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Addicted to the moon: vocal output and diel pattern of vocal activity in two Neotropical nightjars is related to moon phase

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The moon phase affects the ecology and vocal activity of nightjars (Caprimulgidae). However, some studies have found contradictory results regarding the impact of the moon phase on the vocal activity of nightjars. To increase our knowledge on this topic, we monitored the vocal behavior of two Neotropical nigthjars, the Little nightjar (*Setopagis parvula*) and the Common pauraque (*Nyctidromus albicollis*), over 5 lunar cycles in the Brazilian Pantanal. We tested the relationships between the moon phase and daily vocal output (number of calls uttered) and the proportions of calling activity at dusk, midnight, and dawn. Our results suggest that moonlight stimulated the vocal output of both species, since it was between 6 and 8 times higher during full moon nights than during new moon nights. Likewise, the proportion of calling activity at midnight was significantly higher during full moon nights. In contrast, the proportion of calling activity of both species was higher at dawn during new moon nights than under the full moon. The calling activity of the Common pauraque was also higher at dusk during new moon nights. These findings might be partly related to the much lower vocal output at midnight during full moon nights and therefore higher proportions of vocal activity at dusk and at dawn under new moon scenarios. This is the first study comparing the vocal behavior of two Neotropical nightjars over different moon phases and shows that the impact of moonlight may differ between species and at

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a daily scale when analyzing the periods with the highest and lowest illumination. The consequences of the increase in vocal output under moonlight are unknown and should be assessed.

KEY WORDS: acoustic monitoring, Kaleidoscope Pro, moon cycle, *Nyctidromus*, Pantanal, *Setopagis*.

INTRODUCTION

Lunar periodicity affects physiological and behavioral patterns across a wide range of organisms (Kronfeld-Schor et al. 2013) and has a large impact on avian ecology. There are documented effects of lunar cycle on avian activity patterns (Brigham et al. 1999), space use (Milsom et al. 1990), migration (Pyle et al. 1993; Norevik et al. 2019), corticosterone concentration (Tarlow et al. 2003), body temperature (Portugal et al. 2019), and reproduction (Perrins & Crick 1996). It is also well known that bird vocal behavior can be influenced by the lunar cycle, with a general increase in vocal activity during full moon nights, including both, diurnal (La 2012; York et al. 2014) and nocturnal species (Penteriani et al. 2010; Mori et al. 2014). Bird vocalizations play an important role in mate attraction and territory defense (Marler 2004; Catchpole & Slater 2008), and thus the study of the avian vocal behavior may be useful to understand the function of birds' vocal activity.

The effect of the lunar cycle on bird behavior has been especially well studied in nightjars (Caprimulgidae, e.g., Martin 1990; Reino et al. 2015; Norevik et al. 2019; Evens et al. 2020). Nightjars are nocturnally active insectivorous birds that use visual cues to detect prey; therefore, light conditions are an important factor affecting their foraging ecology. Indeed, nightjars usually forage during crepuscular periods (dusk and dawn) but extend their daily foraging activities into the night when a high percentage of the moon is illuminated (Mills 1986; Brigham & Barclay 1992; Brigham et al. 1999; Thurber 2003; Perlman 2008). The moon phase also affects other aspects of nightjar ecology. Previous studies have found a synchrony between the lunar cycle and reproductive behavior in some species, allowing the first 2 weeks of the nestling period to coincide with the greatest moonlight intensity (Mills 1986; Vilella 1989; Brigham & Barclay 1992; Perlman 2008), as well as a high intensity of migration (Norevik et al. 2019; Evens et al. 2020) and use of roads during full moon nights (De Felipe et al. 2019). Similarly, a large number of studies have concluded that the vocal activity of several Caprimulgidae taxa is higher during full moon periods than on new moon nights, including nightjars, sensu stricto, (Caprimulginae, Vilella 1989; Perrins & Crick 1996; Reino et al. 2015) and nighthawks (Chordeilinae, Sidler 2017), but including also caprimulgids of different families, such as the potoos (Nyctibiidae, Pérez-Granados & Schuchmann 2020a). However, some studies have not found a relationship between the moon phase and vocal activity of nightjars, such as the European nightjar (*Caprimulgus europaeus*, Cadbury 1981; Reino et al. 2015), and others have found contradictory results regarding the impact of the moon phase on the vocal activity of the same species (e.g., Kavanagh & Peake 1993; Debus 1997), and among sympatric and closely-related species (Reino et al. 2015; Pérez-Granados & Schuchmann 2020a). Therefore, the impact of the moon phase on nightjar behavior is a topic that deserves more study.

