RESEARCH ARTICLE

Passive acoustic monitoring of the diel and annual vocal behavior of the Black and Gold Howler Monkey

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Abstract

Passive acoustic monitoring, when coupled with automated signal recognition software, allows researchers to perform simultaneous monitoring at large spatial and temporal scales. This technique has been widely used to monitor cetaceans, bats, birds, and anurans but rarely applied to monitor primates. Here, we evaluated the effectiveness of passive acoustic monitoring and automated signal recognition software for detecting the presence and monitoring the roaring behavior of the Black and Gold Howler Monkey (*Alouatta caraya*) over a complete annual cycle at one site in the Brazilian Pantanal. The diel pattern of roaring activity was unimodal, with high vocal activity around dawn. The howler monkey showed a clear seasonal pattern of roaring activity, with most of the roars detected during the wet season (74.9%, peak activity during November and December). The maximum vocal activity occurred during the period of maximum flowering and fruit production in the study area, suggesting a potential role of roaring in defending major feeding sites, which is in agreement with the findings of previous studies on the species. However, we cannot rule out the possibility that roaring may serve different purposes. Vocal activity was negatively associated with relative air humidity, which might be related to lower vocal activity on wetter and rainy days, while vocal activity was not related to minimum air temperature. Automated signal recognition software allowed us to detect the species in 89% of the recordings in which it was vocally active, but with a reduced time cost, since the time investment for data analyses was 2% of recording time. The good performance of the recognizer might be related to the long and loud roars of the howler monkey. Further research should be performed to evaluate the effectiveness of automated signal recognition for detecting the calls of different species of primates and under different environmental conditions.

KEYWORDS
Atelidae, autonomous recording unit, diel activity, mammal, primate, seasonality

1 | INTRODUCTION

In recent years, the emergence of and progress in passive acoustic monitoring have changed the way that vocally active wildlife species are monitored (Pijanowski et al., 2011; Shonfield & Bayne, 2017; Sugai et al., 2019). Among the most remarkable transformations resulting from passive acoustic monitoring is the possibility of studying cryptic and rare species (Miller et al., 2015; Pérez-Granados et al., 2018; Schroeder & McRae, 2020), as well as monitoring taxa at night and at sites that are difficult to access, such as tropical forests or oceans (Deichmann et al., 2017; Miller et al., 2015; Pérez-Granados & Schuchmann, 2020a; Willacy et al., 2015). Another great

advantage of passive acoustic monitoring is that this technique allows researchers to perform monitoring simultaneously at large spatial and temporal scales and therefore opens the door for unraveling ecological patterns that are difficult or impossible to assess using traditional field surveys (Sugai et al., 2019; Willacy et al., 2015). The employment of effective automated signal recognition software is paramount to analyzing long-term acoustic data sets (e.g., Kalan et al., 2015; Knight et al., 2017; Stowell et al., 2019). Despite the exponential increase in studies using passive acoustic monitoring, this technique has been mainly used to monitor cetaceans, bats, birds, and anurans, while its use for monitoring other vocally active taxa, such as nonflying mammals, has been limited (ca. 6% of the studies, see review for terrestrial wildlife in Sugai et al., 2019).

Among nonflying mammals, this technique has been applied to monitor wolves (Suter et al., 2017) and different species of marine mammals (Sousa-Lima et al., 2013; Todd et al., 2015) and primates (Enari et al., 2019; Heinicke et al., 2015). However, very few studies have proven the effectiveness of automated signal recognition software for detecting different primates (but see Aide et al., 2013; Heinicke et al., 2015; Kalan et al., 2015). Currently, approximately 60% of primate species are threatened with extinction, and 75% of them have declining populations (Estrada et al., 2017). Therefore, the use of automated software may contribute to the long-term monitoring of primates. Kalan et al. (2015) used automated signal recognition software to detect three species of primates in recordings collected over 6 months on the Ivory Coast and used that technique to assess the relationships between the vocal activity of the species and climatic variables. However, our current knowledge about the species and the circumstances for which passive acoustic monitoring can be employed to monitor primates is still limited, and there is more room for improvement. Indeed, the effectiveness of automated detection software for detecting primates seems to differ among species. For example, Heinicke et al. (2015) found that automated software performed well in detecting the calls of Diana Monkeys (*Cercopithecus diana*) and King Colobus Monkeys (*Colobus polykomos*; 32%–49% of the calls of both species were automatically detected), but it detected a very small proportion of Red Colobus (*Procolobus badius*) and Chimpanzee (*Pan troglodytes*) vocalizations (0%–11% of the calls of both species were automatically detected). The low detection rate of these latter species might be likely related to the short- and low-intensity calls in the case of the Red Colobus and to high variability among individuals for the Chimpanzee (Heinicke et al., 2015).

