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Vocal behavior of the Undulated Tinamou (*Crypturellus undulatus*) over an annual cycle in the Brazilian Pantanal: New ecological information

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Abstract

Tinamous (Tinamidae) are a group of Neotropical birds for which little information is available. The Undulated Tinamou (*Crypturellus undulatus*) is one of the most widespread species but also declining. Due to its secretive habits, ecological knowledge regarding the species relies on few anecdotal descriptions. We used automated recorders to monitor the vocal activity of the species over an annual cycle at four sites in the Brazilian Pantanal. We provide a description and analyze the diel and seasonal patterns of the calling activity in this species and provide new ecological information. The daily cycle showed two significant peaks in calling activity during the early morning and late afternoon, in agreement with the vocal behavior common among tinamous. The species was vocally active throughout the year, but it was significantly higher during September–October and March. This suggests that the breeding period of the Undulated Tinamou in the Brazilian Pantanal extends from September to April. After the months with highest calling activity, there was a strong decrease in activity, which might be related to the silent behavior of male tinamous during incubation. The seasonal pattern and breeding period identified for the Undulated Tinamou in the Brazilian Pantanal are in agreement with those observed in previous studies carried out with other *Crypturellus* species. The use of automated recorders was found to be a useful method for monitoring the calling activity of this secretive group of birds and might be useful in the assessment of future population trends in this and other declining tinamous.

Abstract in Portugese is available with online material.

KEYWORDS

acoustic monitoring, Aves, birds, daily activity, Neotropics, Tinamiformes, vocal behavior

1 | INTRODUCTION

The study of diel and seasonal variation in bird calling behavior may provide insight into the ecology of monitored species. For example, numerous studies in temperate areas have demonstrated that bird vocal activity has an important role in territory establishment and mate attraction, and seasonal changes in vocal activity can therefore be related to the breeding phenology of birds (Catchpole & Slater, 2008). Knowledge regarding daily and seasonal variation in vocal activity in tropical resident species is lower than that in species from temperate areas (Demko & Mennill, 2019; Jahn, Ganchev, Marques, & Schuchmann, 2017), but studies addressing the vocal activity of tropical species are of interest since such activity is usually not restricted to the breeding period (Jahn et al., 2017; Odom et al., 2016; Topp &

Mennill, 2008). Acquired knowledge about bird vocal activity can also be useful to plan surveys and develop effective monitoring protocols for bird species (Pérez-Granados, Bota, Giralt, & Traba, 2018).

The use of automated recorders has revolutionized the way we understand soundscapes and the way we monitor vocally active wildlife species (see review in Sugai, Silva, Ribeiro, & Llusia, 2019). Automated recorders can be used to detect species' presence, monitor wildlife abundance (Pérez-Granados, Bota, et al., 2019; Terry, Peake, & McGregor, 2005) and detect changes at community and landscape level (Burivalova et al., 2019; Pijanowski, Farina, Gage, Dumyahn, & Krause, 2011). That transformation has produced remarkable results for monitoring secretive species and for those that are active under challenging circumstances, such as at night and at sites that are inhospitable or difficult to access, such as forests or wetlands (Celis-Murillo, Deppe, & Ward, 2012; Deichmann et al., 2018).

Tinamous (Tinamidae) represent one of the most ancient living groups of birds (Hackett et al., 2008). They exhibit exclusive male parental care, and in most species, several females lay their eggs in a single nest, which is incubated by the male (Cabot, 1992). This behavior makes these species an interesting group for studying the breeding ecology of birds. However, there is a lack of knowledge on the basic natural history of most tinamous (Cabot, 1992), and even knowledge regarding their breeding ecology is restricted to anecdotal or captive breeding data (Brooks, 2015; Solano-Ugalde, Ordóñez-Delgado, Vits, & Freile, 2018). This is because tinamous are cryptic, shy, and secretive Neotropical birds with mainly crepuscular and nocturnal activity. The vocalizations of tinamous, which are loud and very distinctive, are the only clues usually used to study tinamou ecology (e.g., Lancaster, 1964a; Negret, Garzón, Stevenson, & Laverde-R, 2015; Negret & Laverde-R, 2014). Therefore, tinamous seem to be an interesting model to monitor applying acoustic approaches. Tinamous are especially vulnerable to hunting, habitat loss, and alteration (Schelsky, 2004; Thornton, Branch, & Sunquist, 2012). Indeed, large differences in tinamou population densities have been found between hunted and nonhunted areas (Peres, 2000).