Here, we aimed to elucidate the relationship between the lunar cycle and vocal behavior in two Neotropical nightjars. Our main goal was to evaluate whether the vocal behavior of the species (number of calls uttered throughout the night and at specific periods: dusk, midnight, and dawn) was related to the moon phase. To achieve this, we monitored the nocturnal vocal activity of the Little nightjar (*Setopagis parvula*) and the Common pauraque (*Nyctidromus albicollis*, hereafter Pauraque) during 5 consecutive lunar cycles in the breeding season of 2015 at three different sites in the Brazilian Pantanal. We predicted that the nightjars' vocal output (number of calls uttered) would be higher during full moon nights than during new moon nights if moonlight stimulates the vocal activity of nightjars (Mills 1986; Reino et al. 2015). We also aimed to unravel whether the positive relationship between the lunar cycle and vocal activity remains constant throughout the night. We hypothesized that the impact of moonlight would be maximized during midnight (12:00 am), when the moonlight is maximal, while the influence of the moon phase would be low or even zero at dusk and at dawn due to the low contribution of lunar illumination to the total environmental levels at sunset and at sunrise (York et al. 2014). Therefore, we predicted a large increase in calling activity at midnight during full moon nights in comparison to that on new moon nights. In contrast, we predicted that nightjar calling activity would be similar at dusk and at dawn regardless of moon phase.

MATERIALS AND METHODS

Study species

In this study, we monitored the vocal activity of two Neotropical nightjars, the Little nightjar and the Pauraque. The Little nightjar is a grayish-brown nightjar typical of open woodlands in the lowlands of central and eastern South America. It is a common migratory species that inhabits the study area (Brazilian Pantanal, see below) from early June to late January (Pérez-Granados & Schuchmann 2020b). The species is a poorly known (Cleere 2010), and without detailed territoriality studies (Provost 2020). Nonetheless, previous reports mention that males establish territories and call at night for mate attraction and territorial defence (Johnson 2020). The call of the Little nightjar is composed of a repetition of 5–9 notes that descend in pitch ("Dop dro-dro-dro-dro-dro-dro", Fig. S1 in Supplemental Data). The Pauraque is a long-tailed brown and gray nightjar typical of open woodland and scrub habitats from southern Texas to the lower Paraná River region (Cleere 2010). Most of its subpopulations are year-round residents. The Pauraque is territorial during the breeding season and males vocalize from their accustomed stations (Quesnel 1993), which makes that the probability of detecting the same individual vocalizing from the same location over consecutive days is high (Sandoval & Escalante 2011). The species call is composed of short whistles ("Wheeeow", Cleere 2010, Fig. S1 in Supplemental Data). The annual pattern of calling activity of the Pauraque is clearly related to the breeding season (Quesnel 1993). Both, the Little nightjar and the Pauraque, are highly vocally active. The vocal activity of both species in the Brazilian Pantanal peaks between August and October, which has been proposed to match with the their breeding period (Pérez-Granados & Schuchmann 2020b), following the increase in arthropod abundance that occurs in the Brazilian Pantanal after the first rains (usually in September; Junk et al. 2006; de Deus et al. 2020).

Study area

The study area is comprised of three acoustic monitoring stations located in the Pantanal of Mato Grosso in the northeastern part of the Brazilian Pantanal. Monitoring stations were established within a buffer of 7 km to the SESC Pantanal (Poconé municipality, Mato Grosso, Brazil; 16°29′58″S, 56°24′39″W) and were separated by a distance of 890 m (stations B-C), 2,030 m (stations A-B), and 2,830 m (stations A-C, Fig. 1). The study area is located within the floodplain of the Cuiabá River, one of the main tributaries of the Paraguay River within the Brazilian Pantanal. It is seasonally inundated between October and April due to the flooding of the Paraguay River (Junk et al. 2006), while the dry season extends from May to September. The vegetation is composed of a mosaic of forested and savanna areas. The regional climate in the study area is tropical and humid, with average annual rainfall of 1,000–1,500 mm and a mean annual temperature of ~ 24 °C.

Acoustic recording

At each of the three monitoring stations, we recorded the vocal behavior of the Little nightjar and the Pauraque with autonomous recording units (Song Meter SM2, Wildlife Acoustics, USA) that were active from 8 June 2015 to 31 May 2016. The effective detection radius of the Song Meter SM2 is approximately 150–160 m (Rempel et al. 2013; Pérez-Granados et al. 2019a), which together with the territorial behavior of the monitored species during the breeding season suggest that the risk of recording the same individual at two different stations (minimum separation of 890 m) was low. The recorders were programmed to record (.wav format) the first 15 min of each hour in 24/7 mode, with a sampling rate of 48 kHz and a resolution of 16 bits per sample.

