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Nocturnal vocal behaviour of the diurnal Undulated Tinamou (*Crypturellus undulatus*) is associated with temperature and moon phase

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Some diurnal birds vocalize at night but the reason for this has seldom been studied. We monitored the nocturnal vocal activity of the Undulated Tinamou *Crypturellus undulatus* from June 2015 to May 2016 at three recording stations in the Brazilian Pantanal. We tested whether an index of nocturnal vocal output (number of vocalizations automatically detected) of the species varied over the monitored annual cycle and whether it was related to night temperature and moon phase. The annual pattern of nocturnal vocal output was unimodal, with high vocal activity during September and October (49.9% of the total calls detected) and very low vocal output from January through June (8.5% of the total). The unimodal pattern found suggests that nocturnal vocal activity might be related to mate attraction rather than to territorial defence, for which a more constant pattern would have been expected. The percentage of the moon illuminated was positively associated with nocturnal vocal activity, probably related to the elevated light level on moonlit nights. Nocturnal vocal activity was not associated with minimum air temperature. Nocturnal vocal output was positively associated with vocal output during the preceding night, but not with vocal output during the preceding day, suggesting that it was not directly associated with diurnal calling. This is the first study showing a complete annual cycle of nocturnal vocalizations for a diurnal bird species. Our study provides new evidence regarding the function of and the reasons for nocturnal vocalizations in a diurnal non-passerine bird and has important implications for continued study of reproductive behaviour in tinamous. Further research should examine whether courtship display is associated with nocturnal vocalizations in this and other species.

Keywords: acoustic monitoring, *Crypturellus undulatus*, diurnal bird, mate attraction, moon, Pantanal, territorial defence, vocal activity.

The vocal activity of most diurnal birds peaks prior to sunrise and then ceases or decreases in intensity for the rest of the day (Mace 1987, Catchpole & Slater 2008). This phenomenon of vocal activity concentrated around sunrise is known as a 'dawn chorus' (Gil & Llusia 2020). Reasons for the concentration of vocal activity at dawn (Krebs & Kacelnik 1983, Naguib *et al.* 2016) and the function of vocalizations during this period have been well documented (Møller 1991, Poesel *et al.* 2006, Pérez-Granados *et al.* 2018). The best-supported hypotheses for dawn choruses are that singing at dawn does not interfere with feeding, and plays a role in female mating and territorial defence (Gil & Llusia 2020). Dawn is also the best time of the day for sound transmission (Henwood & Fabrick 1979) because atmospheric conditions before sunrise (low temperatures and low air turbulence) allow better transmission, which may also

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contribute to explaining why birds sing at dawn (e.g. Henwood & Fabrick 1979, Larom *et al.* 1997). In contrast, although several species of diurnal birds vocalize at night (see review by La 2012), nocturnal vocalizations of diurnal birds have been little studied, and their occurrence and function are poorly known (La 2012).

The nocturnal vocal activity of diurnal birds is logistically difficult to monitor and has been proposed to be a continuation of diurnal efforts (La 2012, Foote *et al.* 2017). This difficulty may partly explain the lack of studies and why no study has assessed whether diurnal and nocturnal vocalizations of diurnal birds are correlated. However, the study of nocturnal vocalizations is of interest because their function may differ from diurnal vocal activity. La (2012) stated that nocturnal vocal activity is found in 30% of North American bird species and that 70% of these species were diurnal birds. Similarly, Kułaga and Budka (2020) showed that around 25% of diurnal bird species in a temperate region of central Europe also sing at night. In recent years, the development of automated sound recorders has encouraged researchers to carry out more intensive studies of the nocturnal vocal behaviour of diurnal birds (e.g. Mennill 2014, Celis-Murillo *et al.* 2016a, 2016b, Foote *et al.* 2017, 2018, Kułaga & Budka 2020).

