The vocal repertoire of oilbirds

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ABSTRACT

The social complexity hypothesis states that social complexity drives the evolution of complex communication systems; in this sense, the vocal repertoire can be studied to measure vocal complexity and, ultimately, social complexity. Oilbirds (*Steatornis caripensis*) are nocturnal, frugivorous birds that live in colonies inside caves. Their vocal repertoire was studied to test the social complexity hypothesis in this species. Recordings were made in three known colonies in Santander, Colombia. For categorization and a complete description of the vocal repertoire, a consensus between manual categorization and an unsupervised classification was reached. I found that the vocal repertoire is comprised of nine unique vocalization types. This vocal repertoire is larger than that of many other passerine and non-passerine species. There were both short-distance vocalizations that may serve as contact vocalizations, and long-distance vocalizations that may serve as alarm, aggressive, or group coordination vocalizations. The relatively large vocal repertoire and the structurally and functionally distinctive vocalization types support the social complexity hypothesis, suggesting a high social complexity in oilbirds supported by a highly complex communication system.

RESUMEN

La hipótesis de la complejidad social afirma que la complejidad social conduce a la evolución de sistemas de comunicación complejos; de esta manera, el repertorio vocal puede ser estudiado para medir la complejidad vocal y, en última estancia, la complejidad social. El guácharo (*Steatornis caripensis*) es un ave frugívora, nocturna y que vive en colonias dentro de cuevas. Se estudió su repertorio vocal para probar la hipótesis de la complejidad social en esta especie. Se realizaron grabaciones en tres colonias conocidas en Santander, Colombia.

Para la categorización y la descripción completa del repertorio vocal, se realizó un consenso entre una categorización manual y una categorización no supervisada. Encontré que el repertorio vocal está conformado por nueve tipos de vocalización únicos. Este repertorio es más amplio que el de muchas aves paseriformes y no paseriformes. Se encontraron vocalizaciones de corta distancia que pueden servir como vocalizaciones de contacto, y vocalizaciones de larga distancia que pueden servir como vocalizaciones de alarma, agresión o de coordinación de grupo. El repertorio vocal relativamente amplio y los tipos de vocalización estructural y funcionalmente distintos apoyan la hipótesis de la complejidad social, sugiriendo una alta complejidad social en los guácharos apoyada por un sistema de comunicación altamente complejo.

KEYWORDS

Communication system, non-passerine, social complexity, vocal complexity.

PALABRAS CLAVE

Complejidad social, complejidad vocal, no paserinos, sistema de comunicación.

INTRODUCTION

The social complexity hypothesis states that social complexity drives the evolution of complex communication systems (Freeberg et al., 2012). According to this hypothesis, more socially complex groups—those with larger group size, group density, diversity in roles or status of group members, or diversity of relations in social networks—will exhibit greater vocal complexity compared with groups with a relatively simple sociality. This is because a larger number of individuals need more complex communication systems with many structural and functionally distinct signals (Krams et al., 2012). This hypothesis has been tested mainly in passerines (i.e., songbirds) (Boucherie et al., 2019; Freeberg, 2006), but very little has been explored in non-passerines (Grieves et al., 2015; Seddon et al., 2002). As a result, there is a large amount of uncertainty about whether the social complexity hypothesis applies to this non-singing group and, if so, how it works.

The lack of knowledge in non-passerines communication is explained by the lack of studies about the vocal behavior and repertoires of these birds. Non-passerines constitute an important missing link in our understanding of communication systems, representing about 40% of total avian diversity (Oliveros et al., 2019), of which vocal behavior remains relatively unknown. Furthermore, non-passerines, have been characterized by exhibiting a diverse array of social structures and behaviors (Malacarne et al., 1991; Trillmich, 1976), and to possess a unique non-social and social behaviors that vary greatly from passerine birds (Jedlikowski et al., 2021; Pérez-Granados & Schuchmann, 2021). Vocalizations in both, passerines and non-passerines, facilitate multiple functions in territorial interactions, coordination of reproductive activities, paternal care, feeding, predator avoidance, pair formation and maintenance, among others (Kroodsma & Miller, 2020).This complex array of social behaviors has to be coupled with a complex communication system through a high level of vocal complexity (Freeberg, 2006; Freeberg et al., 2012). And this diverse array of avian vocalizations suggests that we can expand our knowledge of non-passerine bird behavior by studying its vocalizations.