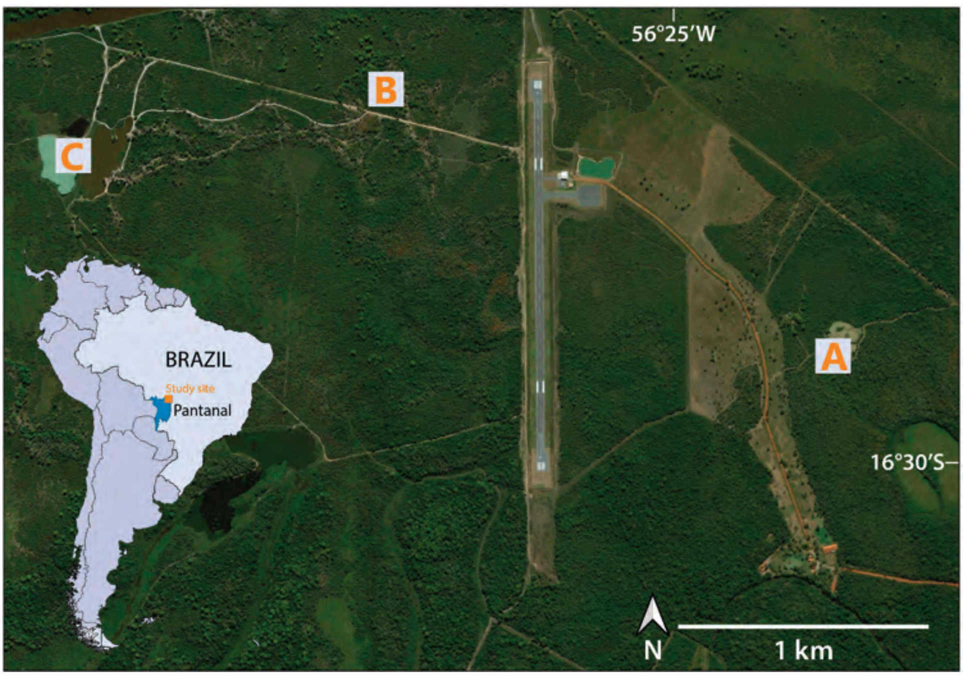

Fig. 1. — Location of the three acoustic monitoring stations in the Brazilian Pantanal (Pantanal of Mato Grosso, Poconé municipality, Mato Grosso, Brazil). The inset shows the location of the study area (red square) and the Brazilian Pantanal. Scale bar: 1 km.

To analyze the impact of the moon cycle on the calling behavior of the two nightjar species, we selected the recordings made between 6:00 pm and 5:00 am during the 2-day interval before and after the moon was totally new or full during 5 consecutive lunar cycles (Fig. 2, see concrete monitoring dates in Supplemental Table S1). We defined a monitoring day as the period that elapsed between 6:00 pm and 5:00 am, which was selected as the optimum monitoring period because 99.9% of the calls of both nightjar species are uttered between 6:00 pm and 5:00 am (Pérez-Granados & Schuchmann 2020b). Moon phase data were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.html). The percentage of the moon illuminated during the 2-day interval varied between 0 and 8% during new moon surveys and between 92 and 100% on full moon nights.

Acoustic data analyses

Recordings were analyzed using Kaleidoscope Pro 5.1.8, an automated signal recognition software program (Wildlife Acoustics, USA). Kaleidoscope scans recordings searching for signals according to the defined signal parameters. The detected signals are automatically clustered according to their similarity and are then sorted by similarity within the clusters. This facilitates the reviewing process since the first sounds of each cluster are the most representative of each