Nocturnal singing activity of diurnal passerines has been related to mate attraction ('mate attraction hypothesis', Amrhein *et al.* 2002, Celis-Murillo *et al.* 2016a). For example, Common Nightingale *Luscinia megarhynchos* males ceased nocturnal singing after pair formation, and this singing can resume if mates desert, which suggests that nocturnal song serves to attract a mate (Amrhein *et al.* 2002). However, nocturnal vocalizations, as with diurnal vocalizations, may have sexual functions (Amrhein *et al.* 2002, La 2012, Celis-Murillo *et al.* 2016a), so birds may benefit from vocalizing at night by extending their daily territorial defence into the night ('territory defence hypothesis', La 2012). La (2012) hypothesized that nocturnal vocalizations of diurnal birds might be a consequence of elevated light levels and that birds with relatively large eyes and/or birds that vocalize early in the dawn chorus may vocalize on nights with elevated light levels due to their ability to detect dim light (La 2012, Table 1). Nocturnal vocal activity of diurnal birds might be also related to better sound transmission at lower temperatures (Larom *et al.* 1997, Mennill 2014), so that birds may prefer to vocalize at night to reach more receivers without an extra cost ('enhanced sound transmission hypothesis', La 2012). Similarly, diurnal birds living in noisy environments may prefer to vocalize at night, when acoustic competition might be lower and conditions quieter ('reduced acoustic competition hypothesis', La 2012). Most of these hypotheses are not incompatible with each other, and may have synergistic effects in promoting nocturnal vocalization by diurnal birds (La 2012).

Our current knowledge regarding the nocturnal vocal activity of diurnal non-passerines is very basic (but see La 2012, Mennill 2014, Kułaga & Budka, 2020). We therefore wished to test whether the functions of nocturnal singing activity of diurnal passerines can be extrapolated to non-passerine behaviour. Likewise, previous studies of the nocturnal vocal activity of diurnal birds were restricted to the breeding season (e.g. Amrhein *et al.* 2002, Celis-Murillo *et al.* 2016, Foote *et al.* 2017, Kułaga & Budka, 2020) or the migration period (Farnsworth 2005, Alessi *et al.* 2010), with very limited information available about whether diurnal birds vocalize at night outside these periods (but see Dickerson *et al.* 2020).

Table 1. List of the four hypotheses tested to assess the function of and the reasons for nocturnal vocal activity of the Undulated Tinamou. A summary with the reasoning, according to La (2012), and our prediction is provided for each of them.

Hypothesis	Reason	Prediction
Mate attraction	Nocturnal vocalizations can be used to attract mates	Nocturnal vocal output would show a seasonal pattern, matching with the breeding season
Territory defence	Nocturnal vocalizations might be used to defend territories during the night	Nocturnal vocal output would remain constant in territorial species
Elevated light level	Nocturnal vocalizations are a consequence of elevated light levels during the night	Higher nocturnal vocal output on nights with an elevated percentage of the moon illuminated
Enhanced sound transmission	Birds may prefer to vocalize at night due to better sound transmission at this time	Higher nocturnal vocal output on nights with lower minimum air temperature

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Ratites are a flightless group of birds that includes ostriches, emus, rheas, cassowaries, kiwis and tinamous (Davies 2002), and they represent one of the most ancient living groups of birds (Hackett *et al.* 2008). Although common in the Neotropics, nocturnal vocalizations of the ratites have rarely been studied (see Pérez-Granados & Schuchmann 2020a). Here, we selected the Undulated Tinamou *Crypturellus undulatus* as a case study species because it is a diurnal bird that often vocalizes at night and for which has been proposed that the nocturnal vocalizations may play an important role in the communication system of the species (Pérez-Granados *et al.* 2020). Previous studies of tinamous indicate that their vocal activity peaks during the breeding period (Lancaster 1964a, 1964b, Solano-Ugalde *et al.* 2018), suggesting that the study of seasonal changes of nocturnal vocal output may be useful to understand the causes of the nocturnal vocalizations of this group of birds. The call of the Undulated Tinamou, its only known vocalization (Pérez-Granados *et al.* 2020), is composed of three distinctive notes (Fig. 1). At the peak of the breeding season in Brazil, which seems to occur during September and October (Pérez-Granados *et al.* 2020), the species may call without a break for at least 30 min (Davies 2002). The Undulated Tinamou has two peaks of vocal activity (at dawn and at dusk, Pérez-Granados *et al.* 2020) and although no information is available on the vocalizations of males and females, it is expected that both sexes vocalize, as described for most tinamou species (Cabot 1992, Davies 2002). The Undulated Tinamou is a resident and elusive bird that is typical of dense tropical habitats in South America (Davies 2002), for which there is little information available about life history patterns. It is a polygynous species. Males maintain a territory and a nesting site during the breeding season, and several females will visit the site and lay their eggs in the same nest (Davies 2002).

Here, we examine the nocturnal vocal activity of the Undulated Tinamou over a complete annual cycle. In this study we aimed to investigate three aspects of vocal behaviour of the species: (1) whether an index of nocturnal vocal output (number of vocalizations automatically detected) of the Undulated Tinamou varied over a complete annual cycle, (2) how variation of nocturnal vocal output relates to the four hypotheses of La (2012) proposed for nocturnal vocalizations of diurnal birds (see Table 1), and (3) whether there is any association between diurnal and nocturnal vocal output.