Howler monkeys (*Alouatta*, Atelidae) are the genus of primates with the broadest geographical distribution in the Neotropical region (10 species; Cortés-Ortiz et al., 2015; Groves, 2001). Howler monkeys exhibit a modified larynx and an enlarged hyoid bone that act as a resonance chamber to amplify their vocalizations (da Cunha et al., 2015). These modifications allow howler monkeys to utter potent, low-frequency roars that are considered the loudest vocalizations produced by a terrestrial mammal and that can be heard at distances >1 km (Baldwin & Baldwin, 1976; da Cunha et al., 2015; Whitehead, 1995). Howler monkeys usually concentrate their roaring behavior around dawn (Baldwin & Baldwin, 1976; da Cunha et al., 2015; Sekulic, 1982; Van Belle et al., 2013; Whitehead, 1995), although some species show a bimodal pattern of vocal activity, with a secondary peak of vocal activity around sunset (Aide et al., 2013; Chiarello, 1995; Cornick & Markowitz, 2002; da Cunha et al., 2015). Long-distance roars are used in intergroup communication, but there is no consensus about their function (Kitchen et al., 2015; Van Belle et al., 2013). Indeed, the function of roaring seems to differ among and within species according to variable socio-ecological contexts, such as food availability and population density (da Cunha & Byrne, 2006; Holzmann et al., 2012; Kitchen et al., 2015). A previous study has assessed the relationships between the vocal activity of howler monkeys and climatic predictors (Sekulic, 1982). However, additional investigations on the external variables that alter the vocal activity of howler monkeys might be useful for improving future survey designs so that surveys can be performed during periods of maximum detection probability, especially when monitoring in remote areas like Neotropical rainforests. Data collection employing standardized techniques over a large temporal scale, such as passive acoustic monitoring, may help advance our understanding of the function of roaring in howler monkeys (da Cunha & Byrne, 2006; Sekulic, 1982; Van Belle et al., 2014) and the relationships of roaring with climatic variables (Van Belle et al., 2013).

The Black and Gold Howler Monkey (*A. caraya*; BGHM hereinafter) is found in the rainforests of eastern Bolivia, southern Brazil, and northern Argentina. It is sexually dimorphic, and males have black hair, while females have a golden coloration, which gives the species its common name. BGHMs are folivores (ca. 60% of their diet) and frugivores (ca. 30%; Bicca-Marques & Calegaro-Marques, 1994), which makes them effective seed dispersers that play an important role in forest regeneration (Bravo, 2012). Like most *Alouatta* species, BGHMs roar in the early morning to define, defend, and claim their home territory (da Cunha & Byrne, 2006). However, there are no previous studies on seasonal changes of roaring behavior of the species at a long temporal scale. The roar of the BGHM can be heard from up to 4.8 km away (Covert, 2019). The species is cataloged as Least Concern according to the International Union for Conservation of Nature (IUCN; Fernandez-Duque et al., 2008), but its population is decreasing; thus, in some countries, such as Argentina, it is classified as Vulnerable (Fernandez-Duque et al., 2008; Oklander et al., 2019). According to the IUCN, more monitoring of its population trends is required to understand how habitat loss may affect the persistence of the species (Fernandez-Duque et al., 2008). In this sense, reliable long-term monitoring methods would be a useful tool for scientists and wildlife managers aiming to monitor the BGHM as well as other primates. The utterance of loud calls with little variability, even among regions (Holzmann & Areta, 2020), suggests that automated signal recognition should be a reliable tool for monitoring the BGHM (Heinicke et al., 2015). Indeed, a previous assessment using automated detection of the calls of the Mantled Howler Monkey (*Alouatta palliata*) showed that the species was automatically detected in 35 of the 43 recordings (81.3%) in which it was present (Aide et al., 2013).

Here, we used passive acoustic monitoring to monitor the vocal behavior of the BGHM over a complete annual cycle in the Brazilian Pantanal. We aimed to (1) evaluate the use of passive acoustic monitoring and automated signal recognition software for monitoring the presence of the BGHM; (2) describe and analyze the diel and seasonal patterns of vocal activity of the species to gain insights into its ecology and to identify the hours and months with the highest vocal activity; and (3) evaluate the relationships between climatic predictors (daily minimum air temperature, relative air humidity, and rainfall) and the vocal activity of the BGHM.