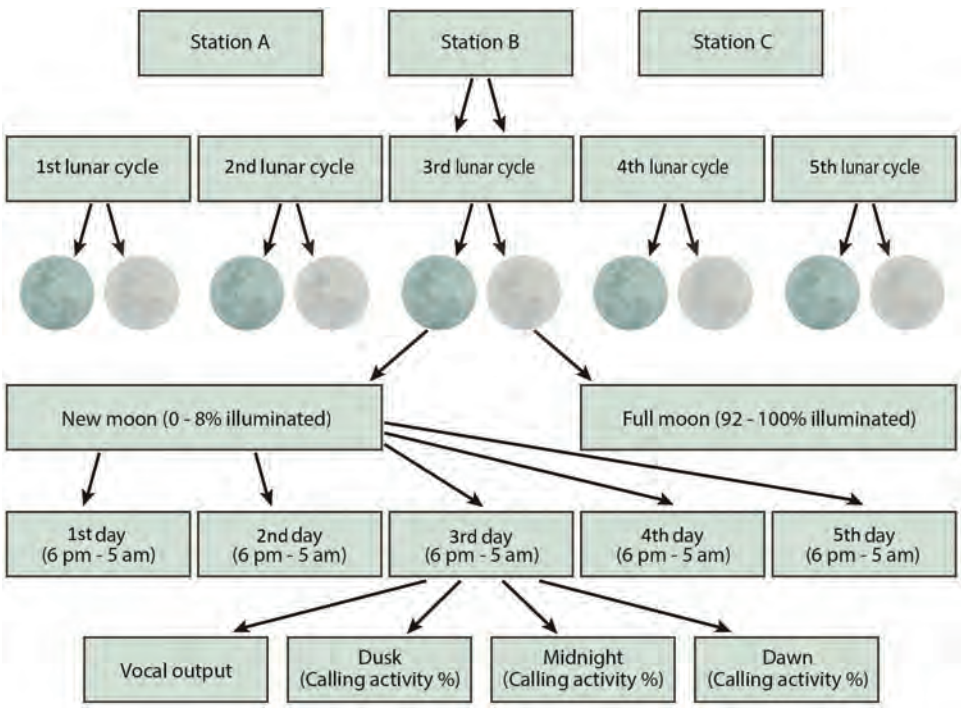

Fig. 2. — Sampling procedure. The calling behavior of the Little nightjar and the Common pauraque was monitored at three different sites in the Brazilian Pantanal during 5 consecutive lunar cycles. During each moon phase, we monitored calling behavior by recording calls for 15 min per hour from 6:00 pm to 5:00 am for 5 consecutive days (the 2-day interval before and after the moon was totally full or new).

group. Therefore, the clusters can be labeled according to whether the target signal was detected within the first sounds of each cluster, and those clusters composed of nontarget signals (other taxa vocalizing within the same frequency band, rainfall, etc.) can be removed.

We first characterized the call structure of the Little nightjar and the Pauraque in the study area (Fig. S1 and Table S2 in Supplemental Data). According to the species' call characteristics, we introduced the following signal parameters in Kaleidoscope:

(1) Little nightjar: minimum and maximum frequency range: 600 and 2,700 Hz, respectively; minimum and maximum detection length: 0.8 and 3 sec, respectively; maximum intersyllable gap: 0.2 sec; distance from the cluster center: 2.0.
(2) Pauraque: minimum and maximum frequency range: 600 and 2,700 Hz, respectively; minimum and maximum detection length: 0.3 and 0.8 sec, respectively; maximum intersyllable gap: 0.2 sec; distance from the cluster center: 2.0.

We created a classifier for each species using a training dataset that consisted of 1,825 15-min training recordings made between May 2015 and February 2016 (randomly selected, not including any recordings used in the study). The first 50 events of each of the clusters created by Kaleidoscope were reviewed and labeled "Little nightjar", "Pauraque" or "other sounds" according to whether a call of the desired species was found (see Table S3 in Supplemental Data). The classifiers were used to sort our dataset based on the labeled training recordings. Finally, each event automatically classified as "Little nightjar" or "Pauraque" was visually and/or acoustically checked to remove undesired signals, while the events classified as "other sounds" were not considered in the study.

We evaluated the performance of the recognizers by calculating their recall rate. The recall rate is defined as the proportion of target species vocalizations automatically detected (Knight et al. 2017). We estimated the recall rate of the recognizer of each species by dividing the number of calls detected by Kaleidoscope by the number of calls in the recordings (Knight et al. 2017; Pérez-Granados & Schuchmann 2020a). The number of calls in sound recordings was annotated after checking visually and acoustically 90 randomly selected recordings. We reviewed a total of 30 recordings per site divided in the three following categories: (A) 10 recordings made at 6 pm, (B) 10 recordings made at 12 am, and (C) 10 recordings made at 5 am. Recordings were reviewed blinded with respect to moon phase, station identification, date of recording, and whether or not the species were detected.

Statistical analyses

To analyze the impact of the moon phase on the calling behavior of the Little nightjar and the Pauraque, we fitted independent generalized linear mixed models (GLMMs). The response variables employed were (a) daily vocal output, measured as the total number of calls detected per monitoring day (recordings made between 6:00 pm and 5:00 am); (b) proportion of calling activity at 6:00 pm (hereafter at dusk); (c) proportion of calling activity at 12:00 am (hereafter at midnight); and (d) proportion of calling activity at 5:00 am (hereafter at dawn). The proportion of calling activity during each period was calculated by dividing the number of calls detected in each recording period by the total number of calls during the monitoring day. GLMMs were fitted independently for each species and for each of the four response variables (log + 1 transformed), and moon phase ("New/Moon") and acoustic monitoring station ("Station A/Station B/Station C") were included as fixed categorical effects, while the monitoring day ("First/Second/Third/Fourth/Fifth") nested in the moon cycle ("First/Second/Third/Fourth/Fifth") was included as random categorical effects to control for daily variations within and among cycles. Station was included to control for variations among sites due to seasonality, but it was included as a fixed effect due to the low number of levels within the factor (see Gelman & Hill 2006). We used the "lmer" function in the R package "lme4" to fit the GLMMs (Bates et al. 2015). All statistical analyses were performed in R 3.6.2 (R Development Core Team 2019), the level of significance was $P < 0.05$.