The Undulated Tinamou (*Crypturellus undulatus*) is a ground-foraging omnivore that is widespread in South America. It is a ubiquitous species that is mainly found in association with riparian forest and secondary growth and is most abundant in the Amazonian basin (BirdLife International, 2016). It is a shy polygynous species for which even basic biological knowledge is lacking (Cabot, 1992; Davies, 2002). The Undulated Tinamou has a negative population trend (BirdLife International, 2016), and additional ecological knowledge is in demand for assessing the current and future status of this taxon.

In this paper, we had four objectives to increase our knowledge about the ecology of the Undulated Tinamou: (a) evaluate the use of automated recorders, a noninvasive technique, as a monitoring method for studying the species; (b) describe the pattern of diel and seasonal variation in calling activity; (c) identify the hours and months with the highest calling output; and (d) elucidate the breeding phenology of the species. The main function of calling activity in the Undulated Tinamou is unknown, but previous research has linked periods with higher calling activity with the breeding conditions of tinamous (Lancaster, 1964b; Negret et al., 2015). Therefore, we expected to find seasonal variation in the calling activity of the species and predicted that those months with the highest calling output would relate to those months during which Undulated Tinamous were establishing territories and attracting mates.

2 | METHODS

2.1 | Study area

This study was carried out in the northeastern part of the Brazilian Pantanal (Pantanal Matogrossense). The study area included four acoustic monitoring stations separated by 890–2,750 m near the SESC Pantanal (Pocone municipality, Mato Grosso, Brazil; 16°29′58″ S, 56°24′39″ W, see Figure S1). The dominant vegetation is a mosaic of different forested and savanna areas (Junk et al., 2006). The regional climate is tropical and humid; the average annual rainfall is 1,000–1,500 mm, and the mean annual temperature is ~24°C. The study area is located on the floodplain of the Cuiaba River, one of the main tributaries of the Paraguay River within the Pantanal, and it is seasonally inundated due to the flooding of the Paraguay River (Junk et al., 2006). Therefore, the study area exhibits marked seasonality, with a pronounced terrestrial phase from May to September and an aquatic phase from October to April (Junk et al., 2006).

2.2 | Acoustic recording

Acoustic monitoring stations operated daily from 8 June 2015 to 31 May 2016, covering one annual cycle at each site. At each acoustic monitoring station, we placed one Song Meter SM2 recorder (Wildlife Acoustics, USA, www.wildlifeacoustics.com). The recorder was programmed to record (.wav format) the first 15 min of each hour in 24/7 mode following the winter local time (GMT −4) and configured with a sampling rate of 48 kHz and a resolution of 16 bits per sample.

2.3 | Acoustic data analyses

Recordings were scanned with Kaleidoscope Pro 5.1.8, an automated signal recognition software program provided by Wildlife Acoustics (Wildlife Acoustics, USA, www.wildlifeacoustics.com). This software is able to identify a target signal by using the signal parameters of the sounds targeted for detection. The call of the Undulated Tinamou is composed of three distinctive notes (Figure 1). Although specific information is not available for the Undulated Tinamou, we expect that calls recorded may have been uttered by both sexes, similar to calling behavior of most tinamous (Cabot, 1992; Davies, 2002). To characterize the call of the species in the study area, we measured 52 calls from eight different recordings (two from each acoustic monitoring

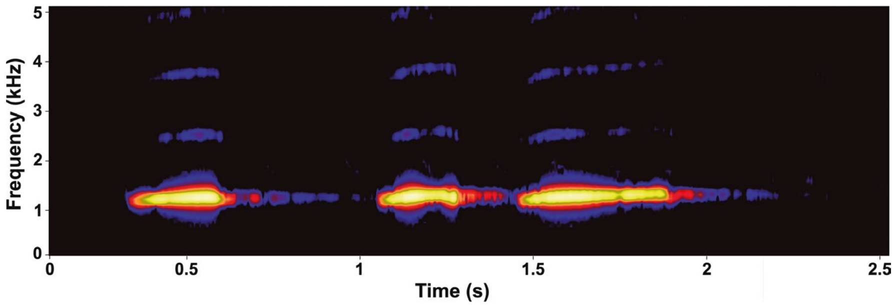

FIGURE 1 Sonogram of a typical Undulated Tinamou call. The call was recorded in Pantanal Matogrossense (Brazil) by a Song Meter SM2 on 5 March 2016

