Bioacoustics

The International Journal of Animal Sound and its Recording

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tbio20

Vocalisations of the Greater Rhea (*Rhea americana*): an allegedly silent ratite

Cristian Pérez-Granados & Karl-L. Schuchmann

To cite this article: Cristian Pérez-Granados & Karl-L. Schuchmann (2021) Vocalisations of the Greater Rhea (*Rhea americana*): an allegedly silent ratite, Bioacoustics, 30:5, 564-574, DOI: 10.1080/09524622.2020.1821399

To link to this article: https://doi.org/10.1080/09524622.2020.1821399

BIOACOUSTICS
2021, VOL. 30, NO. 5, 564–574
https://doi.org/10.1080/09524622.2020.1821399

Vocalisations of the Greater Rhea (*Rhea americana*): an allegedly silent ratite

Cristian Pérez-Granados [a,b] and Karl-L. Schuchmann [a,c,d]

[a]National Institute for Science and Technology in Wetlands (INAU), Federal University of Mato Grosso (UFMT), Computational Bioacoustics Research Unit (CO.BRA), Cuiabá, Brazil; [b]Postgraduate Program in Ecology and Biodiversity Conservation, Institute of Biosciences, Federal University of Mato Grosso, Cuiabá, Brazil; [c]Ornithology, Zoological Research Museum A. Koenig (ZFMK), Bonn, Germany; [d]Postgraduate Program in Zoology, Institute of Biosciences, Federal University of Mato Grosso, Cuiabá, Brazil

ABSTRACT

Our current knowledge of the vocal behaviour of Palaeognathae is limited, although it may increase our understanding of the evolution of avian vocal behaviour. The Greater Rhea (*Rhea americana*) has a complex syrinx, and males produce guttural sounds during the courtship display, which makes this species an interesting model to study vocal behaviour in ratites. We recorded a group of Greater Rheas living in semi-captive conditions at the zoo of the UFMT for eight days. A total of 749 booming calls were detected. The vocal activity of the Greater Rhea was maximum during the first four hours after sunrise, with a second peak before sunset. The species showed nocturnal vocal activity, as also found in a recent study on a diurnal tinamou. The number of vocalising birds during the recording period was unknown, and our data were collected during a restricted time window. Our results suggest that acoustic communication and nocturnal activity of the species might be more relevant than previously described. Passive acoustic monitoring may have further implications for the continued study of vocal activity in ratites. Further research should examine whether the vocal behaviour and nocturnal vocal activity of the Greater Rhea are also important in wild individuals.

ARTICLE HISTORY
Received 29 June 2020
Accepted 2 September 2020

KEYWORDS
Boom; captive; Neotropics; nocturnal; Palaeognathae; Rheida

Introduction

Birds use acoustic signals as their main communication system, and these signals play an important role in mate attraction and territorial defence and maintain group contact or signalling about food or danger (Catchpole and Slater 2008). Studies on the vocalisations in Palaeognathae, the most ancient lineage of birds, are very scarce despite their interesting basal evolutionary position (but see Corfield et al. 2008; Digby et al. 2014; Pérez-Granados et al. 2020). The Palaeognathae is a monophyletic group of birds composed of the flightless ratites and the volant tinamous (Johnston 2011). The ratites are large terrestrial herbivores that include rheas, ostriches, emus, cassowaries, and kiwis (Davies 2002). Among them, the Greater Rhea (*Rhea americana*, hereafter rhea) is the largest bird of South America and

---

CONTACT Cristian Pérez-Granados ✉ perezgranadosc@hotmail.com
Supplemental data for this article can be accessed here.

is native to the Chaco and the Cerrado of northeast Argentina, east Bolivia, Brazil (south of the Amazon Valley), Paraguay and Uruguay (Hodes 2020). With the exception of the kiwis, the ratites are diurnal and silent birds for which nocturnal and vocal activity have been rarely reported (Davies 2002, see diel activity of the rhea in Mercolli and Yanosky 1994; Sales et al. 2000; Oliveira-Santos and Tizianel 2008).

The rhea male is polygamous, and it is the only sex that incubates the eggs and takes care of the nestlings (Davies 2002; Fernández and Reboreda 2003). The nestlings are vocally active and may employ several context-specific calls but lose most of their ability to vocalise a few weeks after hatching due to trachea deterioration (Beaver 1978), which makes adult rheas very silent (Sick 1993; Hodes 2020). However, during the courtship display, rhea males produce a low-pitched, intense guttural sound composed of two syllables that can be audible at great distances (>1 km, Codenotti and Alvarez 2001; Hodes 2020, Fig. 1). Picasso and Carril (2013) stated that the syrinx, the organ responsible for producing vocalisations in birds, has a more complex morphology in the rhea than that in other Palaeognathae. However, despite its complex syrinx and the known vocalisations of the species, the vocal behaviour of the rhea has been little studied (see Mercolli and Yanosky 1994). It is an interesting species to study and may contribute to a better understanding of the evolution of vocal behaviour in birds (Corfield et al. 2008; Picasso and Carril 2013).