METHODS

Study area

The study area was located in the northeastern part of the Brazilian Pantanal (Pantanal of the state of Mato Grosso), which is the largest seasonal floodplain in the world. The study area was close to the SESC Pantanal (Poconé municipality, Mato Grosso, Brazil; 16°30′S, 56°25′W, Fig. 2) and close to the Cuiabá River, one of the main tributaries of the Paraguay River within the Pantanal. The

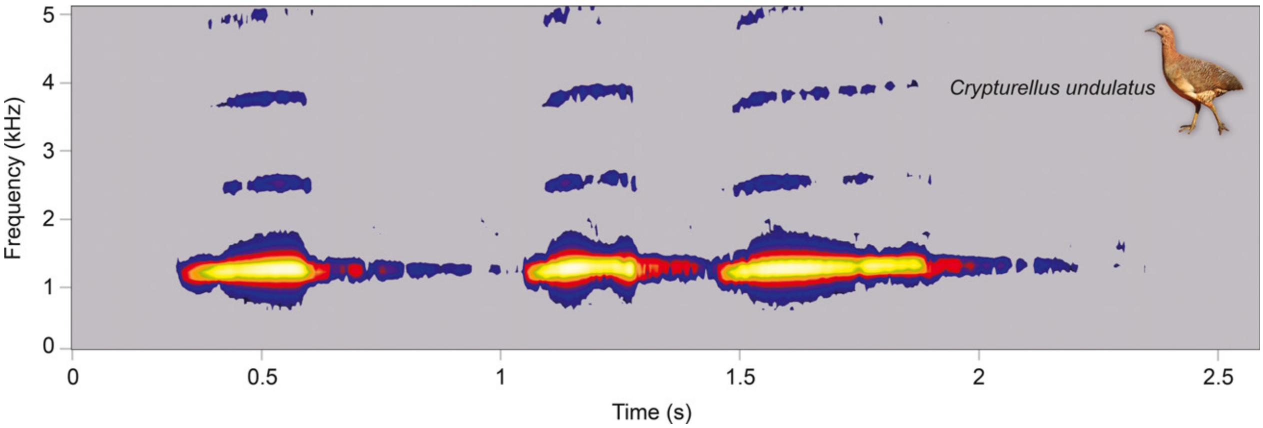

Figure 1. Spectrogram of a typical Undulated Tinamou call in the Brazilian Pantanal. The darkest section shows the frequencies at which the energy of the call of the species is at a maximum. [Colour figure can be viewed at wileyonlinelibrary.com]

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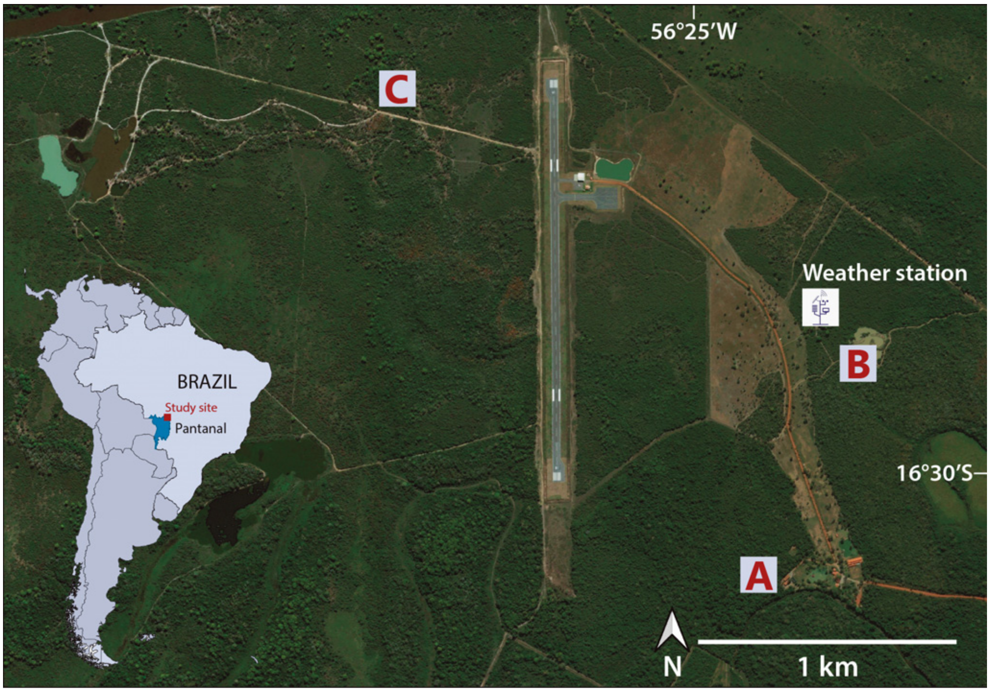