Vocal complexity can be measured in terms of information (bits) in a vocal signaling system, individual usage of vocal signals, and vocal repertoire size (Peckre et al., 2019). A vocal repertoire is the complete library of vocalizations an individual or species can produce (Catchpole & Slater, 2008) that allows for different types of recognition, such as individual recognition (Benti et al., 2019; Lefevre et al., 2001) or kin differentiation (Briefer et al., 2008; Peterson et al., 2023). The number of distinct vocalizations reported for most species of birds ranges from 5 to 14 (Gill et al., 2019), so a large vocal repertoire can be considered one that approaches or exceeds the high end of this range and thus has a high vocal complexity (Grieves et al., 2015). A wider repertoire provides more capability to express more types of signals and convey more complex messages (Trainer & McDonald, 1993). Non-passerine birds can adjust to spatial and environmental characteristics, thus exhibiting vocal plasticity that allows for acoustic variations (Seddon et al., 2002). This high variation in vocal characteristics can create individual signatures that can support processes like group (Monteiro et al., 2021) or kin recognition (Wanker et al., 2005), which suggest processes linked to a high social complexity that can be measured by evaluating the vocal repertoire and its characteristics.

In this study, I described the vocal repertoire of *Steatornis caripensis,* Humboldt 1799 (Aves: Caprimulgiformes), commonly known as the Oilbird. Oilbirds are nocturnal, frugivorous, monomorphic birds that live in colonies in caves and canyons in tropical forests (Snow, 1961). Their colony-living habits, colony size, group density and the restricted space of the places where they live suggest that oilbirds may have a socially complex structure, thus becoming an interesting study subject for exploring the evolution of vocal communication. Previous research in oilbird communication has focused on the echolocation clicks (Brinkløv et al., 2017; Konishi & Knudsen, 1979), but little has been done to understand their vocal diversity and the functionality of their vocalizations. Oilbird vocalizations have been described only as a range of clucks and rather low-pitched “hawking” sounds (Snow 1961), screams, grunts, and flight contact calls (Hilty et al., 2001); however, I expect them to have a relatively large and complex communication system that allow them to convey messages to other members within the colony inside the caves and allows a high social complexity. The detailed description of the vocal repertoire is a first step to describing the vocal diversity and lays out the baseline to understand the function of vocalizations (e.g., territory establishment, group formation, and colony communication).

METHODS

Study area

Recordings were done on three colonies that inhabit different caves in Santander, Colombia (Figure 1). Carracos (6.0831865, -73.8331374; 2342 m.a.s.l.) is the smallest cave, with 17±4.7 individuals (Pineda Dueñas, 2023), it is relatively narrow, and the nests are located around 15 meters from the ground. Palmas (6,0716111, -73,8609722; 2288 m.a.s.l.) is the largest cave with 1129±342 individuals (Pineda Dueñas, 2023). It has a main wide chamber and several smaller chambers with different heights, and nests are located around 15 to 30 meters from the ground. Finally, Berlín (6,1413333, -73,7430277; 1572 m.a.s.l.) is a medium size cave with 339±132 individuals (Pineda Dueñas, 2023). It has one long chamber, and the nests are located around 15 to 20 meters from the ground.