Here, we employed passive acoustic monitoring coupled with automated signal recognition software to create a thorough description of the vocalisation and the vocal behaviour of the rhea. We aimed to (1) assess the effectiveness of passive acoustic monitoring for monitoring the vocal behaviour of the rhea, (2) perform a detailed description of the vocalisation (booming call) of the species, and (3) describe the diel pattern of booming activity of the rhea.

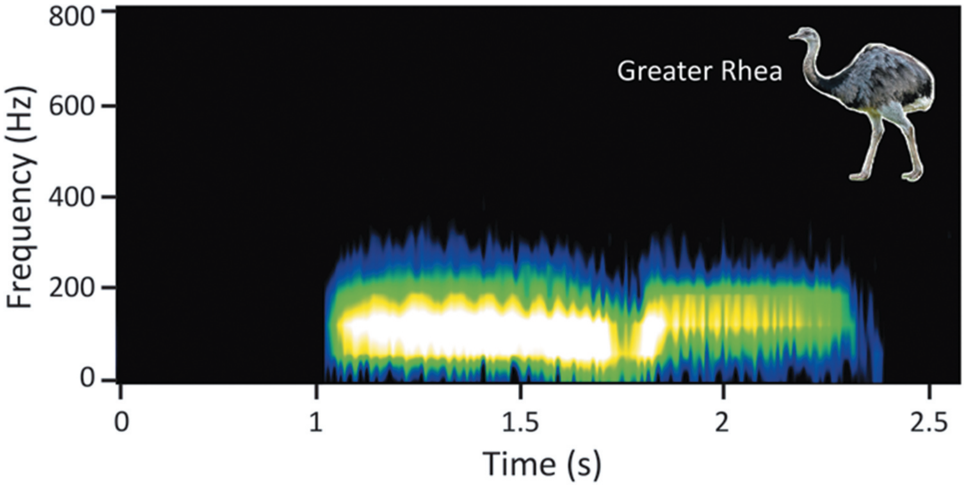

Figure 1. Audiospectrogram (frequency range, Hz) of the booming call of a Greater Rhea (*Rhea americana*) recorded on 30 July 2019 at UFMT Zoo (Cuiabá, Mato Grosso, Brazil). The booming call was recorded using a Song Meter SM2 at 6:37 a.m. The figure was created using Raven Pro 1.5 and following the same configuration as described in the methods (Jet Black color scheme).

Material and methods

Study area

The study was carried out at the zoo of the Federal University of Mato Grosso (UFMT), which has an extension of 12 ha and is located within the campus of the UFMT in Cuiabá (Cuiabá, Mato Grosso, Brazil; 15°36′26″ S, 56°03′55″ W). The study area was located at the lake in the zoo, where a group of three adult males and eight adult females lived in a semi-captive area (Navarro and Martella 2002) in an enclosed area of 2 ha, which was shared with a small group of capybaras (*Hydrochaeris hydrochaeris*) and Brazilian tapirs (*Tapirus terrestris*) (see Supplemental Material S1). The lake is commonly used by wild birds for feeding and roosting, such as Black-bellied Whistling Ducks (*Dendrocygna autumnalis*), Wood Storks (*Mycteria americana*), and Great Egrets (*Ardea alba*), among others. In previous years, the species attempted to breed with some rhea females laying their eggs on nests built by the male, although the reproductive cycle was artificially interrupted. 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.

Acoustic recording

We placed one Song Meter SM2 recorder (Wildlife Acoustics, USA, www.wildlifeacoustics.com) close to the middle of the lake at 3 m height attached to trees (see Supplemental Material S2). Previous studies have stated that the effective detection radius of the Song Meter SM2 recorder is approximately 150–160 m (Rempel et al. 2013; Pérez-Granados et al. 2019a). The distance at which recorders are able to record bird vocalisations varies among studies according to habitat type and main frequency of bird vocalisations (Yip et al. 2017). However, due to low-frequency sounds uttered by the rhea and the open habitat of the surveyed area (see Supplemental Material S1), most of the booming calls uttered within the enclosed area should have been detected. The recorder was programmed to record continuously (files of 30 min) in stereo and .wav format from 28 July to 4 August 2019 and was configured with a sampling rate of 48 kHz and a resolution of 16 bits per sample. The monitoring period corresponded to the main mating period of the species in southern Brazil (Codenotti and Alvarez 2001; de Azevedo et al. 2010). The zoo has been closed to the general public since March 2019, and therefore vocal behaviour of the rhea should not have been biased because of the presence of visitors.