RESULTS

Both species were detected at all acoustic monitoring stations for a total of 21,328 Little nightjar calls and 50,616 calls of the Pauraque. Vocal output of both species varied among stations (Table 1, Table S4 in Supplemental Data). The number of Little nightjar calls detected per station ranged between 5,171 and 10,924, while the number of Pauraque calls per station varied between 2,204 and 40,473. Recall rate for the Little nightjar recognizer was 77.4% (2,366 calls detected of the 3,056 calls annotated in the 90 recordings of the validation data set) and 70.9% for the Pauraque (3,068 calls detected of the 4,326 annotated).

There was a significant interrelation between moon phase and calling behavior of both nightjar species (Table 1), with higher vocal output during nights with full moons than on new moon nights (Fig. 3, Table S4 in Supplemental Data). The vocal output of the Little nightjar was 8 times higher during full moon nights (average of 252.3 calls per monitoring day) than on new moon nights (32.0 calls per day). Similarly, the vocal output of the Pauraque was 6 times higher under the full moon (582.3 calls per day) than on new moon nights (92.6 calls per day).

The proportions of calling activity during the different recording periods were related to the moon phase and showed similar patterns in both species (Table 1). The only vocal parameter that showed a different response between the species was the proportion of calling activity at dusk. The proportion of calling activity performed at dusk by the Little nightjar did not differ between the moon phases, while this variable was marginally significantly related to moon phase in the Pauraque ($P = 0.051$, Table 1), with more than double the calling activity at dusk during new moon nights (Fig. 4, Table S4 in Supplemental Data). The proportion of calling activity at midnight was significantly related with the moon phase, with higher calling activity during full moons than during new moon nights for both species (Table 1). The Little nightjar called more at midnight during full moons (8.7%) than during new moon nights (2.4%), and this pattern was also observed in the Pauraque (6.8 and 6.1%, respectively) (Fig. 4). In contrast, the proportion of calling activity performed at dawn was positively associated with new moon nights, since it was higher during new moons than during full moon nights (Table 1). In both species, the proportion of calling activity performed at dawn during new moon nights was 2 times higher than that performed on full moons (Fig. 4, Table S4 in Supplemental Data). The proportion of calling activity at concrete times of the night also varied among stations (Table S4 in Supplemental Data).

DISCUSSION

In this work, we found that the vocal behavior of the Little nightjar and the Pauraque varied according to the moon phase. In accordance with our prediction, the daily vocal output and the proportion of calling activity at midnight of both nightjar species were positively associated with high percent of the moon illuminated, showing higher values during full moon nights than during moonless nights. In contrast, the proportions of calling activity detected at dusk and at dawn were negatively associated with the percent of the moon illuminated, since their value were lowest under moonlight, with the exception of the proportion of calling activity at dusk for the Little nightjar, which did not differ between the moon phases.

Table 1.

Summary of generalized linear mixed model analysis results regarding the effect of the moon phase on the calling behavior of the Little nightjar and the Pauraque in the Brazilian Pantanal. The calling behavior of both species was monitored by recording calls for 15 min per hour from 6:00 pm to 5:00 am during 5 consecutive days (the 2-day interval before and after the moon was totally full or new) during 5 different moon cycles. For each monitoring day, we estimated the vocal output (total number of calls detected) and the proportion of calling activity occurring at dusk (recordings made at 6:00 pm), midnight (recordings made at 0 am) and dawn (recordings made at 5:00 am). Generalized linear mixed models were fitted independently for each species and response variable using the moon phase and acoustic monitoring station as fixed effects and the moon cycle and monitoring day nested in the moon cycle as random effects.