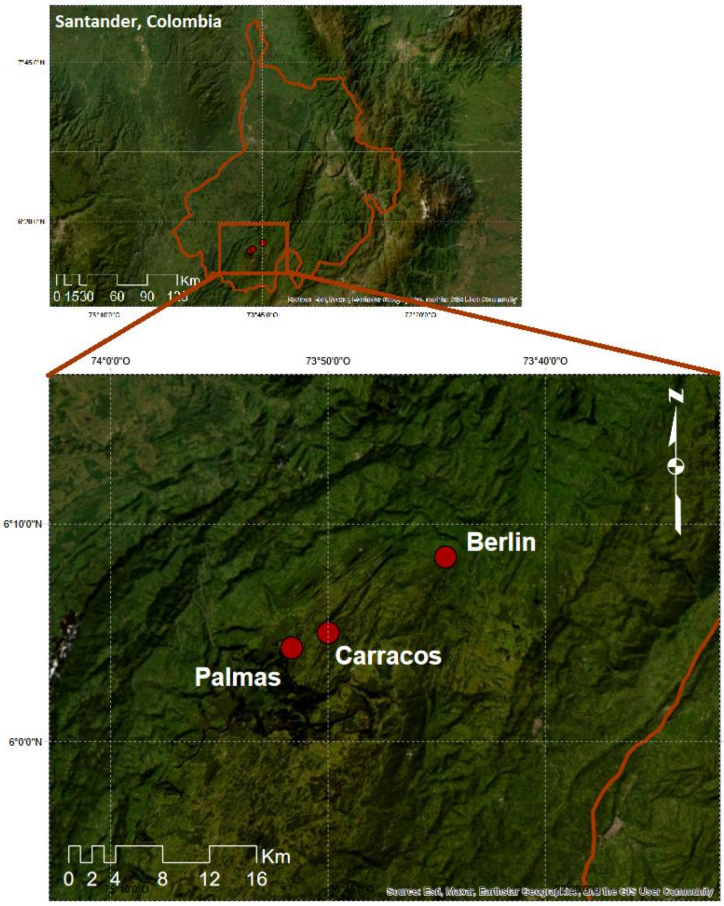


Figure 1. Map of the study area in Santander, Colombia. The red dots indicate the location of the three caves where the studied colonies of oilbirds (*Steatornis caripensis)* are located.

Data collection

Recordings were made using a Zoom H5 Multi-Track Handy Recorder (WAV format; 44.1 kHz; 16 bits) coupled with a Zoom SGH6 shotgun microphone. The recorder was protected with a Ziploc bag and attached to the tip of a 10-meter pole that was directed at the nearest nest located in the cave ceiling (Figure 2). Recordings were done over a six-day period in each of the sampled caves. In each cave, the following sampling scheme was implemented: 1) three hours in the dawn, starting at 5:30 until 8:30, which is when oilbirds return to the cave from their nocturnal foraging trips, and 2) three hours in the dusk, starting at 17:00 until 20:00, which is before and after the departure of the birds to forage at night. This scheme was used to track any vocalizations occurring during the day in different behavioral contexts (e.g., paternal care, couple formation, group coordination etc.).

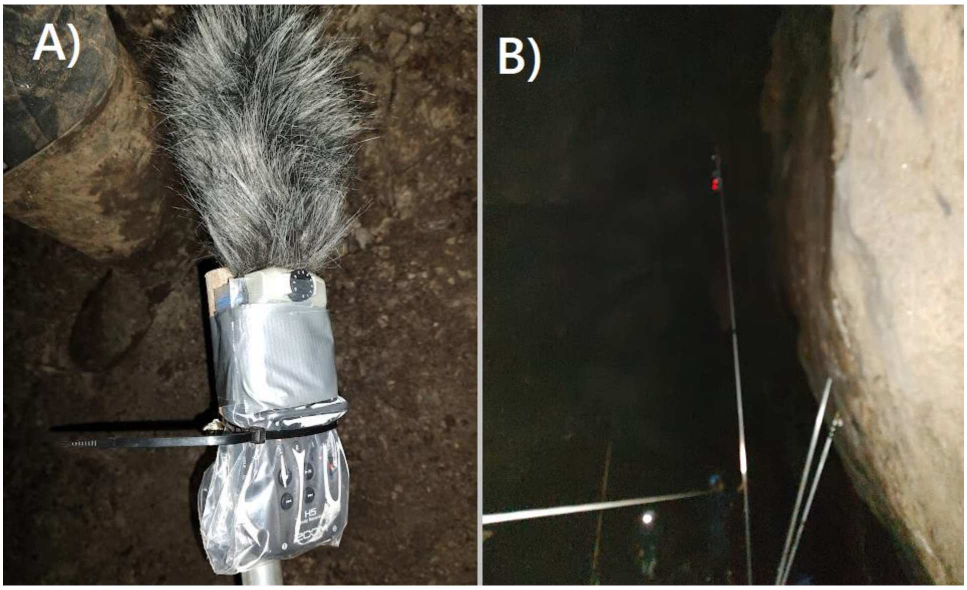


Figure 2. Microphone and recorder placement in the pole and inside the cave for data recording. A) Zoom H5 Multi-Track Handy Recorder coupled with a Zoom SGH6 shotgun microphone covered with a Ziploc bag attached with duct tape and zip ties to the top of the 10-meter pole. B) 10-meter telescopic pole secured and directed to the cave ceiling.

Data analysis

The analysis was done in Raven Pro 1.6.5 (Yang, 2023) following the methodology established in similar studies (e.g., Smeele et al., 2023). Each 3-hour continuous recording from the sampling sessions was subsampled into 5-minute clips and cropped to 11 kHz for subsequent analysis (1204 audio clips in total). Subsequently, I randomly selected an eighth of the audio clips (11:50 hours) to identify discrete vocalizations, and manually annotate them. Clips were visualized on a sound spectrogram (FFT-length, 512; frame, 100%; bandwidth, 88.6 Hz; resolution, 358 Hz, Hann window), using only clips with a signal-to-noise ratio larger than 7dB. For each clean vocalization in each clip, I annotated whether it was overlapped with other vocalization (y/n) and other important sound characteristics such as echolocation clicks (y/n), chick vocalizations (y/n), whether the vocalization was far away (y/n), water or wind in the background (y/n), and if there was another animal (y/n). All subsequent analyses were done in R version 4.3.1 (R Core Team, 2023).