Acoustic data analyses

The left channel of the recordings was analysed using Kaleidoscope Pro 5.1.9 automated signal recognition software (Wildlife Acoustics, www.wildlifeacoustics.com). Kaleidoscope is able to detect a target signal from the signal parameters introduced. The signal parameters introduced for detecting the GR vocalisations were as follows: minimum and maximum frequency range of 0 and 500 Hz, respectively; minimum and maximum length of detection of 0.7 and 3 s, respectively; maximum inter-syllable gap of 1 s and maximum distance from the cluster centre of 2.0. The last parameter ranges from 0 to 2 and has an impact on the number of events detected. The larger the value of this parameter, the larger the number of events detected by Kaleidoscope, including correctly and misclassified signals (see Pérez-Granados et al. 2020 for a quantitative analysis, also using a ratite as the study model, of the number calls detected and the precision of a recogniser using variable values of the maximum distance from the cluster centre parameter). Kaleidoscope reported a series of candidate sounds that match the signal parameters introduced. All candidate sounds were visually and/or acoustically checked by the same observer (GPG) to remove misclassified events.

To evaluate the effectiveness of passive acoustic monitoring when coupled with automated signal recognition software, we estimated the recall rate of the recogniser, which was obtained by dividing the total number of rhea booming calls detected by Kaleidoscope by the total number of booming calls within the recordings (see complete theory in Knight et al. 2017). The number of booming calls within the recordings was annotated after visually and acoustically checking 45 30-min recordings (22.5 hours) from the two following categories: A) 30 recordings randomly selected from those recorded between 5 a.m. and 10 a.m (period of maximum booming activity of the species); and B) 15 recordings randomly selected from those made between 11 a.m and 4 a.m (afternoon and nocturnal recordings). Recordings were reviewed blind with respect to the date of recording and whether the species had been detected by Kaleidoscope.

Booming call measurement

When checking the candidate sounds in Kaleidoscope, a total of 40 high-quality booming calls (no background noise, no rain, no wind) were labelled. The acoustic parameters of the 40 booming calls were measured using Raven Pro 1.5 software (Bioacoustic Research Program 2014) with the following configuration: Hamming window function; 72% brightness; 80% contrast; 512 point DFT size, and 50% time grid overlap. The following spectral traits were measured from spectrograms: dominant frequency (with the peak frequency measurement function); low and high frequency (frequency 5% and frequency 95% functions) and bandwidth (bandwidth 90% function). The booming call duration was measured from the oscillogram. We did not include the description of the booming rate (number of booming calls per unit of time) since we could not be sure about whether the recorded booming calls were uttered by the same or different males. Acoustical measurements are presented as the mean ± standard deviation and the range (minimum and maximum values for all booming calls) for all booming calls pooled.

Statistical analyses

To assess how constant the vocal activity of the rhea was during the monitored period, we created curves of the coefficient of variation (Reed et al. 2002) (CV hereafter) of the daily booming rate for all possible combinations from 1 to 7 monitoring days (see complete theory in Pérez-Granados et al. 2019b). To obtain all possible combinations of monitoring days, we used the package ‘gtools’ (Warnes et al. 2018) in R 3.6.2 (R Development Core Team 2019).

Results

A total of 3,450 candidate sounds were found by Kaleidoscope Pro, of which 749 were classified as booming calls of the rhea. The species was detected on the eight monitored days with a mean daily number of calls detected of 93.6 calls. The recall rate of the recogniser was 86.9%, since it was able to detect 153 of the 176 booming calls annotated in the 45 recordings of the validation data set.

Booming call of the Greater Rhea

The booming call of the rhea had a mean duration of 1.017 ± 0.149 s (0.743–1.315) and was uttered in a narrow, low-frequency band (Fig. 1). The dominant frequency was 123.4 ± 9.9 Hz (62.5–125), while the lowest and highest frequencies were 62.5 Hz (in all cases) and 176.5 ± 30.6 Hz (125–187.5), respectively. The mean bandwidth of the booming call was 114.1 ± 24.1 Hz (62.5–125).