		Little nightjar					Pauraque				
		Estimate	SE	df	t-value	*P*	Estimate	SE	df	t-value	*P*
Vocal output	Intercept	2.61	0.36	55.6	7.20	< 0.001	3.05	0.33	60.81	9.13	< 0.001
	Moon phase (New)	− 0.99	0.25	122.0	− 3.94	< 0.001	− 1.34	0.24	111.68	− 5.40	< 0.001
	Station (B)	0.90	0.31	122.0	2.92	< 0.001	0.69	0.30	117.85	2.24	0.027
	Station (C)	1.08	0.32	121.9	3.50	< 0.001	3.35	0.29	117.30	11.30	< 0.001
% Dusk	Intercept	0.89	0.29	25.78	3.05	0.005	2.06	0.30	12.97	6.90	< 0.001
	Moon phase (New)	− 0.28	0.36	118.0	− 1.10	0.274	0.45	0.23	100.45	1.97	0.051
	Station (B)	0.41	0.33	117.1	1.26	0.212	− 2.15	0.29	101.88	− 7.23	< 0.001
	Station (C)	1.92	0.31	117.7	6.17	< 0.001	0.35	0.27	98.57	1.34	< 0.183
% Midnight	Intercept	0.93	0.22	121.0	4.20	< 0.001	1.25	0.17	115.3	7.10	< 0.001
	Moon phase (New)	− 0.92	0.21	121.0	− 4.33	< 0.001	− 1.28	0.17	102.0	− 7.33	< 0.001
	Station (B)	0.42	0.27	121.0	1.53	0.130	0.46	0.22	104.5	2.05	0.043
	Station (C)	0.75	0.26	121.0	2.89	0.005	0.52	0.20	100.3	2.56	0.012
% Dawn	Intercept	2.00	0.34	103.2	5.88	< 0.001	1.64	0.28	100.9	5.79	0.001
	Moon phase (New)	0.81	0.31	102.3	2.64	0.009	0.86	0.26	99.9	3.31	0.001
	Station (B)	− 0.38	0.39	100.1	− 0.98	0.331	− 0.44	0.34	101.3	− 1.33	0.187
	Station (C)	− 0.69	0.37	102.7	− 1.87	0.065	− 0.32	0.31	98.3	− 1.04	0.302

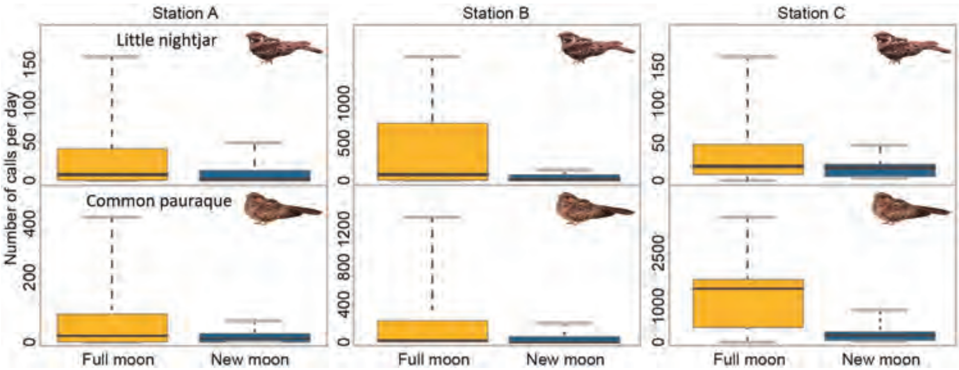

Fig. 3. — Boxplot showing the vocal output of (A) the Little nightjar and (B) the Common pauraque during full and new moon nights in the Brazilian Pantanal. Vocal output (number of calls detected per day) was monitored with recordings obtained at three sites during 5 consecutive lunar cycles between the middle of June and late October 2015. The number of calls detected per day is shown separately for each species and acoustic monitoring station. The boxplot displays the mean (black horizontal line), 25th and 75th percentiles of the data (colored boxes), and the 95% confidence interval (dashed lines).

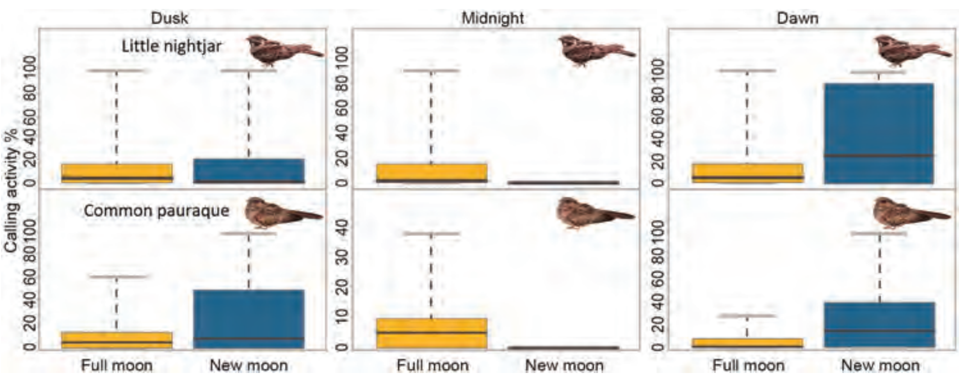

Fig. 4. — Boxplot showing the proportions of calling activity by (A) the Little nightjar and (B) the Common pauraque during full and new moon nights at dusk, midnight and dawn. The proportion of calling activity refers to the number of calls detected during each period divided by the total number of calls detected on each day. Calling activity was monitored with recordings obtained at three sites during 5 consecutive lunar cycles between the middle of June and late October 2015 in the Brazilian Pantanal. The proportion of calling activity is shown separately for each species and period. The boxplot displays the mean (black horizontal line), 25th and 75th percentiles of the data (colored boxes), and the 95% confidence interval (dashed lines).