2 | METHODS

2.1 | Study area

The study area was located in the northeastern part of the Brazilian Pantanal close to the SESC Pantanal (Pantanal Matogrossense, Poconé municipality, Mato Grosso, Brazil; 16°30′S, 56°25′W; Figure S1). The monitored area was in the floodplain of the Cuiabá River, which is one of the main tributaries of the Paraguay River. The Pantanal is the largest wetland in the world (Por, 1992), and it is seasonally inundated for half of the year (from October to April) by the flood pulse increase of the Paraguay River, while the dry season extends from May to September (Junk et al., 2006). The dominant vegetation in the study area includes a mosaic of different forest formations and savannas (Junk et al., 2006). More detailed information about the vegetation communities in the study area can be found in de Deus et al. (2020). The climate in the region is tropical and humid, with an average annual rainfall between 1000 and 1500 mm and a mean annual temperature of approximately 24°C. During the monitored annual cycle, the total annual rainfall in the study area was 1131 mm, and the rainfall regime followed the typical seasonal pattern, with 1025 mm (90.6% of the total) accumulating during the wet season (October–April). The mean annual temperature during the studied year was 25.5°C.

2.2 | Acoustic monitoring

We performed passive acoustic monitoring at six acoustic monitoring stations separated by between 573 and 3750 m (Figure S1). Due to the short distance between stations and because previous studies have pointed out that the roar of the BGHM is audible at a distance >4 km (Covert, 2019), we opted to analyze data from a single acoustic monitoring station to avoid recording the same group of monkeys at two different stations. We selected the station with the largest number of detections of the BGHM, after analyzing the recordings collected at the six stations during November and December (the months with the highest vocal activity, see Section 3). Recordings were analyzed using the same settings and software as described in Section 2.3 section.

We deployed one Song Meter SM2 recorder (Wildlife Acoustics, www.wildlifeacoustics.com) that operated daily from 8 June 2015 to 31 May 2016 and therefore covered almost a whole annual cycle. The recorder was programmed to record (in stereo and .wav format) the first 15 min of each hour (24 h) with the following parameters: hourly time, GMT −4; sampling rate, 48 kHz; and resolution, 16 bits per sample. The device was powered by four 1.5 V alkaline batteries (Duracell MN13000; ~160 h autonomy) and checked weekly to download data and change batteries. A total of 8044 15-min recordings were collected. This study is part of the biodiversity monitoring project Sounds of the Pantanal—The Pantanal Automated Acoustic Biodiversity Monitoring of INAU, Cuiabá, Mato Grosso, Brazil, which was conducted according to Brazilian laws and under SISBIO permit no. 39095 (KLS). The study also agreed with the Principles for the Ethical Treatment of Nonhuman Primates of the American Society of Primatologists (American Society of Primatologists, 2001).

2.3 | Acoustic data analyses

The left channel of the recordings was scanned with Kaleidoscope Pro 5.1.9h (Wildlife Acoustics, www.wildlifeacoustics.com). Kaleidoscope Pro is an automated signal recognition software able to scan recordings for candidate sounds based on the following signal parameters: minimum and maximum frequency ranges (Hz), minimum and maximum times of detection (s), and a maximum intersyllable gap (s). The roar of the BGHM (Figure 1) shows limited geographic variation (Holzmann & Areta, 2020), and thus, we used recent descriptions of the roar of the BGHM to select the best signal parameters (da Cunha et al., 2015; Holzmann & Areta 2020; see a similar approximation in Pérez-Granados et al., 2020). The signal parameters input into Kaleidoscope were as follows: minimum and maximum frequency range (100–800 Hz), minimum and maximum lengths of detection (0.7–20 s), and maximum intersyllable gap (0.05 s). The maximum intersyllable gap is the maximum allowable gap between candidate sounds; thus, roars separated by <0.05 s were considered to be from the same group of monkeys. The signal
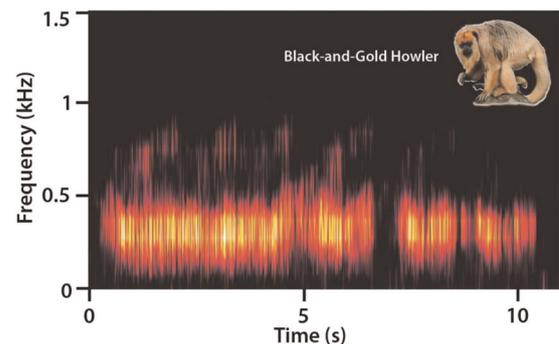