Vocal behaviour

The diel pattern of the booming activity of the rhea showed a bimodal pattern, with the first peak of activity in the first hours before and after sunrise, since 43.6% of the total number of booming calls (N = 311) were detected between 6 a.m. and 9 a.m. (Fig. 2). A second peak of booming activity occurred between 2 and 4 p.m., when 26.9% of the booming calls (N = 204) were detected (Fig. 2). The species vocalised throughout the day and even showed nocturnal booming activity, with 7.2% of the booming calls (N = 55) detected after sunset and before sunrise (between 7 p.m. and 4 a.m., Fig. 1). Our assessment showed that the booming activity rate of the species was relatively constant during the study period, with a CV close to 60% among monitored days. The CV decreased by approximately 20% during four monitored days (Fig. 3).

Discussion

The present study provides a detailed description of the vocal behaviour of the rhea (see also Mercolli and Yanosky 1994) and is one of the first studies on the vocal behaviour of any ratite, excluding kiwis, the most vocal of the ratite species (Davies 2002, see studies on kiwis in Corfield et al. 2008; Digby et al. 2013, 2014; Dent and Molles 2015). Here, we also provide the first thorough description of the spectral and temporal structure of the booming call of the rhea, which might be useful for future studies on the species and to understand how the communication system of the rhea evolved. The booming call was produced at a very low frequency (dominant frequency of 123 Hz) as were the low-frequency sounds described for two species of cassowaries (*Casuarius* spp., Mack and Jones 2003). Low-frequency sounds are expected to experience low degradation and propagate over long distances with minimal attenuation, which may be a good strategy for communication between distant groups of rheas in tropical habitats (Marten and Marler 1977), such as the Cerrado and the Chaco where the rhea lives (Hodes 2020).

According to our few direct observations of individuals vocalising during the study period (c. 30 observations), the booming call was produced by only rhea males (at least

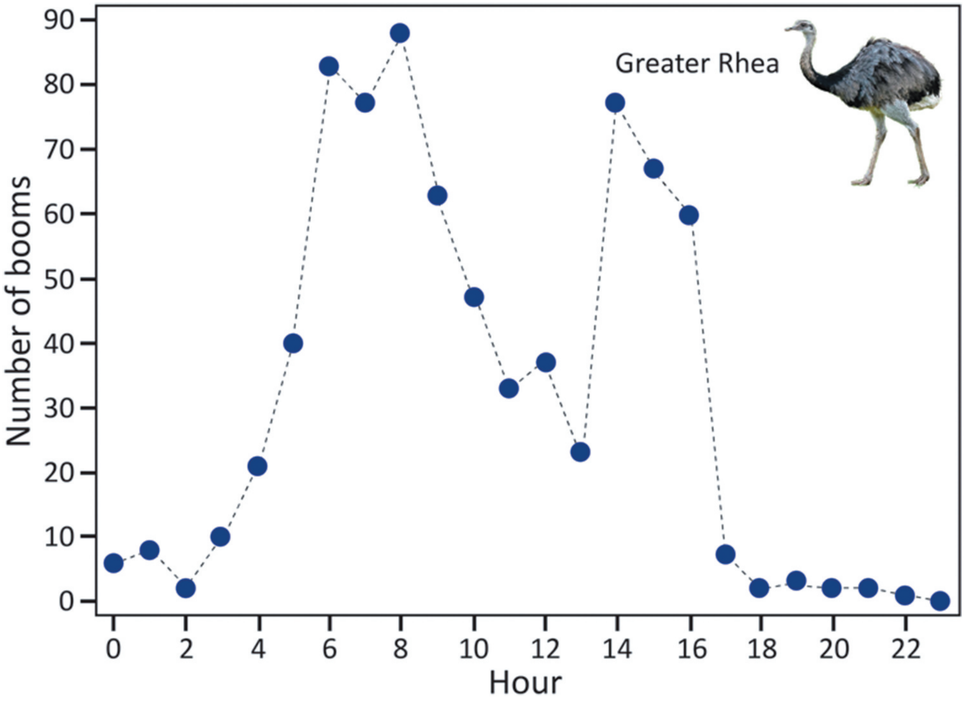

Figure 2. Diel pattern of booming activity of the Greater Rhea (*Rhea americana*) at UFMT Zoo (Cuiabá, Mato Grosso, Brazil). Booming activity was measured by recording continuously from 27 July to 3 August 2019. The diel pattern is expressed as the total number of booming calls recorded per hour. Hours are expressed in UTC -4.