The positive association between moon phase and vocal activity supports most previous studies focused on nightjars (e.g., Cooper 1981; Perrins & Crick 1996; Wilson & Watts 2006; but see Cadbury 1981; Mills 1986; Reino et al. 2015) and other nocturnal bird species (Penteriani et al. 2010; Mori et al. 2014; Pérez-Granados & Schuchmann 2020a). Prior research on the Pauraque also highlighted that the vocal activity of this species was highest when the percent of the moon illuminated was high in comparison with nights with low percentage of the moon illuminated (Quesnel 1993; Thurber 2003). The positive relationship between full moons and the vocal activity of nightjars might be a consequence of the high foraging rates during nights with a full moon (Brigham & Barclay 1992; Brigham et al. 1999; Perlman 2008) related to the increase in nocturnal light (Mills 1986). For example, the Pauraque usually vocalizes stationary just before or after foraging flights (Thurber 2003; K.-L. Schuchmann pers. obs.), which may support a positive relationship between foraging and vocal activity of the monitored species. However, we have no data about foraging activity of the monitored species in the study area to relate both variables. The increase in foraging activity, and therefore vocal activity, on nights with a full moon might be partly related to an increase in prey abundance (Jetz et al. 2003) and improved conditions for visual prey detection (De Felipe et al. 2019). However, it is possible that the increase of vocal output during the full moon nights may also be related to mate attraction. Penteriani et al. (2010) suggested that the Eagle owl (*Bubo bubo*) may use moonlight to increase the conspicuousness of its patch of white throat plumage, since call displays were positively influenced by the amount of moonlight. The same reasoning may apply for the monitored nightjars, since the males of both species have a white band across the primary flight feathers (Cleere 2010). Indeed, Quesnel (1993) previously reported that white wing bars and tail stripes of the Pauraque male and the display behavior of the male would hardly have evolved if the birds were most active in near total darkness. Nonetheless, further research based on observational or experimental studies are needed to disentangle whether moonlight have an impact on the effectiveness of the visual communication of the monitored nightjars.

The variation of vocal output among sites it is likely related to different bird abundance around autonomous recording units, since the relationship between the number of bird vocalizations in sound recordings and bird abundance around autonomous recording units is expected to be density-dependent (Farnsworth et al. 2004). Indeed, several studies have proposed the use of the number of bird vocalizations in sound recordings as a reliable index of bird density (e.g. Oppel et al. 2014; Borker et al. 2015; Pérez-Granados et al. 2019b). A feasible solution for future research using autonomous recording units but aiming to control for the number of vocalizing individuals around recorders might be to discriminate among individuals on the different call parameters of each individual (Ehnes & Foote 2015; Dent & Molles 2016).

The diel pattern of vocal activity in the Little nightjar and the Pauraque was correlated with the moon phase. Both nightjar species showed a higher proportion of calling activity at midnight on nights with a full moon, in agreement with the increase in vocal output explained above and previous studies using also the Pauraque as study species. Quesnel (1993) found that calling activity of the Pauraque, apart from dusk and dawn, was highly dependent on the presence of moonlight. The higher proportion of calling activity at dusk and at dawn during new moon nights, when compared to full-moon nights, might also be a consequence of an increased crepuscular activity during new moon periods. Perlman (2008) found that on full moon nights, the Nubian nightjar (*Caprimulgus nubicus*) foraged through most of the night, while on new moon nights the species foraged only during the twilight of dusk and dawn. Jetz et al. (2003) also showed that two species of tropical nightjars increased twilight foraging activity during new moon periods. Nightjars use visual cues to detect prey, whose detection is lower during new moon nights (De Felipe et al. 2019). During new moon nights elevated light levels are reached just during the crepuscular period, and thus nightjars may increase their foraging activity to compensate for the shorter nocturnal foraging window in the days around the new moon (Jetz et al. 2003). Although a negative association might be expected between time devoted for hunting and singing (trade-off), the increased general activity at dusk and at dawn during the crepuscular period during new moon nights may partly explain our results, since both monitored target species usually vocalize between successive hunting events (Thurber 2003; K.-L. Schuchmann pers. obs.)