station) using Raven Pro 1.5 (Bioacoustics Research Program 2014) (Table S1). According to the call parameters of the species, we introduced the following signal parameters in Kaleidoscope: minimum and maximum frequencies of 1,150 and 1,350 Hz, respectively, minimum and maximum detection durations of 1.3 and 3 s (to include overlapping signals and birds duetting), respectively, and a maximum intersyllable gap of 0.6 ms. Kaleidoscope also requires an additional parameter that may impact the number of detected signals: the distance from the cluster center. Large values will result in a relatively large number of detected target signals (true positives) but also a number of false positives (misclassified signals). This parameter ranges from 0 to 2, and a value between 1.0 and 1.4 is recommended by Wildlife Acoustics. We used a value of 2. We are aware that this selection will increase the number of false positives, but we selected this value in order to detect as many tinamou calls as possible. A sensitive quantitative analysis of tinamou calls detected employing variable values of the parameter "distance from the cluster center" can be found in Table S2.

A total of 744,967 detections matched the signal parameters. Each event was visually and/or acoustically checked, always by the same observer (CPG), to separate Undulated Tinamou calls from undesired signals. A total of 305,581 detections were classified as Undulated Tinamou calls, which were used in subsequent analyses. The undesired signals were bird songs composed by different notes separated less than 0.6 s (maximum intersyllable gap used in our analyses). Most of the false positives were calls of the Little Nightjar (*Setopagis parvula*) and the Chaco Chacalaca (*Ortalis canicollis*). The number of calls detected per station ranged between 51,088 and 95,715 (Table S3).

2.4 | Statistical analyses

To identify the hours with significant high and low Undulated Tinamou calling activity, we fitted a generalized linear mixed model (GLMM) using the percentage of calls detected per hour during each month as the response variable, recording hour as a fixed effect (24 levels) and site (four categorical levels) and month (12 categorical levels) as random effects to control for calling variation owing to site and seasonality. An independent GLMM was fitted to identify months with significantly higher and lower calling activity in the species. In that case, we used the mean number of calls detected per day in each month as the response variable, month (12 categorical levels) as a fixed effect and site (four categorical levels) as a random effect to control for intersite variation. We employed the mean number of calls detected per day instead of the mean number of calls detected per month as a standardized measurement to reduce variation among months due to the variable number of monitoring days per month (e.g., the study began on 8 June). Model performance was evaluated by plotting standardized residuals versus fixed variables, normal Q–Q plots and histograms of residuals. No concrete pattern was found in any case. When a fixed effect was found to be significant, Tukey's post hoc test was performed to test for differences among levels. All statistical analyses were performed with R 3.4.1 (R Development Core Team, 2016). We used the packages "lme4" (Bates, Maechler, Bolker, & Walker, 2015) for the GLMM construction, "lmerTest" (Kuznetsova, Brockhoff, & Christensen, 2014) to calculate the significance of fixed effects and "multcomp" (Hothorn, Bretz, & Westfall, 2008) for post hoc comparison tests. The level of significance was $p < .05$, and the results are expressed as the mean ± *SE*.

3 | RESULTS

3.1 | Diel pattern

The Undulated Tinamou was detected during 99.9% of the monitored days (Table S3). We found a clear diel calling activity pattern in this species. The daily cycle showed a bimodal pattern, with the first peak of activity occurring in early morning (0500–0600 hr, 18.1% of all calls were detected at these recording times) and a second, and slightly higher, peak in the late afternoon (26.6% of the calls were detected in the period between 1600 and 1800 hr) (Figure 2). The species continued to call during the middle of the day but showed much lower activity when compared to that during the sunrise and sunset periods (Figure 2) (Table S4 for hourly call production). The nocturnal calling activity of the species, although low, continuously increased every hour after a strong decrease in activity that occurred at 1900 hr (0.3% of the total for this hour) (Figure 2). According to the GLMM analysis, there were significant differences in calling activity among hours (Table 1). The highest vocal output occurred at 0600 and 1700 hr, with no significant differences among them (Tukey post hoc test, see Figure S2). The period between 1900 and 0300 hr was the interval with significantly lowest calling activity (Table 1), according to Tukey's post hoc test (Figure S2).

3.2 | Seasonal pattern

The Undulated Tinamou was vocally active throughout the year, but calling seasonality also showed a bimodal pattern. The highest vocal output occurred in the months of October and March (372.2 and 343.1 calls per day, respectively) (Figure 3). A strong decrease in calling activity was detected in the months preceding the ones with the highest calling activity, but the lowest vocal activity occurred in February (Figure 3) (see Table S5 for monthly call production). Even in February, a mean number of 94.7 calls were detected per day and station (Table S5). There were significant differences among months in the calling activity of the species (Table 1). According to Tukey's post hoc test, the highest calling activity occurred during March and September–October, while the lowest vocal output occurred during February and July (Figure S3).