FIGURE 1 Spectrogram of a typical roar of the Black and Gold Howler Monkey recorded in the Brazilian Pantanal. Frequency range is expressed as kHz

parameters were extended in relation to the description of the roar of the species, which should maximize the possibility of detecting weaker roars (see a similar approximation in Pérez-Granados et al., 2020). Kaleidoscope identified a total of 39,021 candidate sounds that matched the signal parameters. Every candidate sound was visually and/or acoustically checked by the same observer (Cristian Pérez-Granados) to verify the detection of the species. We opted to use detection/no detection per recording as a response variable rather than the number of roars per recording, since the mean duration of roaring bouts lasts several minutes in howler monkeys (Cornick & Markowitz, 2002; Van Belle et al., 2013), including the BGHM (Cristian Pérez-Granados personal observation). We considered the species as detected when at least one roar was detected in a recording.

To assess the performance of the analyses performed with Kaleidoscope, we estimated the recall rate of the recognizer (Knight et al., 2017) by dividing the number of recordings in which the BGHM was detected by Kaleidoscope by the total number of recordings in which the species was vocally active. The number of recordings in which the BGHM was vocally active was estimated by visually and acoustically checking the spectrograms of a selected number of recordings, always by the same experienced observer (Cristian Pérez-Granados). A total of 100 15-min recordings were checked. The recordings were randomly selected from those made between October and January and between 5 a.m. and 6 a.m. to increase the probability of detecting the species.

2.4 | Environmental variables

Weather data were collected from a weather station located in the study area at a distance of 955 m from the acoustic monitoring station (see location in Figure S1). The following daily information was collected during the study period: daily maximum, mean (24 h period) and minimum air temperatures (°C), accumulated daily rainfall (mm), and mean (24 h period) relative air humidity.

2.5 | Statistical analyses

To identify the months with significantly high roaring activity of the BGHM, we fitted a generalized linear model (GLM; Poisson error structure). In the model, the daily number of recordings in which the species was detected was introduced as the response variable and month (seven levels) as a factor. The periods June–August 2015 and April–May 2016 were not included in the analyses due to low vocal activity (see Section 3). Thus, we reduced the number of levels in the factor analyzed and the number of zeros in our analyses, thereby improving our analytical approach. A Tukey's post hoc test was performed to identify the month with the highest roaring activity.

The potential collinearity among climatic variables was reduced by removing variables whose Spearman correlation coefficients were higher than 0.7 (Dormann et al., 2013). Daily mean air temperature

and daily maximum air temperature were highly positively correlated (Spearman correlation coefficient of 0.85). Likewise, daily maximum air temperature was highly and negatively correlated with daily mean relative air humidity (Spearman correlation coefficient of −0.89). Therefore, we decided to remove daily mean air temperature and daily maximum air temperature from further analyses because we expected to find a greater impact of relative air humidity on the vocal behavior of the species, since mean and maximum air temperatures are reached during the central hours of the day when the BGHM is almost vocally inactive. Daily minimum air temperature, usually reached at dawn, should be the best temperature variable for assessing the relationship between BGHM vocal activity and air temperature. To assess the impact of climatic variables on the vocal activity of the species, we fitted a logistic regression using the daily occurrence (detected/undetected) of vocalizations as a response variable and climatic variables (minimum air temperature, relative air humidity, and daily rainfall) as covariates. We focused our analyses on the four consecutive months with the highest vocal activity of the species (October–January, see a similar approximation in Pérez-Granados & Schuchmann, 2020b). All statistical analyses were performed in R 3.6.2 (R Development Core Team, 2019), using the package "multcomp" (Hothorn et al., 2008) for post hoc comparison tests.

3 | RESULTS

The time required to analyze the data collected (2011 h) was approximately 42 working hours, including time for scanning recordings (9 h, automatically done by Kaleidoscope Pro) and manually reviewing candidate sounds (33 h). The BGHM was detected in 211 recordings and on 148 monitoring days (41.1% of the monitored days), with a mean value of 0.10 detections per hour of monitoring (211 detections in 2011 recording hours). The recall rate of the recognizer was 89.2%, since the species' presence was automatically detected in 33 of the 37 recordings in which it was annotated among the 100 recordings in the validation data set. Although the candidate sounds that did not belong to the BGHM were not labeled, most of these sounds were bird vocalizations of common species that sang at the same frequency as the BGHM, mainly the Chaco Chachalaca (*Ortalis canicollis*) and the White-tipped Dove (*Leptotila verreauxi*).