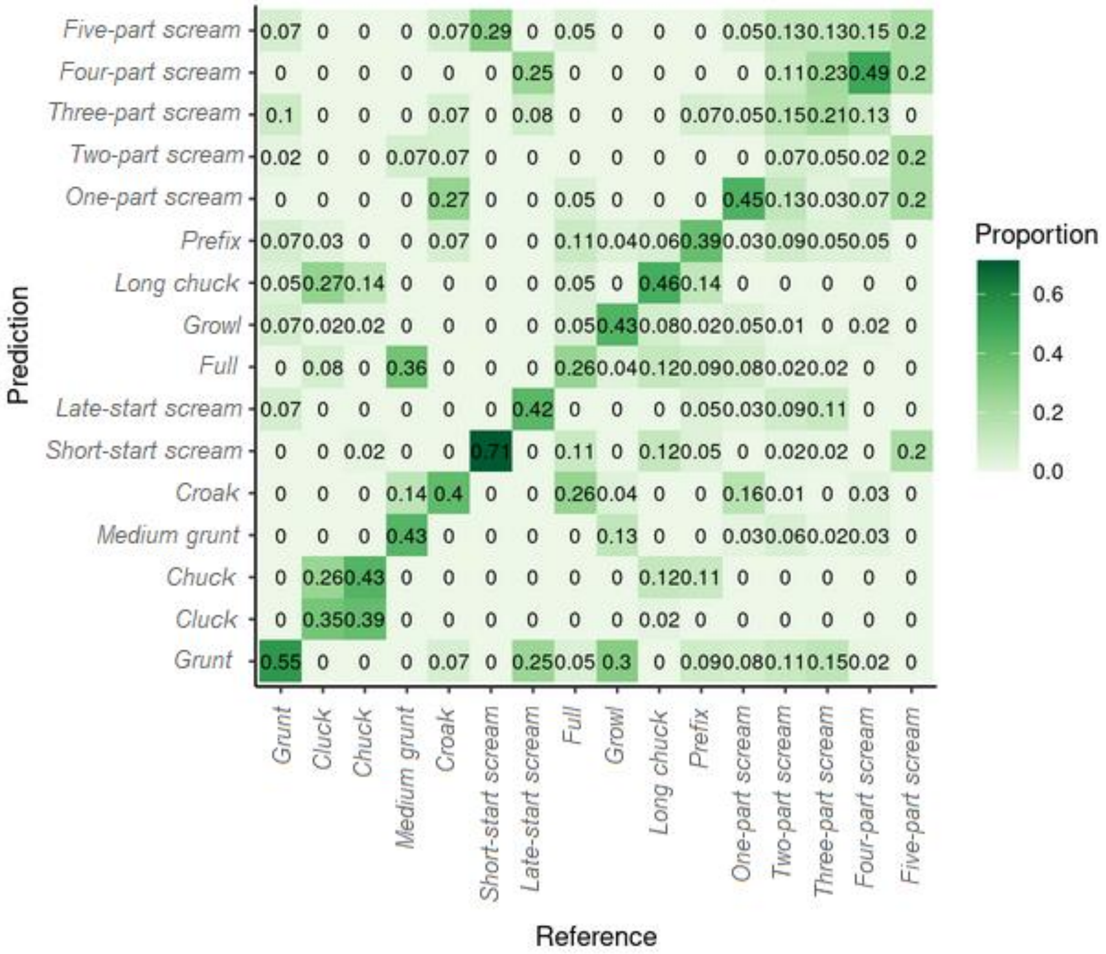
Next, I manually classified the clean vocalizations based on the visual and auditive information of each spectrogram extracted with the package Rraven 1.0.13 (Araya-Salas, 2021). This classification was then tested using a random forest procedure using the package randomForest (Liaw & Wiener, 2022). For this, I used the 25% of the data as the training set (reference data) and the other 75% as the testing set (predicted data). I used the acoustic features and Mel-frequency cepstral coefficients (MFCCs) to run a supervised classification of the data and used the 75% to make predictions of the classification for each vocalization. The prediction parameters were measured with the package warbleR (Araya-Salas & Smith-Vidaurre, 2023). Lastly, I evaluated the accuracy of the predictions versus the manual classification using a confusion matrix in the package caret (Kuhn, 2023).