Figure 2. Locations of the three acoustic monitoring stations and of the meteorological station (white square) in the Brazilian Pantanal (Poconé municipality, Mato Grosso, Brazil). The inset shows the location of the study area (red square) in Brazil. Scale bar: 1 km. [Colour figure can be viewed at wileyonlinelibrary.com]

Brazilian Pantanal is inundated from October to April due to flooding of the Paraguay River, and the area exhibits a pronounced dry season between May and September (Junk *et al.* 2006). We placed three acoustic monitoring stations within the study area, and stations were separated by 1530 and 2017 m (Fig. 2). Although no specific information about territorial behaviour of the study species is available, we expect that territorial males would not be recorded at two different stations due to separation between sampled stations and the known effective detection radius of the autonomous sound recorders employed (see below). The dominant vegetation in the study area involves a mosaic of forested and savanna areas (Junk *et al.* 2006). The regional climate is tropical and humid, with an average annual rainfall of 1000–1500 mm (1130 during the studied year) and a mean annual temperature of approximately 24 °C (25.5 °C during the studied year).

Acoustic monitoring

At each of the three acoustic monitoring stations, we placed one Song Meter SM2 recorder (Wildlife Acoustics, USA, www.wildlifeacoustics.com), which was active from 8 June 2015 to 31 May 2016 and therefore covered a whole annual cycle. The distance at which bird vocalizations can be recorded varies among species according to their different frequencies and amplitudes, and also varies with habitat surveyed and weather conditions (see Yip *et al.* 2017). Previous field tests using the SM2 recorder have proven its utility for recording most bird vocalizations at a distance of 150–160 m (Rempel *et al.* 2013, Pérez-Granados *et al.* 2019). However, this range may be limited in closed (forested) areas (Yip *et al.* 2017), as in our study area. These assumptions, together with the fact that we did not find overlapping calls of the species among the two closest stations (separated by 1530 m), suggest that the risk of recording the same individual from two different stations might be low. The recorders were programmed to record (in stereo and uncompressed .wav format) the first 15 min of each hour in 24/7 mode. The automated recorders were configured with a sampling rate of 48 000 Hz, a resolution of 16 bits per sample, and gain of +0 dB. Recordings were stored on microSD memory cards capable of storing ~250 h

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of recording. Recorders were powered by four 1.5 -V alkaline batteries (Duracell MN13000) (~160 h-autonomy) and checked weekly to download data and change batteries. The study was carried out according to Brazilian laws and the SISBIO permit (KLS No. 39095).

Acoustic data analyses

The left channel of the recordings was scanned with Kaleidoscope Pro 5.1.8, an automated signal recognition software program provided by Wildlife Acoustics (www.wildlifeacoustics.com). Kaleidoscope Pro is able to examine recordings for signals of interest according to the signal parameters introduced in the software. We established the following signal parameters in Kaleidoscope according to prior knowledge about the vocalization of the Undulated Tinamou in the study area (Pérez-Granados *et al.* 2020): minimum and maximum frequency range: 1150 and 1350 Hz; minimum and maximum length detection: 1.3 and 3 s (to include overlapping signals and birds duetting); maximum intersyllable gap: 0.6 ms; and 'distance from the cluster centre': 2.0. A description of the call structure of the species in the study area and an analysis of the impact on the number of Undulated Tinamou calls detected using different values of the 'distance from the cluster centre' parameter were provided by Pérez-Granados *et al.* (2020). All candidate sounds identified by Kaleidoscope were visually and/or acoustically checked and only those identified as tinamou calls were used in subsequent analyses. Our response variable was the total number of tinamou calls automatically detected by Kaleidoscope Pro. It represents an index of vocal activity of the species, rather than the absolute number of vocalizations made by the species. To evaluate the effectiveness of the automated detection applied by Kaleidoscope Pro we estimated the recall rate of the recognizer, defined as the proportion of target species vocalizations detected by the recognizer (Knight *et al.* 2017). The recall rate was estimated by dividing the total number of tinamou calls detected by Kaleidoscope by the total number of calls detected by CPG, after visually and acoustically checking 240 recordings of a selected dataset (Knight *et al.* 2017, Pérez-Granados & Schuchmann 2020b). We randomly selected a total of 120 15-min nocturnal recordings with presence of the species, according to Kaleidoscope Pro (40 recordings per station) and 120 15-min recordings randomly selected within the dataset (40 recordings per station). The observer had no information about whether the species was detected or the number of calls detected by Kaleidoscope while reviewing the recordings.