3.1 | Diel activity pattern

The diel activity pattern of the BGHM in the Brazilian Pantanal was concentrated around dawn, with 76.4% of the detections made between 5 a.m. and 7 a.m. (Figure 2). The species was detected during all hours of the day except for two (9 p.m. and 10 p.m.; see hourly roar production in Table S1). The hour with the highest vocal activity was 6 a.m., with 71 detections (33.5% with respect to the total).
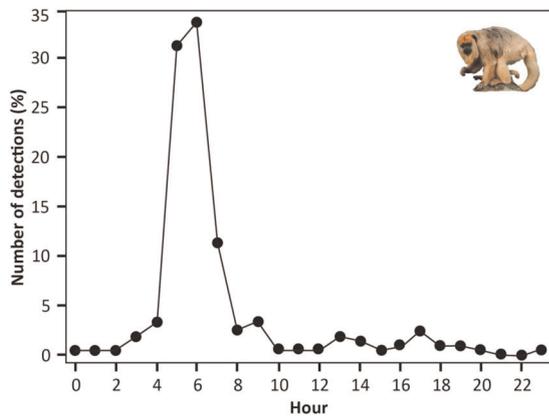
FIGURE 2 Diel roaring activity pattern of the Black and Gold Howler Monkey in the Brazilian Pantanal. Roaring activity was monitored using autonomous recording units from June 8, 2015 to May 31, 2016 at one site. The diel pattern refers to the % of detections (respect to the total) in which the species was detected during each recording period. Hours are expressed in winter local time (UTC-4)

TABLE 1 Estimates from a generalized linear model testing the effect of month on the roaring activity of the Black and Gold Howler Monkey in the Brazilian Pantanal

	Estimate	Std. error	Z value	p
(Intercept)	−1.204	0.333	−3.61	<0.001
October	0.714	0.405	1.77	.077
November	1.386	0.373	3.72	<0.001
December	1.381	0.372	3.71	<0.001
January	0.660	0.408	1.62	.106
February	0.881	0.398	2.21	.027
March	0.989	0.389	2.54	.011

Note: Roaring activity was monitored using autonomous recording units from June 8, 2015 to May 31, 2016 at one site, although the analysis was restricted to the period between September 2015 and March 2016.

greatest roar production (34.6% with respect to the total, see Figure S2).

3.2 | Seasonal activity pattern

The BGHM was vocally active throughout the year but showed higher vocal activity during the wet season (October–April, 74.9% with respect to the total number of detections) than during the dry season (May–September, 25.1% of the total; Figure 3 and see monthly roar production in Table S2). The peak vocal activity of the BGHM was observed between October and March, a period during which 73.9% of the detections occurred (Figure 3). The vocal activity of the BGHM varied seasonally (Table 1), and according to Tukey's post hoc test, November and December were the months with the
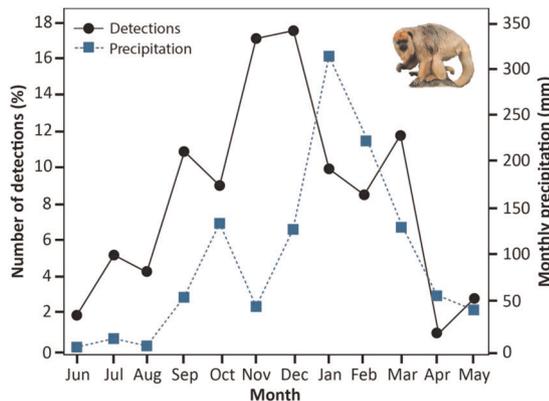
3.3 | Environmental variables

Logistic regression revealed that the vocal activity of the BGHM was significantly associated with daily relative air humidity (Table 2), with the species being more vocally active on days with a low relative air humidity (Figure 4). However, the daily occurrence of species calling was not related to daily minimum air temperature or daily rainfall (Table 2).