two of the three males were vocally active during the study period) and was not specifically directed at any sex or individual. Our observations are in agreement with a previous description of how wild rheas vocalise in southern Brazil (Codenotti and Alvarez 2001). The vocal activity of the rhea was restricted, at least as a common behaviour, to the beginning of the mating season, which occurs between July and September in south Brazil (during the dry season, Codenotti and Alvarez 2001; de Azevedo et al. 2010; Gasparri 2016). Although recorders were not placed in the zoo, we walked the external fence of the lake of the zoo twice per day (5–10 min of walking at 7 a.m. and at 4 p.m.) between mid-June and late November 2019. We did not detect any booming calls until 24 July, and the last booming call was detected on 18 August, which suggests that the vocal behaviour of the rhea plays an important role in the communication system of the species but during only a short period of time. Our assumption is in agreement with the annual pattern of vocal activity described for wild rheas in Argentina, since vocalisations were only detected from mid August to late October, with no calls detected during the rest of the year (Mercolli and Yanosky 1994). Further research should try to assess whether the booming calls have an intra- or intersexual function since we cannot rule out either possibility with the current knowledge of the vocal behaviour of the species (Mercolli and Yanosky 1994). Future studies should also evaluate whether individual recognition of recorded birds is possible in the rhea (see application in a ratite using autonomous recording units in Dent and Molles (2016), and see also Ehnes and

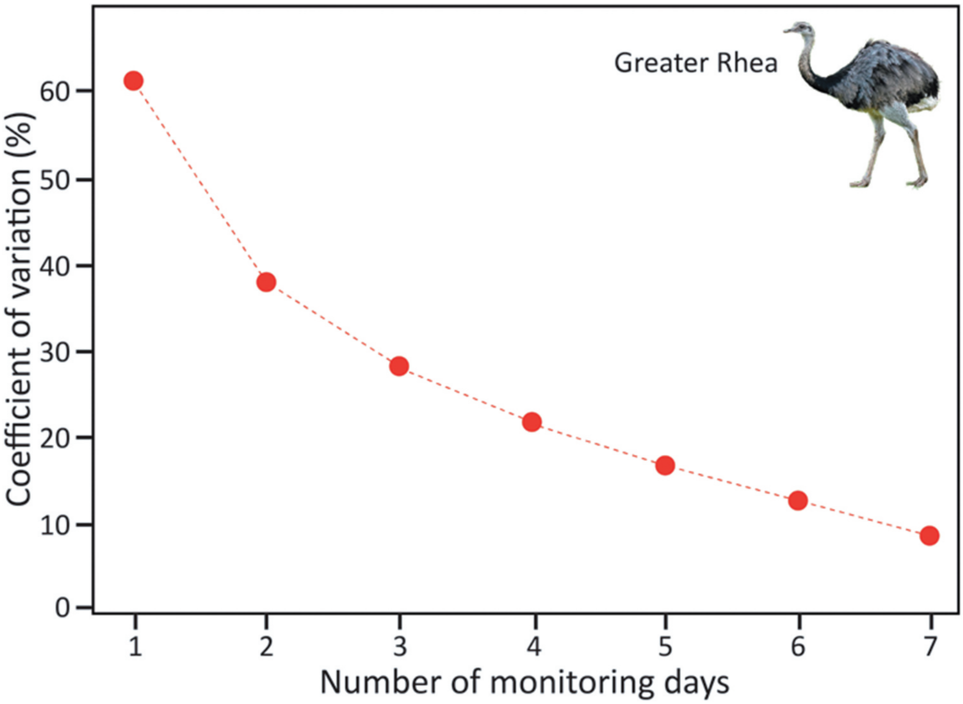

Figure 3. Coefficient of variation (%) of the daily booming activity rate of the Greater Rhea as a function of monitoring days. Booming activity was measured by recording continuously from 27 July to 3 August 2019 at UFMT Zoo (Cuiabá, Mato Grosso, Brazil).

Foote 2015), which may allow researchers to control for the number of birds vocalising around recorders.

The rhea showed the typical bimodal pattern of vocal activity found in most bird species, with a first and high peak of vocal activity after sunrise and a second peak before sunset (Catchpole and Slater 2008). The bimodal pattern found in our study, with the highest calling activity after sunrise, is in agreement with the diel pattern described for wild rheas in Argentina (Mercolli and Yanosky 1994). Nonetheless, in the later study the second peak of vocal activity before sunrise was much reduced than in our study. Surprisingly, we also found that the species vocalised at night, as nocturnal activity has not been previously reported for this species (see diel pattern of activity the species described by 24-h monitoring with camera traps in Oliveira-Santos and Tizianel 2008, and see diel pattern of vocal behaviour described during 24-h monitoring throughout field observations in; Mercolli and Yanosky 1994). The nocturnal vocal behaviour of the species is similar to a recent study that used passive acoustic monitoring to study the vocal behaviour of another diurnal Palaeognathae, the Undulated Tinamou (*Crypturellus undulatus*). Pérez-Granados et al. (2020) found a high rate of nocturnal calling activity of the Undulated Tinamou and suggested that it should ‘play an important role in the communication system of the species’. The same reasoning might be true for the rhea, although the proportion of nocturnal vocalisations produced by the rhea at night (7.2% between 7 p.m. and 4 a.m.) was half the proportion of nocturnal vocalisations produced by the Undulated Tinamou (14.3% between 7 p.m. and 4 a.m.). The study of nocturnal vocal activity of diurnal birds is an interesting topic that deserves more attention, especially for nonpasserines for which exist very limited information (La 2012; Celis-Murillo et al. 2016; Foote et al. 2017, but see Kułaga and Budka 2020). The monitored zoo was located within the campus of the UFTM, and thus there was some artificial light at night, which may have positively influenced the nocturnal vocal behaviour of the monitored rheas (Miller 2006; Byrkjedal et al. 2012; Watson et al. 2016). Therefore, further research involving recording wild individuals during the night, in the absence of anthropogenic light, is required to provide a reliable measure of the relative importance of nocturnal vocalisations in the communication system of the species.