Environmental variables

Weather data were collected from a meteorological station located between 150 and 1900 m from acoustic monitoring stations (Fig. 2). We sampled the daily minimum air temperature (°C, used as a surrogate of night temperature) and daily rainfall (mm) throughout the study period. We added the daily percentage of the moon illuminated as an index of the moonlight intensity. The daily percentage of the moon illuminated was extracted from www.timeanddate.com.

Statistical analyses

We considered the night length to be the time elapsed between evening and morning nautical twilight (Foote *et al.* 2017), as extracted from www.timeanddate.com. To standardize the number of hours of recordings analysed per day and to control for seasonal variation in night length, we used only nocturnal vocalizations detected in recordings made between 20:00 and 04:15 h (UTC −4), which was always between the evening and morning twilight times. We assumed a survey night to start with the recording made at 20:00 h and end after the recording at 04:15 h, with the diurnal period occurring between the recordings at 05:00 and 19:15 h.

To identify whether nocturnal vocal activity of the Undulated Tinamou varied over the monitored annual cycle we fitted a negative binomial generalized linear model (NBGLM). The number of nocturnal calls detected per night was used as the response variable, 'month' (12 categorical levels) was included as a factor, and 'station' (three categorical levels) was also included as a factor to control for variation between sites. We accounted for temporal autocorrelation in nocturnal calling activity by including an autocovariate (Lichstein *et al.* 2002), as the vocal output on one night can be correlated to the vocal output on the preceding night. The autocovariate included in the analyses

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represented the total number of vocalizations detected during the previous night. A Tukey's post hoc test was performed to identify the months with high nocturnal vocal activity.

Second, we assessed whether environmental variables and vocal output during the preceding day had an impact on the nocturnal vocal output (number of vocalizations detected per night). We again fitted an NBGLM using the number of nocturnal vocalizations detected per night as the response variable; environmental variables (daily minimum air temperature, and percentage of the moon illuminated), the autocovariate, and the vocal output during the preceding day (to ascertain whether diurnal and nocturnal vocal outputs of the same day were correlated) were included in the model as predictors, and 'station' (three categorical levels) and 'month' (five categorical levels) were considered as a factor to control for site-based and seasonal variations in weather conditions. We did not include daily rainfall in the analysis because we had only daily (24-h) values and therefore accumulated daily rainfall may not be an adequate surrogate of rainfall events during the night. Because nocturnal vocal activity of the Undulated Tinamou is very seasonal (see Results and Fig. 3), we focused the analyses on the period between 1 August 2015 and 31 December 2015, the five months with significantly high and consistent vocal activity of the species during the night (see similar approximation in Pérez-Granados & Schuchmann 2020b, 2020c). Nocturnal vocal activity outside this period was too low to permit analysis of differences related to weather or moon illumination.

All statistical analyses were performed in R 3.4.1 (R Development Core Team 2016). The level of significance was $P < 0.05$, and the results were expressed as the mean ± se. We used the package 'multcomp' for post hoc comparison tests (Hothorn *et al.* 2008) and the package 'glmmTMB' for NBGLM analysis (Brooks *et al.* 2017).

RESULTS

Kaleidoscope detected a total of 620 486 potential signals, of which 254 493 events were identified as Undulated Tinamou vocalizations and 29 702 (11.7% of the total) were detected during the night. The numbers of nocturnal vocalizations detected per station, our estimated index of vocal activity, were 3187 (Station A), 8725 (Station C) and 17 790 (Station B). The recall rate of the recognizer was 0.74 (1545 calls detected of the 2097 calls annotated in the validation dataset).