4 | DISCUSSION

In this study, we describe and analyze the vocal behavior of the BGHM over a complete annual cycle in the Brazilian Pantanal and validate the use of passive acoustic monitoring coupled with automated signal recognition software as a useful tool for detecting the presence and monitoring the vocal behavior of the species. The vocal activity of the BGHM varied with the time of day, the time of season, and relative air humidity. We are aware that we performed acoustic monitoring just at one site and therefore some of our generalizations may require further validation to provide more robust conclusions about seasonal changes of roaring behavior of the BGHW. Similarly, we were unable to control for group size or number of individuals roaring around recorders, so future studies being able to control for such covariates may provide a better understanding about the roaring behavior of the species. We obtained a mean value of 0.10 detections of presence per hour of monitoring (211 detections in 2011 recording hours). This estimate seemed low according to the famous roaring behavior of howler monkeys (reviewed by da Cunha et al., 2015). However, our estimate is exactly the same as that previously described by da Cunha and Byrne (2006) when performing long-term monitoring surveys of the BGHM in the Brazilian

FIGURE 3 Seasonal roaring activity pattern of the Black and Gold Howler Monkey in the Brazilian Pantanal. Roaring activity was monitored using autonomous recording units from June 8, 2015 to May 31, 2016 at one site. The seasonal pattern is expressed as the % of detections (respect to the total) in which the species was detected per month (black circles). The monthly accumulated rainfall (blue squares) is shown on the right *Y*-axis

TABLE 2 Summary results of a logistic regression performed to assess the relationships between the daily occurrence (detected/undetected) of vocalizations of the Black and Gold Howler Monkey and climatic variables (daily minimum air temperature, relative air humidity, and daily rainfall) in Pantanal Matogrossense (Brazil)

	Estimate	Std. error	Z value	p
(Intercept)	5.491	3.139	1.744	.088
Minimum air temperature (°C)	0.016	0.133	0.122	.903
Air humidity (%)	−0.071	0.034	−2.076	.038
Daily rainfall (mm)	−0.042	0.028	−1.494	.135

Note: Roaring activity was monitored using autonomous recording units from June 8, 2015 to May 31, 2016 at one site, although the analysis was restricted to the period between October 1, 2015 and January 31, 2016.

Pantanal (219 detections in 2250 observation hours, 0.10 detections per hour of monitoring). Likewise, our estimate is comparable to estimates obtained in long-term monitoring programs of other howler monkeys, such as the Brown Howler Monkey (*Alouatta fusca*, 47 detections in 730.5 observation hours, 0.06 detections per hour of monitoring; Chiarello, 1995) and the Black Howler Monkey (*A. pigra*, 359 detections in 2523 observation hours, 0.14 detections per hour of monitoring; Van Belle et al., 2013). Holzmann et al. (2012) also monitored the BGHM and detected 34 roars in 145 days (23.4% of the monitored days), a lower value than our estimate. However, Holzmann et al. (2012) did not provide specific details about the number of hours monitored every day; thus, direct comparisons cannot be made. Despite the different methodologies employed, our findings suggest that passive acoustic monitoring might be a reliable
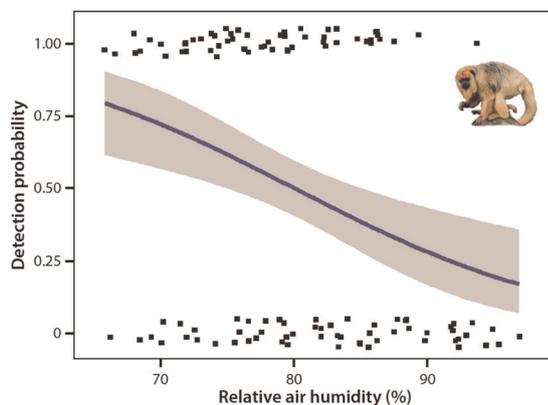

FIGURE 4 Probability of detecting the presence of the Black and Gold Howler Monkey in the Brazilian Pantanal as a function of daily relative air humidity. Roaring activity was monitored using autonomous recording units from June 8, 2015 to May 31, 2016 at one site, although the analysis was restricted to the period between October 1, 2015 and January 31, 2016. The blue line shows the estimates of logistic regressions performed using the daily detection/no detection of the species (black squares) as the response variable and relative air humidity as the predictor variable. The 95% confidence intervals are shown in gray

tool for monitoring the spontaneous vocal behavior of howler monkeys. In our study, we were unable to discern between the days on which the BGHM decided not to vocalize and those on which the species might have been far beyond the effective detection radius of the recorder and thus may have produced vocalizations that went undetected. A potential solution for avoiding such missed detection might be the deployment of spatially dispersed microphone arrays, which may allow researchers to track the spatial movements of the monitored groups (reviewed by Blumstein et al., 2011).