The assessment of the decreasing pattern of the CV of the booming activity rate of the rhea showed a CV of 60% among days, which can be considered low when compared to other bird species (see Pérez-Granados et al. 2019b; Pérez-Granados and Schuchmann 2020a). Although the CV of birds' vocal activity has been published for only three bird species (a European songbird and two Neotropical nightjars), the pattern found in our study suggests that the vocal activity of the rhea was relatively constant. Our assessment might also be useful for further research on ratites using passive acoustic monitoring as a starting point to evaluate the minimum number of monitoring days needed to estimate a reliable diel pattern or a low-error estimate of the vocal activity rate.

Passive acoustic monitoring, coupled with automated signal recognition software, has proven to be a useful technique for monitoring the vocal behaviour of the rhea. This technique allowed us to monitor the vocalisations of the species using a standardised approach over eight consecutive days and detect around 87% of their calls in a much reduced amount of time (c. 1 hour for data analyses and reviewing the candidate sounds, 0.5% of the recording time). The recall rate estimated in our study can be considered as high when compared to previous studies using automated detection of calls of ratites (recall rate of 40% for the Little Spotted Kiwi, *Apterys owenii*, Digby et al. 2013) and with prior research that used Kaleidoscope Pro for detecting bird calls (e.g., recalls rates between 74% and 85% for two potoos, *Nyctibius* spp., Pérez-Granados and Schuchmann 2020b; 81% for the Western Capercaillie, *Tetrao urogallus*, Abrahams 2019; 11–22% for two vocalisations type of the King Rail, *Rallus elegans*, Schroeder and Mcrae 2020). Our results are in agreement with prior studies that proved the utility of autonomous sound recorders for monitoring the vocal activity of different Palaeognathae (Digby et al. 2013, 2014; Dent and Molles 2015; Pérez-Granados et al. 2020). For example, Digby et al. (2013) found that visual inspection of sonograms detected 85% of the calls of the Little Spotted Kiwi heard by human listeners in the field. Therefore, when able to create a recogniser with a high recall rate, passive acoustic monitoring might be useful for continued study of the vocal activity of ratites (e.g., cassowaries) as well as to evaluate the importance of vocal behaviour in wild rheas over a large temporal scale.

Our study shows that the rhea is a vocally active species with a booming call structure similar to that of cassowaries and with a diurnal and nocturnal pattern of vocal activity similar to that described for other diurnal Palaeognathae, such as the Undulated Tinamou (Pérez-Granados et al. 2020). Our results might be useful to understand how vocal behaviour evolved in ratites and its function and therefore may provide insights into the evolutionary process of avian vocal behaviour. Nonetheless, we are aware that our study was restricted to a short period (8 days) of time, and used a reduced number of captive birds as study model, and therefore, there is still much to be learned about how rheas use booming calls for communication (Mercolli and Yanosky 1994). We hope that our study may encourage researchers to study vocal behaviour in other birds from basal lineages to increase our current knowledge of this intriguing phenomenon (Benedict and Krakauer 2013).

Acknowledgements

We thank Prof. Marinêz Isaac Marques for her constant support and help and to Ana Silvia Tissiani and Filipe Ferreira de Deus for their technical assistance. We also thank the whole zoo staff, and especially the zoo coordinator, Prof. Sandra Helena Ramiro Côrrea, for permission to conduct our research at the zoo. We wish to thank two anonymous reviewers for their comments that helped to improve the manuscript. 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 under SISBIO permit no. 39095 (KLS). We are also grateful to the Cornell Lab of Ornithology for the license for Raven Pro: Interactive Sound Analysis Software.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior–Brasil [Finance Code 01];Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas; Brehm Funds for International Bird Conservation.