Additionally, I run an unsupervised classification using model-based clustering (ellipsoidal, varying volume, shape, and orientation) for all the clean vocalizations in the selected clips using the package mclust (Scrucca et al., 2023). Then, I compared the manual classification to the unsupervised classification to find matches between the categories using a proportion matrix. Projections of both classifications were made with Uniform Manifold Approximation and Projection (UMAP) with the package umap (Konopka, 2023) and all visual representations of data were made using the package ggplot2 (Wickham, 2016).

RESULTS

A total of 34 recordings adding up 94:32 hours of audio were recorded across the three caves. Some of the recordings were shorter due to battery and time limitations, so 8 hours (from the 102 hours expected) were lost. All recordings had a high signal-to-noise ratio (> 7dB). In the set of randomly selected clips, I identified a total of 2710 clean vocalizations available for further classification, of which 1575 (58.11%) vocalizations were from Carracos, 778 (28.72%) from Palmas, and 357 (13.17%) from Berlín.

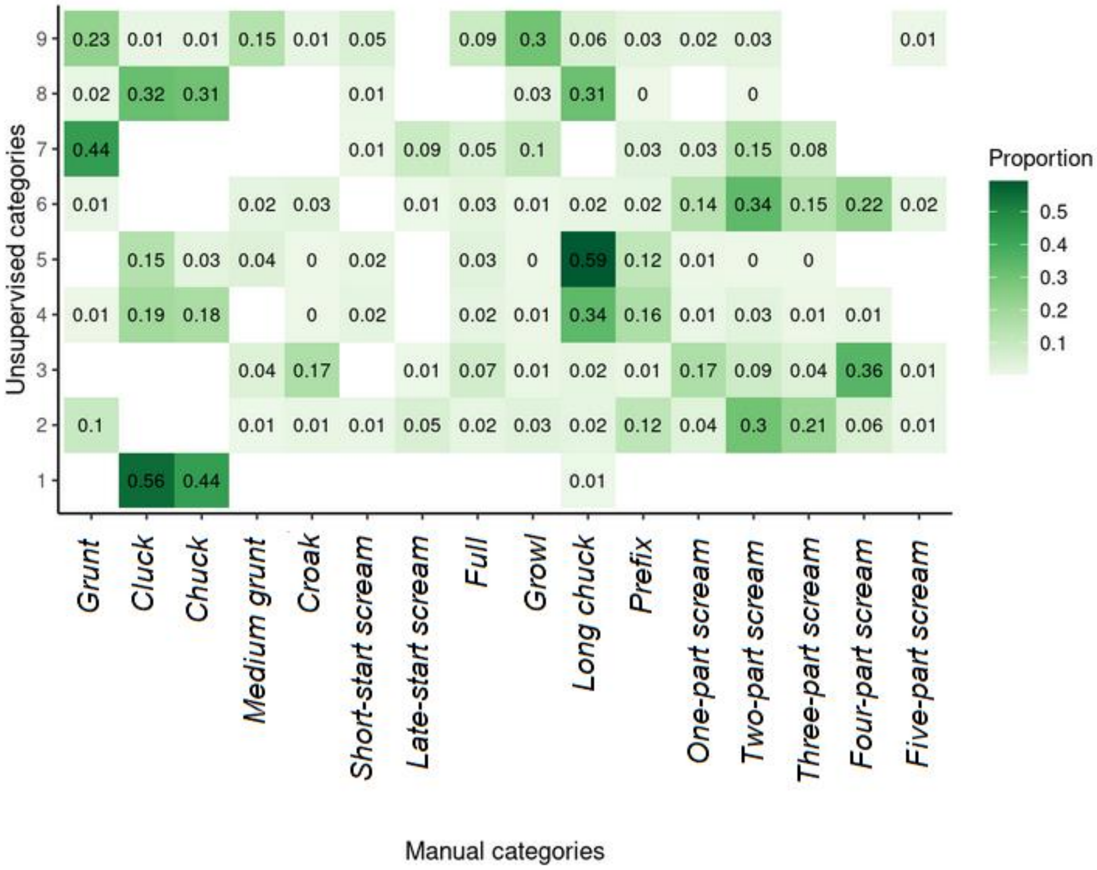
The manual classification of the vocalizations resulted in 16 different types of vocalizations (*Grunt* n = 168, *cluck* n = 270, *chuck* n = 205, *medium grunt* n = 58, *croak* n = 60, *short-start scream* n = 29, *late-start scream* n = 50, *full* n = 77, *growl* n = 95, *long chuck* n = 388, *prefix* n = 180, *one-part scream* n = 154, *two-part scream* n = 459, *three-part scream* n = 249, *four-part scream* n = 245, *five-part scream* n = 23). The random forest predictions of the manual classification correctly identified 11 categories and overall had low but significant accuracy (35.22%, $p < 0.001$). The confusion matrix, which shows the accuracy of the prediction for each category, showed that *short-start scream* (0.71), and *grunt* (0.55) had the highest accuracy, and that *two-part scream* (0.07), *three-part scream* (0.21), *five-part scream* (0.2), and *full* (0.26) had the lowest accuracy overall (Figure 3). *Cluck* and *chuck* had high accuracy within themselves and between each other, meaning there was no substantial discrimination between them, suggesting both have similar acoustic features.