The BGHM concentrated its vocal activity around dawn, following the typical pattern described for the genus (Baldwin & Baldwin, 1976; da Cunha et al., 2015; Sekulic, 1982; Van Belle et al., 2013; Whitehead, 1995). The diel pattern found in our study is fully in agreement with that previously described for other populations of the BGHM in the Brazilian Pantanal (da Cunha & Byrne, 2006). However, several howler monkeys species show a bimodal pattern of vocal activity, with a secondary peak of vocal activity around sunset (Aide et al., 2013; Chiarello, 1995; Cornick & Markowitz, 2002; da Cunha et al., 2015). The reason for a secondary afternoon peak in some other species or populations is still unknown (da Cunha et al., 2015). The low vocal activity of howler monkeys during the day, especially at midday, has been related to the long resting and sleeping periods described for the genus (Cornick & Markowitz, 2002; Milton, 1980). The BGHM was vocally active throughout the day, since it was detected in 22 of the 24 recording periods. Nonetheless, vocal activity outside the dawn period was very limited, and these sporadic roars might be related to direct encounters with neighboring groups that may occur randomly during the day (Van Belle et al., 2013).

The vocal activity of the BGHM showed clear seasonality, with 74% of the roars uttered during the wet season. This result is in disagreement with that from a previous study on the Brown Howler Monkey in southeastern Brazil in which the number of roars during the dry season was similar to that during the wet season (Chiarello, 1995). The vocal activity increased from October onward with the onset of rains (Figure 3). The early wet season is a period with high leaf and fruit production in the Brazilian Pantanal (Ragusa-Netto, 2004; Ragusa-Netto & Silva, 2007). The higher vocal activity during the fruiting season suggests that roaring in the BGHM might be related to the defense of major feeding sites, as has been previously suggested for a large number of howler monkeys (Chiarello, 1995; Hopkins, 2013; Sekulic, 1982; Van Belle et al., 2014). Our findings are consistent with the main conclusion reached by da Cunha and Byrne (2006) when studying the function of roaring in the BGHM: that roaring in the BGHM "apparently functions in intergroup competition, by regulating use of space." However, we were unable to assess the relationship between vocal activity and reproduction of the species to test other plausible hypotheses, such as the mate defense hypothesis and the infant avoidance hypothesis (reviewed by Kitchen et al., 2015). Further research involving the collection of observational data and/or the use of playback tests is required to provide useful insights into the function of roaring in the BGHM (but see da Cunha & Byrne, 2006; Holzmann et al., 2012).

Here, we provide one of the first assessments of the relationships between climatic variables and the daily vocal activity of howler monkeys (but see Sekulic, 1982). We found that the daily occurrence of vocalizations of the BGHM was negatively related to air humidity. This result was surprising since we did not expect to find a relationship between the two variables. Sound attenuation in forests is increased under high humidity (Fricke, 1984; Marten et al., 1977), which may partly explain the negative relationship found between the vocal activity of the BGHM and relative air humidity. This suggests that the BGHM may choose to call on days with lower air humidity to communicate more efficiently. Nonetheless, the negative relationship found between the vocal activity of the BGHM and relative air humidity might be explained by the high correlation between relative air humidity and daily rainfall (Spearman correlation coefficient of 0.64; $p < .0001$). Indeed, when we removed relative air humidity from our analyses, the negative relationship between the vocal activity of the BGHM and daily rainfall became significant (see Table S3). Sound transmission on rainy days might be decreased due to the masking effect of rain (Brumm & Slabbekoorn, 2005; Mennill, 2014), which may partly explain why the BGHM may decide to vocalize less on wetter/rainy days. This result is in agreement with previous studies showing that the vocal activity of two gibbon species (*Hylobates* genus) was negatively affected by rain (Cheyne, 2008; Clink et al., 2020). However, a previous study assessing the relationship between daily rainfall and vocal activity in three primates did not find a significant relationship between these variables for any of the species (Kalan et al., 2015). The minimum air temperature was not related to the vocal activity of the BGHM. This result is in agreement with that obtained by Sekulic (1982) for the Red Howler Monkey (*Alouatta seniculus*) during the wet season. However, Sekulic (1982) found a significant positive relationship between roaring activity and temperature in the dry season. Our analyses were restricted to the 4 consecutive months of maximum vocal activity that occurred during the wet (rainy) season; therefore, our results are in agreement with those observed in other howler monkeys. Similarly, Kalan et al. (2015) did not find a relationship between air temperature and vocal activity for two of three primates monitored. Nonetheless, the vocal activity of the Diana Monkey was positively and significantly related to mean air temperature, which suggests that the impact of climatic conditions may differ among sympatric species. Further research is required to improve our knowledge about the relationships between primate vocal activity and climatic predictors.

