowledge of the effects of environmental predictors on

anuran activity and whether populations of the same species respond similarly to environmental variables.

Among anurans, the recently described *Elachistocleis matogrosso* Camaraschi, 2010 (Microhylidae) is outstanding due to its restricted known distribution, which is bounded to a few localities in midwestern Brazil (Caramaschi 2010; Pansonato et al. 2011; Dorado-Rodrigues et al. 2018) and to a single locality in northern Paraguay (Brouard et al. 2015). So far, only the morphology (Caramaschi 2010) and the advertisement call of this species have been described (Marinho et al. 2018; Pansonato et al. 2018), thus the biology is unknown. *Elachistocleis matogrosso* has a small body size and immaculate belly, and its advertisement call is very characteristic (lasts 1.3–3.6 s and is mainly uttered between 4,000 and 4,800 Hz; Marinho et al. 2018; Pansonato et al. 2018; Supplemental Figure S1).

In the present study, we aimed to assess how the calling activity and production of advertisement calls of *E. matogrosso* in the northeastern Pantanal (Brazil) vary in response to the meteorological environment during a complete annual cycle at four sampled sites. Specifically, we tested the relative importance of air temperature and relative air humidity, rainfall and moon phase on the calling activity and number of calls produced by this species. This double-scale study will provide a better overview of the gamut of factors determining whether the species is vocally active and the number of calls produced in addition to how the effects of environmental predictors differ among sites. We also constructed and transferred models of calling activity among sites to evaluate whether the effects of environmental variables were constant or differed among the sampled sites. The evaluation of the transferability of models will allow us to identify whether the vocal activity of the species differs among sites according to site-specific conditions or whether the effects of the environmental predictors are consistent among sites regardless of the local environment.

Material and methods

Study area

The study was carried out in the northeastern part of the Brazilian Pantanal (Pantanal Matogrossense), the largest seasonal floodplain in the world. The study area is located near the SESC Pantanal (Poconé municipality, Mato Grosso, Brazil; 16°30'S, 56°25'W, see Supplemental Figure S2) and the Cuiabá River, one of the main tributaries of the Paraguay River within the Pantanal. This area is seasonally inundated due to the flooding of the Paraguay River and exhibits a pronounced dry season from May to September and a rainy season from October to April (Junk et al. 2006). The dominant vegetation in the study area is composed of a mosaic of different forest formations and savannas (Junk et al. 2006). The climate in the region is tropical humid with an average annual rainfall between 1,000 and 1,500 mm, and the mean annual temperature is approximately 24°C.

Acoustic monitoring and analyses

Four acoustic monitoring stations were established in the study area and separated by between 400 and 2,800 m (Supplemental Figure S2). The monitoring stations were monitored daily from 8 June 2015, to 2 June 2016, comprising one complete annual cycle. We

placed one Song Meter SM2 recorder (Wildlife Acoustics, www.wildlifeacoustics.com) programmed to record in 24/7 mode at each acoustic monitoring station. The Song Meter recorded sounds during the first 15 min of each hour. The recorders were programmed to record during the whole year according to the winter local time (GMT -4) and using the same settings (sample rate of 48 kHz and resolution of 16 bits per sample).

The recordings were automatically scanned with Kaleidoscope Pro 5.1.8. (Wildlife Acoustics, www.wildlifeacoustics.com). This software is able to examine recordings for signals of interest based on selected signal parameters of the sounds to be detected. We used recent descriptions of *E. matogrosso* advertisement calls to select the best signal parameters (Marinho et al. 2018; Pansonato et al. 2018). The signal parameters input into Kaleidoscope were as follows: minimum and maximum frequency range (3,600–6,100 Hz), minimum and maximum length of detection (0.76–15 s), and maximum intersyllable gap (0.03 ms). These signal parameters were extended in relation to the description of the call of the species to maximise the possibility of detecting weaker, overlapping and successive calls uttered by multiple individuals (Marinho et al. 2018; Pansonato et al. 2018). We fitted the 'distance from cluster center to include outputs in cluster.csv' as 1.8. This distance ranges from 0 to 2 and has an impact on the number of detected signals. Larger values result in an increase in the number of detected signals, including improved detection of *E. matogrosso* calls but also a larger number of false positives (not targeted signals). The instructions from Wildlife Acoustics advise using a value between 1 and 1.4, but we chose a higher value to detect a large number of *E. matogrosso* calls.