4 | DISCUSSION

Here, we report the results of a year-long study of the vocal behavior of the Undulated Tinamou, one of the most ancient living birds (Hacket et al., 2008). The use of automated recorders allowed us to quantify vocal production across an annual cycle and at different times of day, including the nocturnal period, at four monitoring stations. The calling activity of the species significantly differed among months as well as throughout the day. At the daily scale, the species called at any time of the day but at a higher rate in the early morning and late afternoon. This diel pattern is consistent with that found among other genera of tinamous, such as *Crypturellus* (Lancaster, 1964a; Skutch, 1963), *Nothoprocta* (Lancaster, 1964b; Pearson & Pearson, 1955), and *Tinamous* (Kuhnen, Lima, Santos, & Machado Filho, 2013; Lancaster, 1964a). In the only reference found for the Undulated Tinamou, Pearman (2001) stated that, in Argentina, the species was only found to vocalize for 15 min at dawn and dusk. However, no more information was provided, and this seems to be an anecdotal observation.

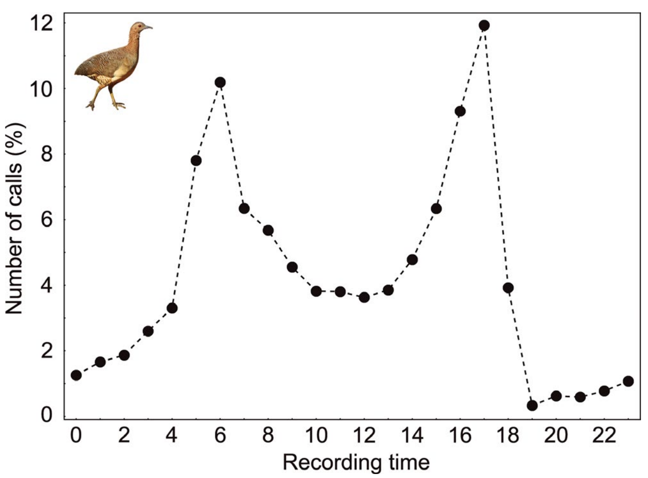

FIGURE 2 Diel calling activity pattern of the Undulated Tinamou in Pantanal Matogrossense (Brazil). Calling activity was measured by acoustic monitoring from 8 June 2015 to 31 May 2016 at four acoustic monitoring stations. Diel pattern is expressed as the mean percentage of calls detected during each recording time per station. Hours are expressed in winter local time (GMT −4)

Several authors have reported that nocturnal calling by tinamous is an intermittent and occasional behavior (e.g., Aldrich & Bole Jr., 1937; Beebe, 1925; Lancaster, 1964a; Skutch, 1963). In contrast, the nocturnal calling activity of the Undulated Tinamou, although significantly lower than the calling activity during the day, seems to play an important role in the communication system of the species (>42,000 calls were detected between 2000 and 0400 hr the next day, Table S4). We are aware that vocal behavior may vary among closely related species (e.g., Francis, Ortega, & Cruz, 2011). However, we strongly believe that the greater nocturnal activity observed in our study than in previous studies is related to the use of automated recorders. Prior research on the nocturnal calling activity of tinamous was based on auditory surveys, and calling activity was rarely monitored beyond sunset or, if so, only for short periods (Lancaster, 1964a, 1964b; Skutch, 1963). In contrast, we monitored the nocturnal calling behavior of Undulated Tinamous with the same intensity as that for the diurnal calling activity. Future research should include detailed analyses of nocturnal calling activity to elucidate whether calling in the night is a rare or common behavior among tinamous.

The detection of the greatest calling activity during September–October and March suggests that the breeding period of the Undulated Tinamou in the Brazilian Pantanal during the monitored year extended from at least September to April. This is in agreement with the seasonal pattern found in other tinamou species that are also vocally active throughout the year but show a peak in vocal activity during the breeding period (Lancaster, 1964a). However, other tinamou species show marked calling seasonality and only call during the breeding period (Lancaster, 1964b). The suggested breeding period of the Undulated Tinamou (September–April) is similar to that indicated for the closely related Yellow-legged Tinamou (*Crypturellus noctivagus*) in Venezuela (August–April, Friedmann & Smith, 1950) and for the Little Tinamou (*Crypturellus soui*) in Costa Rica. Tinamous

TABLE 1 Summary table of type-III partitioning of variances testing the effects of recording time and month on the calling activity of the Undulated Tinamou in Pantanal Matogrossense (Brazil)

Fixed effect	*df*	Den *df*	Sum Sq	Mean Sq	*F*	*P*
Recording time	23	1,128	12,775	555.4	47.57	<.001
Month	11	1,369.1	8,521,689	774,699	18.36	<.001

Note: The effects of recording time and month were fitted using independent generalized linear mixed models. Calling activity was monitored with recordings conducted for 15 min every hour between 8 June 2015 and 31 May 2016 at four acoustic monitoring stations.