ORCID

Cristian Pérez-Granados http://orcid.org/0000-0003-3247-4182
Karl-L. Schuchmann http://orcid.org/0000-0002-3233-8917

Data accessibility

Raw data employed for creating graphs and data analyses can be found at: 10.6084/m9.figshare.12789152

References

Abrahams C. 2019. Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.). J Ornithol. 19:685–697. doi:10.1007/s10336-019-01649-8.

Beaver PW. 1978. Ontogeny of vocalization in the greater rhea. Auk. 95(2):382–388. doi:10.1093/auk/95.2.382.

Benedict L, Krakauer AH. 2013. Kiwis to pewees: the value of studying bird calls. Ibis. 155(2):225–228. doi:10.1111/ibi.12049.

Bioacoustics Research Program. 2014. Raven Pro: interactive Sound Analysis Software. Version 1.5. Computer software. Available from. Ithaca (NY): The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven

Byrkjedal I, Lislevand T, Vogler S. 2012. Do passerine birds utilise artificial light to prolong their diurnal activity during winter at northern latitudes? Ornis Norvegica. 35:37–42. doi:10.15845/on.v35i0.269.

Catchpole CK, Slater PJ. 2008. Bird song: biological themes and variations (2nd edition). Cambridge: Cambridge University Press.

Celis-Murillo A, Benson BT, Sosa-López JR, Ward MP. 2016. Nocturnal songs in a diurnal passerine: attracting mates or repelling intruders? Anim Behav. 118:105–114. doi:10.1016/j.anbehav.2016.04.023.

Codenotti TL, Alvarez F. 2001. Mating behavior of the male Greater Rhea. Wilson J Ornithol. 113 (1):85–89.

Corfield J, Gillman L, Parsons S. 2008. Vocalizations of the North Island brown kiwi (*Apteryx mantelli*). Auk. 125(2):326–335. doi:10.1525/auk.2008.06234.

Davies SJJF. 2002. Ratites and tinamous. Oxford Univ. New York (New York): Oxford Univ. Press.

de Azevedo CS, Ferraz JB, Tinoco HP, Young RJ, Rodrigues M. 2010. Time–activity budget of greater rheas (*Rhea americana*, Aves) on a human-disturbed area: the role of habitat, time of the day, season and group size. Acta Ethol. 13(2):109–117.

Dent JM, Molles L. 2015. Sexually dimorphic vocalisations of the Great Spotted Kiwi (*Apteryx haastii*). Notornis. 62:1–7.

Dent JM, Molles L. 2016. Call-based identification as a potential tool for monitoring Great Spotted Kiwi. Emu-Austral Ornithol. 116(4):315–322. doi:10.1071/MU15079.

Digby A, Bell BD, Teal PD. 2013. Vocal cooperation between the sexes in Little Spotted Kiwi *Apteryx owenii*. Ibis. 155:229–245. doi:10.1111/ibi.12031.

Digby A, Towsey M, Bell BD, Teal PD. 2014. Temporal and environmental influences on the vocal behaviour of a nocturnal bird. J Avian Biol. 45:591–599. doi:10.1111/jav.00411.

Ehnes M, Foote JR. 2015. Comparison of autonomous and manual recording methods for discrimination of individually distinctive Ovenbird songs. Bioacoustics. 24:111–121. doi:10.1080/09524622.2014.994228.

Fernández GJ, Reboreda JC. 2003. Male parental care in Greater Rheas (*Rhea americana*) in Argentina. Auk. 120(2):418–428. doi:10.1093/auk/120.2.418.

Foote JR, Nanni LK, Schroeder R. 2017. Seasonal patterns of nocturnal singing by ovenbirds and white-throated sparrows. Behav. 154:1275–1295. doi:10.1163/1568539X-00003468.

Gasparri B. 2016. Biología y Ecología del Ñandú (*Rhea americana*). In: Gasparri B, Athor J, editors. El Ñandú (*Rhea americana*). Buenos Aires (Argentina): Fundación de Historia Natural “Félix de Azara”; p. 11–64.

Hodes C. 2020. Greater Rhea (*Rhea americana)*, version 1.0. In: Schulenberg TS, editor. Birds of the World. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.grerhe1.01 .

Johnston P. 2011. New morphological evidence supports congruent phylogenies and Gondwana vicariance for palaeognathous birds. Zool J Linn Soc. 163:959–982. doi:10.1111/j.1096-3642.2011.00730.x.

Knight E, Hannah K, Foley G, Scott C, Brigham R, Bayne E. 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. Avian Cons Ecol. 12(2):14.

Kułaga K, Budka M. 2020. Nocturnal singing by diurnal birds in a temperate region of central Europe. J Ornithol. doi:10.1007/s10336-020-01794-5

La VT. 2012. Diurnal and nocturnal birds vocalize at night: a review. Condor. 114:245–257.