The moon effect may be low in partially diurnal nightjars, such as the Lesser nighthawk (*Chordeiles acutipennis*) and the Common nighthawk (*Chordeiles minor*) (Mills 1986). However, the Little nightjar and Pauraque are strictly nocturnal species (Pérez-Granados & Schuchmann 2020b), which may partly explain the effect found in this study. Contradictory results found at the intraspecific level regarding the relationship between moon phase and the proportion of calling activity at dusk might be related to the different diel patterns of vocal activity in each species. The peak of vocal activity in the Little nightjar is significantly higher at dawn than at dusk (21.5% of the 64,233 calls detected throughout an annual cycle were recorded at 5:00 am, while only 4.4% were recorded at 6:00 pm, Pérez-Granados & Schuchmann 2020b), while the diel pattern of Pauraque is more constant throughout the night (11 and 7.8% of the 133,939 calls detected throughout an annual cycle were recorded at 5:00 am and 6:00 pm, respectively, Pérez-Granados & Schuchmann 2020b). The lower vocal activity of the Little nightjar at dusk, when compared to that of the Pauraque (Table S4 in Supplemental Data), may contribute to explain why the proportion of calling activity at dusk of the Little nightjar did not differ between the moon phases for such species. The negative association found between full moon nights and calling activity at dusk and at dawn in the Pauraque agrees with a prior study in the species, since Quesnel (1993) found that moonlight influenced the number of calls at dusk just as it did at dawn. Finally, the variation among sites in the proportion of calling activity at dawn and at dusk (Table S4 in Supplemental Data) might be related to microhabitat variations that may alter the light level perceived by the nightjars at each station. Among these factors, it is worth highlighting the forest canopy cover and main habitat type (savanna or forest). However, we do not have habitat data to deep further into such relationship, but further research should evaluate whether microhabitat variables may have an impact on the relationship between moon phase and birds' vocal activity.

The use of autonomous recording units coupled with automated signal recognition has proven to be an effective tool for nightjar monitoring (Zwart et al. 2014) and enabled us to simultaneously monitor the vocal activity of the Little nightjar and the Pauraque. The recall rate of the created recognizers were of 71 and 77%, values than can be considered as high when compared to previous studies (e.g., Swiston & Mennill 2009; Digby et al. 2013; Bobay et al. 2018; Shonfield et al. 2018; Pérez-Granados et al. 2019b); and that are in agreement with the recall rate of recognizers created for monitoring the vocal activity of two other caprimulgids in the study area (74–85%, Pérez-Granados & Schuchmann 2020a). Monitoring the vocal activity of both monitored species over the study period would have been difficult by applying traditional field surveys. We encourage researchers aiming to evaluate the impacts of the moon phases on bird vocal activity to use this technique. Previous studies found that birds with high retinal sensitivity are more sensitive to dim light than other species (Thomas et al. 2002; McNeil et al. 2005). Therefore, the use of autonomous recording units might be useful for evaluating the relationship between eye size and the impact of moonlight on vocal activity in a large number of bird species (e.g., nightjars, potoos, owls) recorded under the same environmental conditions. This technique would also be useful for considering the effects of other exogenous factors that may have a marked effect on the level of singing under the moon, such as air temperature, cloud cover or breeding status (e.g., Robbins 1981; Amrhein et al. 2002). In our study we were unable to control for cloud cover, which may have influenced the light level perceived by the nightjars and thus may have influenced our results.

In summary, our results show an interrelation between moon phase and vocal behavior in the two monitored species and that the relationship between moonlight and vocal activity in birds may differ among species and at a daily scale. Bird vocal behavior is usually related to individual quality (Catchpole & Slater 2008). Therefore, further research should evaluate whether high vocal activity under moonlight is related to the quality of individuals and mate attraction, and thus it may have implications at the fitness level (Catchpole & Slater 2008). Future studies should evaluate whether higher vocal activity of nightjars during full moon nights might be a related to mate attraction, rather than a consequence of increasing foraging activity. For such purpose, recording birds with known breeding status and the development of light autonomous recording units able to be mounted on GPS-marked individuals (see application in Yan et al. 2019) would be desirable, as a feasible solution to evaluate whether moonlight has a direct impact on vocal activity of nightjars or if it is a consequence of increasing foraging activity during full moon nights. Likewise, further research should also analyze, when possible, the consequences of higher vocal output during full moon nights on mate attraction, territorial defense and foraging behavior of these and other nightjars, to unravel whether changes in vocal activity in relation to the moon phase have consequences at the fitness level.

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DISCLOSURE STATEMENT

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SUPPLEMENTAL DATA

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