Annual pattern of nocturnal vocal activity

The annual pattern of nocturnal calling activity of the Undulated Tinamou showed a seasonal, unimodal pattern (Fig. 3). Nocturnal vocal output differed significantly between months (Table 2) and was significantly higher during September and October (Fig. 3), when 49.9% of the total of the nocturnal calls were detected (see Table S1 for monthly calling production per month and site). After this period, there was a decrease in nocturnal vocal output with significantly lower nocturnal vocalization between January and June (8.5% of total nocturnal calls were detected in this 6-month period). February was the month with significantly

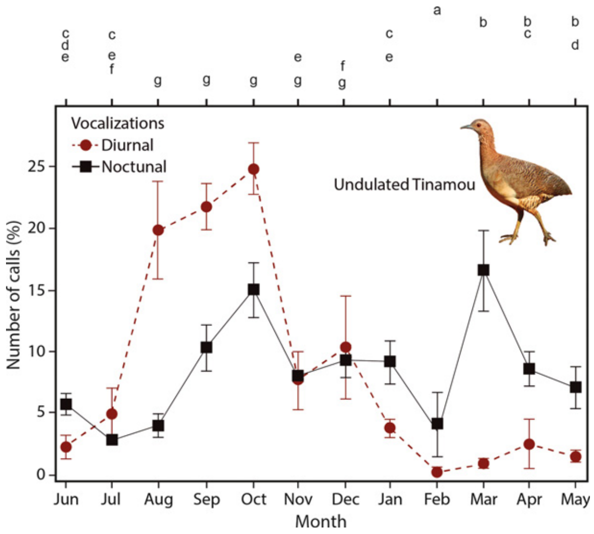

Figure 3. Seasonal pattern of nocturnal and diurnal vocal output of the Undulated Tinamou over an annual cycle in the Brazilian Pantanal. Vocal output was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at three acoustic monitoring stations. Night was defined as the period between 20:00 and 04:15 h, and day as the time elapsed between 05:00 and 19:15 h. Vocal output is expressed as the mean (±se) percentage of total calls detected over the year at all sites per month. Letters on the top indicate significant differences between month in the nocturnal calling activity of the Undulated Tinamou from Tukey's post hoc test.[Colour figure can be viewed at wileyonlinelibrary.com]

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Table 2. Estimates of the negative binomial generalized linear model testing the effect of month on the nocturnal vocal output of the Undulated Tinamou in the Brazilian Pantanal. Nocturnal vocal output was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at three acoustic monitoring stations. Night was defined as the period between 20:00 and 04:15 h. Estimates are expressed as the differences from the intercept, which was estimated using the recordings made during the month of June and Station A as reference values.

Vocal output	Estimate	se	*z*-value	*P*
(Intercept)	1.350	0.258	5.24	<0.001
Vocal output night before	0.006	0.001	5.87	<0.001
July	0.385	0.315	1.22	0.221
August	1.568	0.319	4.29	<0.001
September	1.674	0.325	5.15	<0.001
October	1.902	0.327	5.82	<0.001
November	0.948	0.317	2.99	0.003
December	1.242	0.317	3.91	<0.001
January	0.262	0.316	0.83	0.406
February	−3.956	0.452	−8.77	<0.001
March	−1.280	0.324	−3.953	<0.001
April	−0.378	0.320	−1.18	0.237
May	−0.698	0.320	−2.18	0.029
Station B	1.003	0.160	6.26	<0.001
Station C	0.479	0.154	3.11	0.001

the lowest vocal activity, according to a post hoc comparison (Fig. 3).

Environmental correlates of nocturnal vocal output

The Undulated Tinamou was vocally active during the whole night but showed a continual increase in vocal output as the night progressed. The peak of nocturnal vocal activity occurred in the hours before sunrise (Fig. 4). Nocturnal vocal output increased with the percentage of the moon illuminated, but there was no significant relationship with minimum air temperature (Table 3, Fig. 5). Nocturnal vocal output was not related to diurnal vocal output of the preceding day but was positively associated with vocal output during the preceding night (Table 3).

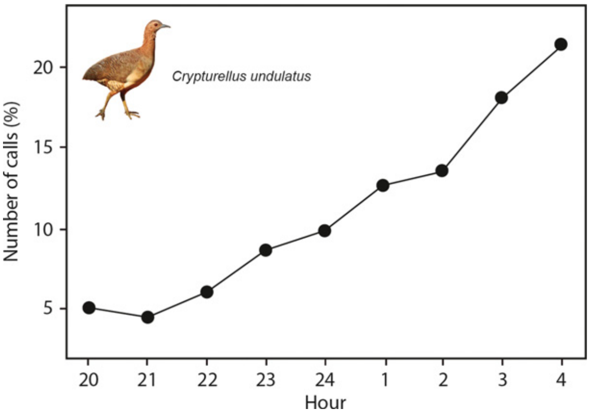

Figure 4. Diel pattern of nocturnal vocal output of the Undulated Tinamou. Vocal output was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at three acoustic monitoring stations. Night was defined as the period between 20:00 and 04:15 h, and diurnal period as the time elapsed between 05:00 and 19:15 h. Vocal output is expressed as the percentage of total calls detected over the year at all sites per hour. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 3. Estimates of the negative binomial generalized linear model to test the effects of environmental predictors on the nocturnal vocal output of the Undulated Tinamou in the Brazilian Pantanal. Nocturnal vocal output was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at three acoustic monitoring stations. Night was defined as the period between 20:00 and 04:15 h. Estimates are expressed as the difference from the intercept, which was estimated using the recordings made during the month of August and Station A as reference values.