Mack AL, Jones J. 2003. Low-frequency vocalizations by cassowaries (*Casuarius* spp.). The Auk. 120(4):1062–1068. doi:10.1642/0004-8038(2003)120[1062:LVBCCS]2.0.CO;2.

Marten K, Marler P. 1977. Sound transmission and its significance for animal vocalization. Behav Ecol Sociobiol. 2(3):271–290. doi:10.1007/BF00299740.

Mercolli C, Yanosky AA. 1994. Vocalizaciones del ñandú común *Rhea americana* (Aves: rheidae) en Argentina. Revista De Biología Tropical. 42(3):759–760.

Miller MW. 2006. Apparent effects of light pollution on singing behavior of American robins. Condor. 108:130–139. doi:10.1093/condor/108.1.130.

Navarro JL, Martella MB. 2002. Reproductivity and raising of Greater Rhea (*Rhea americana*) and Lesser Rhea (*Pterocnemia pennata*): a review. Archiv fur Geflugelkunde. 66(3):124–132.

Oliveira-Santos LGR, Tizianel FAT. 2008. Influence of temperature on Greater Rhea *Rhea americana* activity in restinga habitat, southern Brazil. Revista Brasileira De Ornitologia. 16 (1):29–31.

Pérez-Granados C, Bota G, Giralt D, Albarracín J, Traba J. 2019a. Cost-effectiveness assessment of five audio recording systems for wildlife monitoring: differences between recording distances and singing direction. Ardeola. 66(2):311–325. doi:10.13157/arla.66.2.2019.ra4.

Pérez-Granados C, Gómez-Catasús J, Bustillo-de la Rosa D, Barrero A, Reverter M, Traba J. 2019b. Effort needed to accurately estimate vocal activity rate index using acoustic monitoring: a case study with a dawn-time singing passerine. Ecol Ind. 107:105608. doi:10.1016/j.ecolind.2019.105608.

Pérez-Granados C, Schuchmann K-L. 2020a. Illuminating the nightlife of two Neotropical nightjars: vocal behavior over a year and monitoring recommendations. Ethol Ecol Evol. 32 (5):466–480. doi:10.1080/03949370.2020.1753117.

Pérez-Granados C, Schuchmann K-L. 2020b. Monitoring the annual vocal activity of two enigmatic Neotropical birds: the Common Potoo (*Nyctibius griseus*) and the Great Potoo (*Nyctibius grandis*). J Ornithol. doi:10.1007/s10336-020-01795-4

Pérez-Granados C, Schuchmann K-L, Marques MI. 2020. Vocal behavior of the Undulated Tinamou (*Crypturellus undulatus*) over an annual cycle in the Brazilian Pantanal: new ecological information. Biotropica. 52(1):165–171. doi:10.1111/btp.12742.

Picasso MBJ, Carril J. 2013. The peculiar syrinx of *Rhea americana* (Greater rhea, Palaeognathae). Verteb Zool. 63(3):321–327.

R Development Core Team. 2019. A language and environment for statistical computing R foundation for statistical computing. Vienna: R Development Core Team.

Reed GF, Lynn F, Meade BD. 2002. Use of coefficient of variation in assessing variability of quantitative assays. Clin Diagn Lab Immunol. 9:1235–1239.

Rempel RS, Francis CM, Robinson JN, Campbell M. 2013. Comparison of audio recording system performance for detecting and monitoring songbirds. J Field Ornithol. 84(1):86–97. doi:10.1111/jofo.12008.

Sales J, Deeming DC, Van Deventer PJU, Martella MB, Navarro JL. 2000. Diurnal time-activity budget of adult Greater Rheas (*Rhea americana*) in a farming environment. Archiv für Geflügelkunde. 64(5):207–210.

Schroeder KM, Mcrae SB. 2020. Automated auditory detection of a rare, secretive marsh bird with infrequent and acoustically indistinct vocalisations. Ibis. 162(3):1033–1046. doi:10.1111/ibi.12805.

Sick H. 1993. Birds in Brazil: a natural history. Princeton: Princeton University Press.

Warnes GR, Bolker B, Lumley T, Warnes MGR 2018. Package ‘gtools’. R Package version 3.8.1.

Watson MJ, Wilson DR, Mennill DJ. 2016. Anthropogenic light is associated with increased vocal activity by nocturnally migrating birds. The Condor. 118(2):338–344. doi:10.1650/CONDOR-15-136.1.

Yip D, Leston L, Bayne E, Sólymos P, Grover A. 2017. Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. Avian Conserv Ecol. 12(1):11. doi:10.5751/ACE-00997-120111.