Our results provide evidence of the effectiveness of employing automated signal recognition software for detecting the presence of primates and nonflying mammals, a group of taxa under monitored using this technique (Sugai et al., 2019). This technique might be useful for monitoring such a threatened group of vertebrates (Estrada et al., 2017). Kaleidoscope Pro was able to automatically detect the presence of the species in 89.2% of the recordings in which it was present (33 of 37 recordings in the validation data set), a recall rate very similar to that previously obtained for four bird species using the same software (range 74%–85%; Abrahams, 2019; Pérez-Granados & Schuchmann, 2020b, 2020c). The recall rate of the recognizer obtained in that study is similar to that obtained by the algorithm developed by Aide et al. (2013), which automatically detected 81.3% of the calls of the Mantled Howler Monkey in the validation data set (35 of 43 calls detected). However, a previous study employing automated detection of calls of four species of primates obtained much lower recall rates, which ranged between 0% and 49% (Heinicke et al., 2015). Heinicke et al. (2015) suggested that the low recall rate obtained for some of the species included in their study might have been related to the short duration and low sound intensity of their calls (Red Colobus) and to the large call variability among individuals (Chimpanzee). Our recall rate refers to the percentage of recordings that the species was automatically detected, while previous studies of primates used number of calls. Although this precludes us from making direct comparisons, our findings, together with those obtained by Aide et al. (2013), provide strong evidence of the effectiveness of automated signal recognition software for detecting the presence of howler monkeys. The effectiveness of automated software for monitoring howler monkeys might be partly explained by the long and loud calls of the genus (da Cunha et al., 2015), as well as limited variability of calls among populations (Holzmann & Areta 2020). Indeed, the few instances when the BGHM was detected by the observer but not by Kaleidoscope Pro, in our study, were cases in which the species was presumably calling at long distances from the recorder, according to the low sound pressure level of these calls detected in the spectrograms (Cristian Pérez-Granados personal observation). The weak pattern shown on the spectrograms might have reduced the ability of Kaleidoscope Pro to identify the long-distance roars as candidate sounds. We were unable to estimate the precision of the recognizer (i.e., number of BGHW roars divided by the total number of candidate sounds; Knight et al., 2017) since our approach aimed to rapidly process the database (once the species was detected within a recording no more candidate sounds were checked). This recognizer index should be included in future studies whenever possible. Automated detection of calls was performed in 2.1% of the total time required to listen to the recordings. This estimate clearly suggests that automated recognition software can be used to process recordings in a timely manner. The proportion of time invested in automated detection of calls of the BGHM was very similar to that reported by Heinicke et al. (2015) for three different primates (3.5%).

Here, we employed and validated the use of passive acoustic monitoring, coupled with automated signal recognition software, to detect the presence and study the diel and seasonal changes in the vocal activity of the BGHM. We hope that our results will encourage scientists and managers to consider passive acoustic monitoring as a reliable tool for monitoring primates, a group of taxa with more than 60% of their species threatened by extinction (Estrada et al., 2017; Mittermeier et al., 2009). This tool might be especially useful for detecting species presence or studying diel activity patterns of monitored species. However, its utility for behavioral studies might be somewhat reduced due to the lack of field observations under the circumstances relevant for species vocalizations, which are needed to determine the reasons for and the functions of wildlife vocal

activity. Therefore, passive acoustic monitoring cannot replace traditional field surveys for monitoring primates in several types of projects, but a combined method using sound recorders (e.g., monitoring the species' presence at potential sites and long-term surveys) and traditional field surveys (e.g., characterizing group composition and breeding status) might be a promising method for future survey designs.

AUTHOR CONTRIBUTIONS

Cristian Pérez-Granados: conceptualization (equal); data curation (equal); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (lead); project administration (supporting); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Karl-Ludwig Schuchmann**: conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the analyses reported in this article are available in the following link: https://figshare.com/s/8250550be8d25cd5f07a. DOI: 10.6084/m9.figshare.13235201

PEER REVIEW

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