Vocal output	Estimate	se	*z*-value	*P*
(Intercept)	2.875	0.534	5.38	<0.001
Vocal output night before	0.002	0.001	2.53	0.011
Vocal output day before	0.001	0.001	0.80	0.424
Minimum air temperature	−0.046	0.038	−1.22	0.222
% of the moon illuminated	0.009	0.002	4.18	<0.001
September	0.235	0.281	0.83	0.404
October	0.343	0.334	1.03	0.304
November	−0.478	0.374	−1.28	0.201
December	−0.352	0.370	−0.951	0.342
Station B	1.612	0.201	8.00	<0.001
Station C	1.279	0.180	7.10	<0.001

DISCUSSION

Our results show that nocturnal vocal output of the Undulated Tinamou was seasonal but also related to moon phase during the period analysed (August–December). The annual pattern of nocturnal vocal output showed significantly the highest vocal activity during the months of September and October and very low output between January and June.

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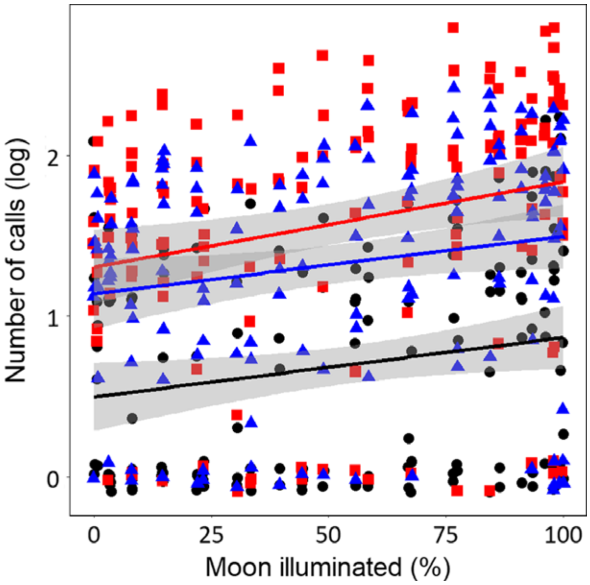

Figure 5. Scatterplot showing variation in the nocturnal vocal output of the Undulated Tinamou as a function of the percentage of the moon illuminated during August–December 2015. Nocturnal vocal output was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at three acoustic monitoring stations. Night was defined as the period between 20:00 and 04:15 h. Data are shown with different colours representing the different monitored stations. The linear regression (solid line) between vocal output and percentage of the moon illuminated is shown for each station. The 95% confidence intervals are shown in grey. [Colour figure can be viewed at wileyonlinelibrary.com]

However, the diurnal seasonal pattern of vocal activity of the species was much more constant (Fig. 2). The unimodal pattern and clear seasonality of nocturnal vocalizations of the species suggests that they may play a role in mate attraction. A peak of calling activity during the breeding season has been previously found in several tinamous (Lancaster 1964a, 1964b, Solano-Ugalde *et al.* 2018) and the proposed role in mate attraction is in agreement with the role proposed for nocturnal vocalizations for a large number of diurnal passerines (Amrhein *et al.* 2002, Celis-Murillo *et al.* 2016a, Foote *et al.* 2017, Dickerson *et al.* 2020). We would have expected a more constant seasonal pattern, as found during the day (Fig. 3), if nocturnal vocalizations were primarily related to territorial defence. Further research, including field observations of the breeding biology of the species and breeding status of recorded birds would be needed to prove the role of nocturnal vocalizations in mate attraction.