The Kaleidoscope output reported a total of 101,838 events that matched the signal parameters. These events were visual and/or acoustically checked, always by the same observer (CPG), to separate false positives from true positives (correct detections made by Kaleidoscope). A total of 8,278 events were classified as *E. matogrosso* advertisement calls and used in posterior analyses.

Environmental variables

We collected environmental data from a weather station located in the study area at a distance of between 180 and 2,630 m to the acoustic monitoring stations (see Supplemental Figure S2). The following daily information was gathered: minimum air temperature (°C), mean air temperature (°C), maximum air temperature (°C), rainfall (mm) and relative air humidity (%). As anuran calling activity is usually related to rainfall in the preceding days (Lemckert et al. 2013; Plenderleith et al. 2018), we incorporated the accumulated rainfall from the previous three days as a variable. We also obtained the daily percent of the moon illuminated from the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.html>), and used it as an index of moonlight intensity.

Statistical analyses

Although we used the same environmental predictors for all monitored sites, we conducted analyses independently for each site since site-specific conditions can alter the calling behaviour of the species (Brooke et al. 2000). After testing for data normality, we reduced the potential collinearity among environmental variables by removing

those whose Spearman correlation coefficients were higher than 0.7 (Dormann et al. 2013). Daily mean air temperature was highly correlated with minimum and maximum air temperature. We decided to remove mean air temperature from further analyses because we expected a greater impact of minimum air temperature on the calling behaviour of the species due to nocturnal calling activity of the species. Likewise, maximum air temperature may have an impact on anuran mobility and water temperature, which may affect the calling activity of the species. We focused our analyses during the reproductive season, (1 December 2015–31 May 2016), since the species was not detected during any of the other months (see Supplemental Table S1). Thus, we reduced the number of days in the analysis by removing the days when activity of the species did not occur, thereby improving our analytical approach.

A hierarchical partitioning (hereafter HP) approach was used to identify the environmental variables that had a major influence on whether or not the species was vocally active at each particular station during a complete annual cycle. This method is able to identify the independent relationships (as opposed to partial ones) between environmental predictors and the target variable (Mac Nally 2002); in our case the occurrence of *E. matogrosso* on one day. A logistic regression with log likelihood was applied as the goodness-of-fit measure. The statistical significance of the independent contribution of each environmental predictor was evaluated by randomisation with 999 bootstraps (Mac Nally 2002). We took into account temporal autocorrelation in calling activity in the HP analysis by including an autocovariate (Lichstein et al. 2002), since we consider that the probability of detecting the species on one day can be correlated to the presence or absence of the species on the previous day. Thus, the autocovariate represented the number of consecutive days during which the species was previously detected.

We also evaluated whether the environmental predictors had a similar effect at all monitored stations. Therefore, a zero-inflated Poisson (ZIP) regression was conducted using the presence/absence of the species on each day as the response variable and environmental variables as potential predictors. We created specific models for each site and followed a model-averaging strategy (Cade 2015). We assessed the similarity in the effects of the environmental predictors among sites by transferring models among them. To do this, we ranked all possible models according to Akaike's information criterion adjusted for small samples (AICc). Models were selected with $\Delta\text{AICc} < 2$ (Burnham and Anderson 2002) and averaged their estimates by weighting the predictions of the models by their AICc value (Cade 2015). Averaged prediction was used to assess the similarity among the models using area under the curve (AUC) estimation (Sing et al. 2005), since larger values of AUC are related to higher estimate-observation agreement (Fielding and Bell 1997). For the spatial validation, we applied the set of models constructed for each station using the vocally active-inactive data sets from the other sites.

We fitted a zero-inflated negative binomial generalised linear mixed model (GLMM hereafter) using the number of calls detected per day as the response variable, the environmental predictors as fixed effects and site and month as random effects to control for the site and intermonthly variation. ZIP and GLMM were fitted after testing different distribution families (binomial, Poisson, quasi-Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial), and the most appropriate model according to AIC and Vuong test estimates was retained. Model performances were also evaluated by visually checking the residuals and estimating the overdispersion

parameter when possible. All statistical analyses were performed in R 3.4.1 (R Development Core Team 2014). The level of significance was $p < 0.05$, and the results are expressed as the mean \pm SE. We used the packages ‘hier.part’ for HP (Walsh and Mac Nally 2008), ‘MASS’ for AICc estimates (Venables and Ripley 2002), ‘MuMIn’ for model averaging (Barton 2011), ‘ROCR’ for AUC estimation (Sing et al. 2005) and ‘glmmTMB’ for GLMM analysis (Brooks et al. 2017).