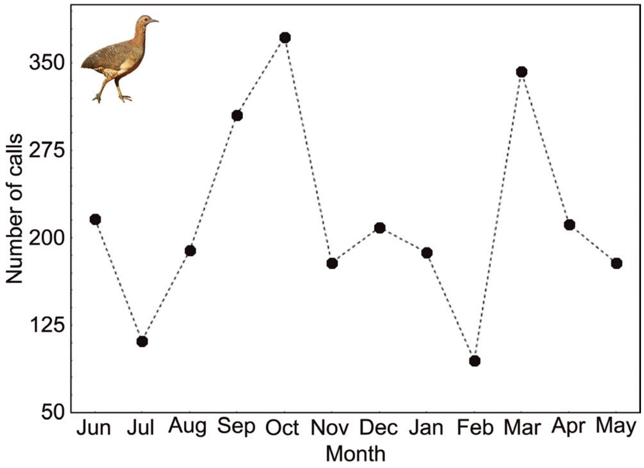

FIGURE 3 Seasonal calling activity pattern of the Undulated Tinamou in Pantanal Matogrossense (Brazil). Calling activity was measured by acoustic monitoring from 8 June 2015 to 31 May 2016 at four acoustic monitoring stations. The seasonal pattern is expressed as the daily mean number of calls detected per month

from other genera seem to breed mainly at the end of the rainy period (March–April) (Lancaster, 1964b; Negret et al., 2015; Solano-Ugalde et al., 2018). The observation of the maximum calling activity of the Undulated Tinamou in September–October and March can be related to the period when males establish territories and seek mates (Lancaster, 1964a), while the decrease in calling activity in the following month might be due to the silent behavior of incubating males, a phenomenon found in other tinamous (Lancaster, 1964a). Another nonexclusive explanation for the decrease in calling activity in the months following the maximum calling activity is that tinamou males may have learned the calls of neighboring individuals (Lancaster, 1964a) and do not answer their calls at high rates later in the season (Dear Enemy Hypothesis, Fischer, 1954). The two peaks in vocalization followed by a decrease of vocal activity in the following months suggest that the Undulated tinamou might be a double-brooded species in the study area. It is in agreement with the two marked peaks of nesting, in September and February, of the Little Tinamou in Costa Rica (Skutch, 1963). However, we have no observational data to confirm that the Undulated Tinamou as a double-brooded species.

Our results highlight that future monitoring programs aimed at detecting the Undulated Tinamou can be performed in the late afternoon. This could increase the flexibility of fieldwork and save significant time for working on other project goals during the early morning, when time is usually more limited. Future studies on tinamous should attempt to determine the specific function of calling seasonality in this group of birds. However, due to the difficulties in regard to performing observational field studies with tinamous and other birds, the use of remote sensing techniques should be considered. In this study, we demonstrated that acoustic monitoring, coupled with automated signal recognition, was useful for studying the presence and the behavior of this group of birds. Acoustic monitoring allowed us to monitor the calling activity over a year, but also to monitor its nocturnal vocal activity obviated the necessity of performing night surveys in the study area. Finally, the vocal activity data presented here can be a useful baseline for future monitoring programs aiming to assess species-specific population trends (Buxton, Major, Jones, & Williams, 2013). Our data can also be used to identify concrete periods (September–October and March–April) during which field surveys can be performed to monitor the species as well as during which hunting pressure should be reduced, especially if the populations continue to decline in the future (BirdLife International, 2016).

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AUTHOR CONTRIBUTION

1. Conceived the idea, design, experiment (supervised research, formulated question or hypothesis): CPG, KLS, and MIM. 2. Performed the experiments (collected data, conducted the research): KLS and MIM 3. Wrote the paper (or substantially edited the paper): CPG, KLS, and MIM. 4. Developed or designed methods: CPG. 5. Analyzed the data: CPG. 6. Contributed substantial materials, resources, or funding: KLS and MIM.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h6t7g (Pérez-Granados, Schuchmann, et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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