	Grunt	Cluck	Chuck	Medium grunt	Croak	Short-start scream	Late-start scream	Full	Growl	Long chuck	Prefix	One-part scream	Two-part scream	Three-part scream	Four-part scream	Five-part scream
Five-part scream	0.07	0	0	0	0.07	0.29	0	0.05	0	0	0	0.05	0.13	0.13	0.15	0.2
Four-part scream	0	0	0	0	0	0	0.25	0	0	0	0	0	0.11	0.23	0.49	0.2
Three-part scream	0.1	0	0	0	0.07	0	0.08	0	0	0	0.07	0.05	0.15	0.21	0.13	0
Two-part scream	0.02	0	0	0.07	0.07	0	0	0	0	0	0	0	0.07	0.05	0.02	0.2
One-part scream	0	0	0	0	0.27	0	0	0.05	0	0	0	0.45	0.13	0.03	0.07	0.2
Prefix	0.07	0.03	0	0	0.07	0	0	0.11	0.04	0.06	0.39	0.03	0.09	0.05	0.05	0
Long chuck	0.05	0.27	0.14	0	0	0	0	0.05	0	0.46	0.14	0	0	0	0	0
Growl	0.07	0.02	0.02	0	0	0	0	0.05	0.43	0.08	0.02	0.05	0.01	0	0.02	0
Full	0	0.08	0	0.36	0	0	0	0.26	0.04	0.12	0.09	0.08	0.02	0.02	0	0
Late-start scream	0.07	0	0	0	0	0	0.42	0	0	0	0.05	0.03	0.09	0.11	0	0
Short-start scream	0	0	0.02	0	0	0.71	0	0.11	0	0.12	0.05	0	0.02	0.02	0	0.2
Croak	0	0	0	0.14	0.4	0	0	0.26	0.04	0	0	0.16	0.01	0	0.03	0
Medium grunt	0	0	0	0.43	0	0	0	0	0.13	0	0	0.03	0.06	0.02	0.03	0
Chuck	0	0.26	0.43	0	0	0	0	0	0	0.12	0.11	0	0	0	0	0
Cluck	0	0.35	0.39	0	0	0	0	0	0	0.02	0	0	0	0	0	0
Grunt	0.55	0	0	0	0.07	0	0.25	0.05	0.3	0	0.09	0.08	0.11	0.15	0.02	0

Figure 3. Confusion matrix for prediction of manual categorization of the 2710 oilbird vocalizations. The matrix was built using a random forest routine with 75% of the total data. The 25% of the data was used for reference.

The unsupervised classification resulted in nine different categories with distinct acoustic features and a different number of occurrences. Matching the manual and the unsupervised classification in a proportion matrix, which directly compares how many manual categories were placed in each unsupervised category, I found that there was some consensus in both classifications, specifically for the manual categories *grunt, cluck, chuck, growl, long chuck, two-part scream,* and *four-part scream* (Figure 4).



Unsupervised categories	Grunt	Cluck	Chuck	Medium grunt	Croak	Short-start scream	Late-start scream	Full	Growl	Long chuck	Prefix	One-part scream	Two-part scream	Three-part scream	Four-part scream	Five-part scream
9	0.23	0.01	0.01	0.15	0.01	0.05		0.09	0.3	0.06	0.03	0.02	0.03			0.01
8	0.02	0.32	0.31			0.01			0.03	0.31	0		0			
7	0.44					0.01	0.09	0.05	0.1		0.03	0.03	0.15	0.08		
6	0.01			0.02	0.03		0.01	0.03	0.01	0.02	0.02	0.14	0.34	0.15	0.22	0.02
5		0.15	0.03	0.04	0	0.02		0.03	0	0.59	0.12	0.01	0	0		
4	0.01	0.19	0.18		0	0.02		0.02	0.01	0.34	0.16	0.01	0.03	0.01	0.01	
3				0.04	0.17		0.01	0.07	0.01	0.02	0.01	0.17	0.09	0.04	0.36	0.01
2	0.1			0.01	0.01	0.01	0.05	0.02	0.03	0.02	0.12	0.04	0.3	0.21	0.06	0.01
1		0.56	0.44							0.01						

Figure 4. Proportion matrix. Comparison between the 16 manual categories and the nine unsupervised categories made using model-based clustering of the 2710 vocalizations for the oilbirds.