Results

The HP analyses showed some consistency in the effects of the environmental variables on the calling activity of the species among acoustic monitoring stations (Table 1 and Figure 1). At all stations, the daily minimum air temperature and the autocovariate had significant effects on whether the species was vocally active, with a positive effect in both cases (Table 1). *Elachistocleis matogrosso* was more vocally active on days with a high minimum temperature and when the species had been detected during a large number of previous days (Table 1). However, at two of the monitored sites, the activity of the species was also significantly affected by the daily rainfall, being more often vocally active on days with greater amounts of precipitation (Table 1 and Figure 1). At one of the stations, the calling activity of the species was also related to the accumulated rainfall, with the species being more often vocally active when a larger amount of precipitation occurred on the previous three days (Table 1 and Figure 1). The other environmental parameters (maximum air temperature, relative air humidity, and percentage of the moon illuminated) were not significantly related to the calling activity of the species (Table 1).

The model predictions agreed very well with the observed calling activity of the species at each station according to the AUC values (0.85 ± 0.01 ; Figure 2). A variable number of plausible models was found for each station (the number of candidate models and number of times each environmental predictor was selected per station

Table 1. Environmental predictors related to the calling activity of *Elachistocleis matogrosso* at four sampled stations in the Pantanal Matogrossense (Brazil) according to hierarchical partitioning analysis. The daily activity of the species (active/inactive) was monitored with recordings conducted 15 min of every hour between December 2015 and May 2016. The individual contribution of each variable is shown as a percentage (%) of the total deviance explained by the predictors. The signs of the effects were obtained from univariate regression models. The z-test column shows the significance level of the randomisation tests for the independent contributions (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). % Dev is the percentage of deviance accounted for by a logistic regression model including all variables.

Environmental predictor	Station A			Station B			Station C			Station D		
	Sign	l%	z-test									
Autocovariate	+	81.2	***	+	82.1	***	+	49.5	***	+	79.1	***
Maximum air temperature	+	0.9		+	3.0		-	2.6		+	0.8	
Minimum air temperature	+	12.5	***	+	6.9	*	+	27.8	***	+	10.1	***
Rainfall	+	3.1		+	2.0		+	12.0	**	+	2.8	*
Accumulated rainfall	+	0.4		+	0.1		+	2.5		+	5.6	***
Relative air humidity	+	1.5		+	0.8		+	3.7		+	1.2	
% of the moon illuminated	+	0.4		+	5.1		-	1.9		-	0.4	
%Dev		56.9			45.0			37.5			58.1	