According to our prediction and the elevated light level hypothesis (La 2012), the nocturnal vocal behaviour of the Undulated Tinamou was positively related to light level. The species was more vocally active on nights with a higher percentage of the moon illuminated. The nocturnal light level at full moon is much higher than at new moon (Kronfeld-Schor *et al.* 2013) and the increase in light level on moonlit nights seems to stimulate the nocturnal vocal activity of several nocturnal (e.g. Wilson & Watts 2006, Penteriani *et al.* 2010, Pérez-Granados & Schuchmann 2020b, but see Cadbury 1981, Reino *et al.* 2015) and diurnal bird species (La 2012, Dickerson *et al.* 2020, but see Foote *et al.* 2017). Vocalizing at night can be risky, especially at elevated light levels, because it may increase predation risk (Mougeot & Bretagnolle 2000, Schmidt & Belinski 2013). Indeed, previous studies of small songbirds have found that diurnal birds reduce their vocal rate under full moons, which might be a response to reduce their predation risk (Foote *et al.* 2017, Pérez-Granados & López-Iborra 2020). However, the Undulated Tinamou is a medium-sized bird (*c.* 500 g) and may be less susceptible to effects of moonlight on predation risk. We did not control for some factors that may have influenced the moonlight intensity perceived by the Undulated Tinamou, such as cloud cover and moon position with respect to the horizon (Digby *et al.* 2014, York *et al.* 2014); future research would ideally include these variables as covariates.

Minimum air temperature was not related to the nocturnal vocal output of the Undulated Tinamou. This finding does not accord with the enhanced sound transmission hypothesis (Larom *et al.* 1997, La 2012). The finding also contrasts with previous research studying nocturnal vocalizations of both non-passerines (Digby *et al.* 2014, Mennill 2014) and passerines (Dickerson *et al.* 2020). La (2012) noted that ‘enhanced sound transmission may apply more to birds that live in open habitats than to those in closed habitats’, as signal degradation due to air turbulence should be low in closed habitats (Slabbekoorn *et al.* 2002). This may partly explain the lack of relationship found for Undulated Tinamou, as our study area was in a mosaic of forest and savanna. Similarly, previous research in the same study area found no relationship between vocal activity of two nocturnal bird species (*Nyctibius* spp.) and nocturnal air

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temperature (Pérez-Granados & Schuchmann 2020b). Moreover, low-frequency sounds, such as the Undulated Tinamou call (dominant frequency of 1280 Hz, Pérez-Granados *et al.* 2020) are less attenuated than higher frequency sounds (Pierce 1981, Larom *et al.* 1997), which may also contribute to the lack of impact of minimum air temperature on nocturnal vocal output found in our study.

Our study also provides evidence that the nocturnal vocal behaviour of the Undulated Tinamou was positively related to vocal output during the preceding night. This result suggests that the species' nocturnal calling activity might be related to endogenous factors, such as hormones (Nowicki & Ball 1989, Hau *et al.* 2000). However, the high correlation of vocal output between consecutive nights could be also related to the low variation in the percentage of the moon illuminated among successive nights, as this factor was associated with nocturnal vocal output. We did not find a significant association between daily and nocturnal vocal output on the same day, thus not supporting the hypothesis that nocturnal vocal activity of diurnal birds might be a continuation of diurnal efforts (La 2012). We are aware that our study was based on a reduced number of sites and that the number of calls detected and vocalization patterns found varied among monitoring stations. Future research seeking to evaluate the relationship between daily and nocturnal vocal activity of diurnal birds should therefore try to perform monitoring in a larger number of sites to obtain more robust data.

In this study we have described the annual pattern of nocturnal vocalizations of a Neotropical diurnal bird and its relationship with night temperature and moon phase. This observation provides new evidence regarding the function of nocturnal calling activity for mate attraction and the reasons why a diurnal bird vocalizes during the night. The use of autonomous recording units allowed us to monitor the nocturnal vocal behaviour of the species over a large temporal and spatial scale. Our definition of night was clearly limited by our recording schedule (one 15-min recording per hour). Future studies employing autonomous recording units may choose to make continuous recordings, which might allow researchers to use night length as a covariate on subsequent analyses. Likewise, we were unable to account for the breeding status and number of birds vocalizing around recorders. Individual recognition of recorded birds (e.g. Ehnes & Foote 2015) might be a feasible solution for future studies employing sound recorders once the method has been validated for the studied species. Likewise, further research on this topic should analyse the effects of other variables (e.g. hormones, number of neighbours and predation risk) to improve our knowledge of the function of and reasons for the nocturnal vocal activity of diurnal birds.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTION

Cristian Pérez-Granados: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (supporting); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Karl-L. Schuchmann:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal);

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Methodology (supporting); Project administration (lead); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal).

Data availability statement

Analyses reported in this article can be reproduced using the data provided in the following link: https://figshare.com/s/9d430818b7e8949345a1; https://doi.org/10.6084/m9.figshare.13208186.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of nocturnal calls of the Undulated Tinamou detected per month and station in the Brazilian Pantanal.

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