Based on both the random forest prediction and the match of unsupervised categories and manual categories, a consensus was reached to establish the complete vocal repertoire. First, the vocal categories *full* and *medium grunt* were removed. *Full* because of its low accuracy in the random forest prediction and because there was no corresponding category in the unsupervised classification. *Medium grunt* because it did not have a significant match with any of the unsupervised categories. *Cluck* and *chuck* were merged into one category given their similarities in the prediction as well as in the unsupervised categories. Also, *two-*

part scream, *three-part scream*, *four-part scream,* and *five-part scream* were merged into a new category: *complex scream*, due to their similarities and low accuracy overall. Finally, *late-start scream* was also merged into this category due to their low consistency, especially in the unsupervised category match.

The final consensus for the vocal repertoire of oilbirds had a total of 2571 vocalizations categorized into nine different vocalization types: *one-part scream*, *complex scream*, *prefix*, *growl*, *croak*, *grunt*, *short-start scream*, *chuck*, and *long chuck* (Figure 5, Table 1). All of them were characterized by their short duration (< 2 s) and high entropy (> 0.8), as well as starting at 0 kHz (Table 2). All vocalizations consisted of a single continuous note and were present in the three caves, except for *short-start scream* that was absent in Berlín. There was also substantial structural variation within each vocalization type (Figure S1), as well as high variation in acoustic features, as shown by the large values of the standard deviation (SD) (Table 1).

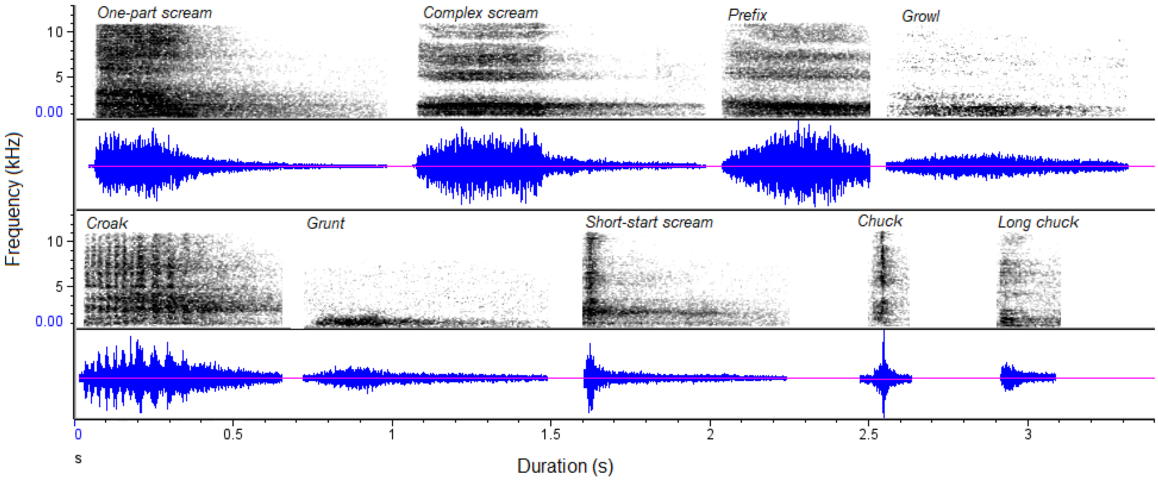


Figure 5. Spectrograms and waveform showing representative samples of the nine oilbird vocalizations, including *one-part scream*, *complex scream*, *prefix*, *growl*, *croak*, *grunt*, *short-start scream*, *chuck* and *long chuck* vocalizations.

Table 1. Spectral, temporal, and structural description of each discrete vocalization type of the vocal repertoire of oilbirds.