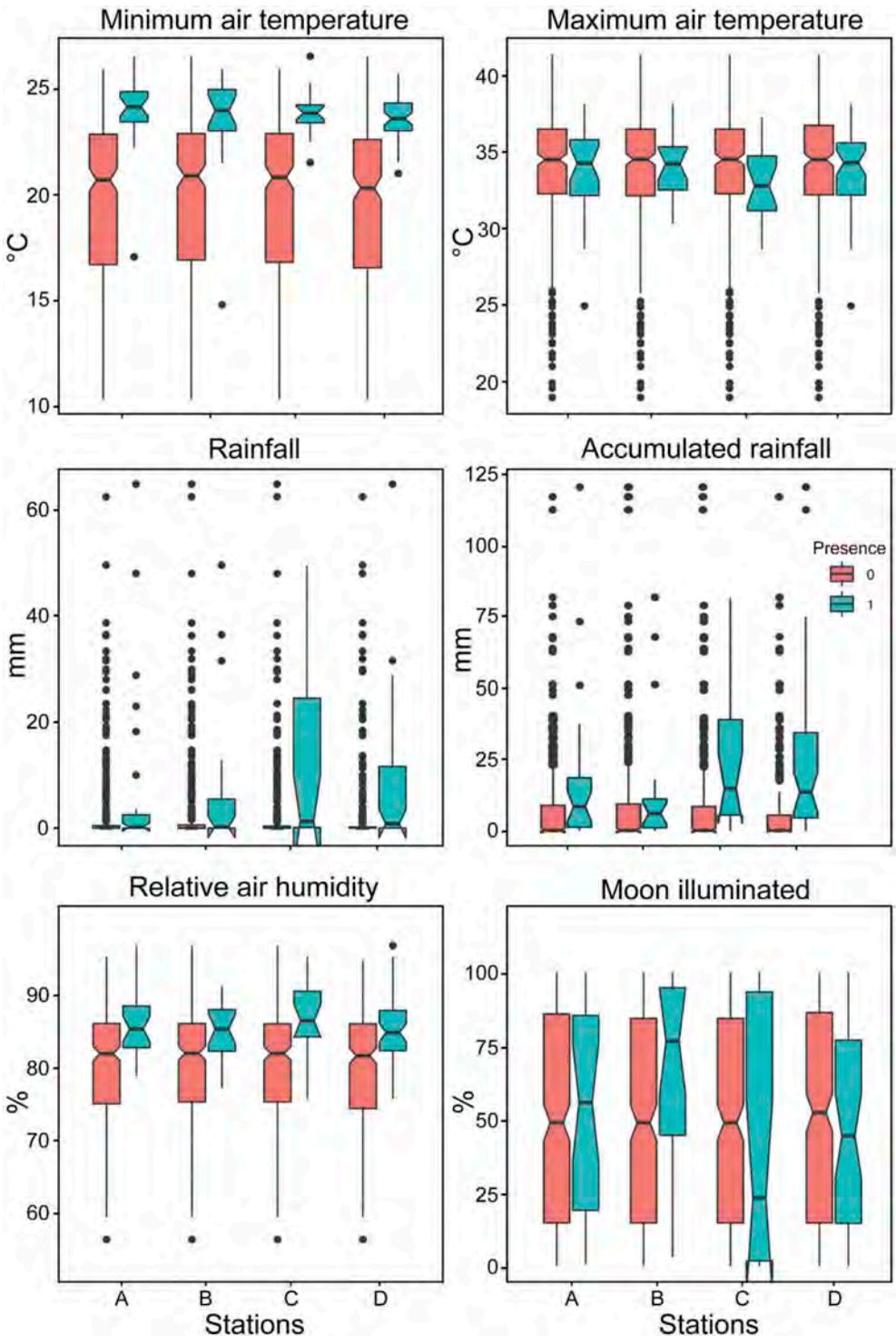


Figure 1. Relationship between environmental variables (minimum and maximum air temperature, rainfall, accumulated rainfall, relative air humidity and percent of the moon illuminated) and calling activity (vocally-active [1] or inactive [0]) of *Elachistocleis matogrossensis* in four sampled stations in the Pantanal Matogrossense (Brazil). Daily number of calls was monitored recording 15 min every hour between December 2015 and May 2016.

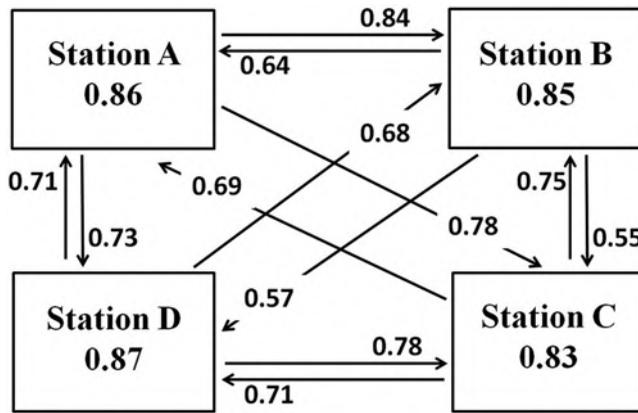


Figure 2. Summary of AUC values of the plausible models for each monitored site. Arrows indicate the direction of the inter-site validation of the models.

Table 2. Estimates of a zero-inflated negative binomial generalised linear mixed model testing the effects of environmental predictors on the daily number of calls uttered by *Elachistocleis matogrosso* in the Pantanal Matogrossense (Brazil). The daily number of calls was monitored with recordings conducted for 15 min every hour between December 2015 and May 2016 at four sampling stations.

Environmental predictor	Df	Estimate	Std. Error	Z value	Pr
(Intercept)	1	-15.03	9.203	-1.63	0.102
Maximum air temperature	1	0.234	0.125	1.86	0.062
Minimum air temperature	1	0.292	0.188	1.55	0.120
Rainfall	1	0.082	0.020	4.01	<0.001
Accumulated rainfall	1	0.026	0.009	2.77	0.005
Relative air humidity	1	-0.002	0.079	-0.02	0.979
% of the moon illuminated	1	-0.010	0.007	-1.40	0.159

can be found in Supplemental Table S2). We found intermediate transferability of the models among stations (averaged AUC value of 0.70 ± 0.02 , Figure 2).

According to the GLMM analysis, the daily rainfall and accumulated rainfall were the only environmental predictors significantly related to the daily production of calls by *E. matogrosso* (Table 2), with a larger number of calls detected on days with a greater amount of precipitation and larger volumes of accumulated rainfall. However, the rest of the environmental predictors (minimum and maximum air temperature, relative air humidity, and percentage of the moon illuminated) were not significantly related to the daily call production of the species (Table 2).

Discussion

Our study provides strong evidence that the calling activity and production of calls of *E. matogrosso* in the Pantanal are related to weather conditions. Moreover, our results reveal that while the minimum air temperature and rainfall are reliable predictors of whether *E. matogrosso* is vocally active or not, rainfall and accumulated rainfall are the only variables related to the daily production of calls. However, the autocovariate, which represents the number of previous days when the species was detected, was the predictor

with a major influence on the calling activity of the species at all monitored stations. This result suggests that the calling activity of *E. matogrosso* is mainly related to endogenous factors, such as hormones (Arch and Narins 2009; Yamaguchi and Kelley 2002).

Regardless of the effect of the autocovariate, minimum air temperature was the most informative variable related to the calling activity of *E. matogrosso*, and its contribution was significant at all monitored stations. This result could be related to the nocturnal calling behaviour of the species, since 44% of the calls were detected during the three hours after dusk (authors' own data). This finding also explains why maximum air temperature had no effect on the calling activity of the species since it occurs in the middle of the day when the species is vocally inactive. This positive relationship between anuran calling activity and air temperature has been found in a large number of anuran species (e.g. Navas 1996; Almeida-Gomes et al. 2007; Cui et al. 2011), and previous studies also described air temperature as the most important environmental factor regulating the calling activities of other species (Pough et al. 1983; Navas 1996), including the congener *E. bicolor* (Martori et al. 2010; Elgue and Maneyro 2017). Cui et al. (2011) proposed that the calling activity of temperate anuran species may cease when the temperature falls below a critical level, but they also noted that this effect could also be related to a decrease in the energy reserved for calling. Our results can be used to corroborate the aforementioned hypotheses. *Elachistocleis matogrosso* did not call when the temperature was below a specific threshold, but temperature had no effect on the number of calls produced, which would be expected if calling was related to energetic cost.

At two of the monitored sites, the calling activity of the species was also related to rainfall (and accumulated rainfall at one of them), which is in agreement with previous studies that described rainfall as a trigger for breeding activity in *E. bicolor* (e.g. Prado et al. 2005; Iop et al. 2012) and calling activity in different anuran species (e.g. Navas 1996; Van Sluys et al. 2012). However, rainfall was not associated with the calling activity of the species in the other monitored populations. These differences could be related to site-specific variations, such as a differential presence of water bodies around the monitored stations. We are aware that our analyses considered only the data collected during the rainy season in the Pantanal, a tropical area, since the species was vocally inactive during the rest of the year. This condition may partly explain why rainfall was not a limiting factor for the calling activity of the species at some of the stations.

In contrast to calling activity, the number of calls produced daily was related to rainfall and accumulated rainfall but not air temperature. These contradictory results could be related to the fact that the detection of a larger number of calls would most likely be related to the number of males calling, since a larger chorus results in a larger number of calls detected (e.g. Henzi et al. 1995; Llusia et al. 2013).

The information available about the reproduction of the genus *Elachistocleis* indicates the use of both temporary and permanent ponds (Rodrigues et al. 2003; Cacciali 2010; Iop et al. 2012; López et al. 2017) and even bromeliads (de Andrade et al. 2009). No information is available about the reproductive behaviour of *E. matogrosso*, but prior observations of calling males have always been collected at temporary ponds (e.g. Marinho et al. 2018; Pansonato et al. 2018), which suggests that the species may use these habitat types for breeding. Thus, the calling and breeding activity of the species might be greater in periods with higher rainfall and accumulated rainfall when the availability of water bodies is greater (e.g. Gottsberger and Gruber 2004; Van Sluys et al.

2012). These findings are in agreement with previous studies carried out on *E. bicolor*, which postulated that the breeding activity of that taxon was also correlated with extensive continuous precipitation (Rodrigues et al. 2003; Cacciali 2010). Surprisingly, we did not find any relationship between the daily number of calls detected and the minimum or maximum air temperature, which is in disagreement with the results found at the calling activity level and with a large number of previous studies that found a positive relationship between call production and temperature (Navas 1996; Almeida-Gomes et al. 2007; Van Sluys et al. 2012). Differences found at the calling activity and call production scale highlight the importance of performing studies at different calling scales since the main results and conclusions may differ according to the scale considered. We did not find any relationship between relative air humidity and the calling activity of *E. matogrosso* at any of the monitored stations, in contrast to results found by different authors who described higher calling activity of anurans during days with greater air humidity (Bellis 1962; Almeida-Gomes et al. 2007). This pattern has been related to a lower risk of desiccation by calling during wetter days (Almeida-Gomes et al. 2007). The mean relative air humidity in the area during the study period was very high (close to 85%) and exhibited low variation among days (Coefficient of Variation, 4.76%). Therefore, the air in the study area might have been hypersaturated, even on the less wet days, and the humidity level would likely have been sufficient to allow calling activity of the species without increasing the risk of desiccation, at least during the wet season (Almeida-Gomes et al. 2007).

Moonlight was not related to any of the calling activity parameters measured, in contrast to the results of some previous research (Johnson and Batie 2001; Buchanan 2006). However, the response to moonlight seems to be species-specific (Johnson and Batie 2001). We cannot disregard that the effects of other social or environmental variables (e.g. cloud cover, photoperiod, rainfall, temperature) could mask a possible effect of humidity and moon phase on *E. matogrosso* calling activity.

The high performance of the calling activity models within stations and intermediate transferability among sites provide strong evidence that the environmental predictors had similar effects on the calling activity of the species regardless of site-specific conditions. We are aware that our study considered only neighbouring populations. It therefore remains unclear whether the effects of environmental variables may differ among populations over a larger geographic scale. The high model performance and transferability among stations suggest that it is possible to reliably predict when *E. matogrosso* will be vocally active according to environmental predictors. Our results might be useful to provide guidelines for monitoring the species. Monitoring surveys for detecting the presence should be conducted on warm nights (temperature > 23°C) after rain during the wet season (December-May).

Our study is one of the first to describe differences in the impacts of environmental variables on the calling activity of anurans at a daily scale among sites and detect a differential effect at the calling-activity or calling-production scale. Further research should include a larger number of species, particularly at the community level, since the same local environmental factors may influence sympatric species in different ways (Oseen and Wassersug 2002). We also encourage researchers analysing the effects of environmental parameters on anuran calling activity to include information on photoperiod, social factors, habitat characteristics, and hormone levels in the analyses to

increase our understanding of animal communication and unravel the relative importance of these factors from that of environmental factors.

Acknowledgements

We greatly appreciate the financial support from the following institutions: This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES)-Finance Code 01; Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (INAU/UFMT/CNPq); Centro de Pesquisa do Pantanal (CPP); Brehm Funds for International Bird Conservation (BF), Bonn, Germany; the Organisation of American States through its Partnerships Program for Education and Training of the Coimbra Group of Brazilian Universities (OAS/PAEC/GCUB, PRP). Furthermore, we thank the SESC Pantanal, Mato Grosso, for permission to conduct research on their property and for their logistical help with our fieldwork. We wish to thank to Prof. Dr. José de Souza Nogueira from Post-Graduate Programme in Physics, UFMT, kindly provided the weather data for the time period of our study and to Ana Silvia Tissiani for her technical support. We are grateful to two anonymous reviewers, whose comments helped to improve the manuscript. This study is part of the biodiversity monitoring project: Sounds of the Pantanal – The Pantanal Automated Acoustic Biodiversity Monitoring Programme of INAU/UFMT, Cuiabá, Mato Grosso, Brazil, conducted under SISBIO permit no. 39095 (KLS).

Disclosure statement

No potential conflict of interest was reported by the authors.

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