Vocalization type	Description
One-part scream (154)	High bandwidth at the start of the vocalization and an abrupt shift to a low frequency ending. It presents the longest mean duration as well as a high peak frequency, always spanning 11 kHz of bandwidth (Table 2). *One-part screams* are structurally similar to three other vocalizations: *complex scream*, *croak*, and *short-start scream* (Fig. 5, Fig. S2, Table 2)
Complex scream (1024)	As the *one-part scream,* it starts with a high bandwidth beginning to an abrupt shift with a low frequency ending, but in contrast, it has a clear harmonic stack at the beginning, having from 1 to 4 distinct harmonics. Long duration always has a bandwidth of 11 kHz (Table 2); sometimes it has subharmonics in between the main harmonics.
Prefix (179)	It is always given as a prefix that can immediately precede *one-part screams, complex screams, croaks,* or *short-start screams*. It can be either low-frequency (~1000 Hz) with no harmonics or have 1-4 harmonics and a bandwidth up to 11 kHz. It has low duration and high entropy (Table 2). Around 14.1% of vocalizations had a *prefix* before them.
Growl (95)	Has low to medium maximum frequency (2 kHz –5 kHz), can have harmonics above 6 kHz, peak frequency, and amplitude towards the middle of the vocalization, unlike *one-part scream*, *complex scream, croak,* and *grunt*. It is structurally similar to *grunts* (Fig. 5, Fig. S2), but with higher amplitude, maximum frequency, and peak frequency (Table 2).
Croak (60)	Very similar structure to *one-part scream* and *complex scream* (Fig. 5, Fig. S2), with a high frequency beginning followed by a low frequency ending, but with rapid amplitude modulation towards the beginning that slows down (Figure 5), always has 11 kHz of bandwidth, has a high peak frequency, and has a high amplitude (Table 2).
Grunt (168)	Has low frequency vocalization, medium duration, low peak frequency (Table 2), never has harmonics, with its peak of frequency and amplitude at the beginning or in the middle.
Short-start scream (29)	Very similar to a *one-part scream* (Fig. S2) but with the section of broad bandwidth at the start with a very short duration (~100 ms), always a bandwidth of 11 kHz, and it can have clear harmonics up to 4, or being a single continuous

	bandwidth, also its duration is considerably lower and has higher entropy than *one-part screams* (Table 2).
Chuck (474)	Has the shortest duration, can be low frequency (2 kHz), as well as having harmonics up to a bandwidth of up to 11 kHz (Table 2), and can be given in succession to a maximum of 18 continuous *chucks*, resembling a low cluck. It is structurally similar to *long chucks* (Fig. 5, Fig. S2, Table 2).
Long chuck (388)	Very similar to a *chuck* but with higher entropy, longer duration, and a lower peak frequency, it can be low-frequency (2 kHz) or have harmonics up to 11 kHz (Table 2). It is usually given singly (in the absence of other vocalization types or individuals vocalizing) or sometimes interspersed with other vocalizations.

Table 2. Mean (± SD) values of duration, peak frequency, mean frequency and entropy measured for the nine oilbird vocalization types analyzed. The numbers in parenthesis after each vocalization type represent the number of vocalizations found for the category.

Vocalization type	Duration (ms)	Peak Frequency (Hz)	Mean Frequency (Hz)	Entropy
One-part scream (154)	794.1±294.3	1518.0±751.6	5291.0±91.7	0.81±0.02
Complex scream (1024)	737.1±269.6	1144.8±372.4	5283.1±113.3	0.80±0.02
Prefix (179)	267.9±111.8	1136.6±679.2	4870.8±1138.9	0.86±0.04
Growl (95)	543.3±202.8	756.2±307.0	856.8±273.8	0.83±0.03
Croak (60)	630.8±261.1	2022.0±1073.4	5271.5±127.7	0.83±0.02
Grunt (168)	699.4±246.1	660.8±201.7	792.1±202.1	0.80±0.02

Short-start scream (29)	391.4±187.5	1403.4±1660.8	5183.8±246.2	0.85±0.03
Chuck (474)	115.3±49.5	1217.8±1031.1	3558.4±1968.4	0.85±0.09
Long chuck (388)	197.7±58.9	1000.2±847.5	4325.9±1638.0	0.90±0.02

DISCUSSION

The vocal repertoire of the oilbird is comprised of nine vocalization types, which include short-ranged contact vocalizations, alarm and aggressive vocalizations, and group coordination vocalizations. The repertoire size is close to the maximum of the range of 5 to 14 discrete vocalizations for most species of birds (Gill et al., 2019), and it is higher than the mean reported by Leighton & Birmingham in 2021 (7.25) that includes the vocal repertoires of other 821 bird species. At a colony level, there was no substantial variation in the vocalization types between the caves, suggesting that there is not strong variation in the communication system between colonies, suggesting that the social system is similar across colonies (Freeberg, 2006; Krams et al., 2012). Oilbirds have a large repertoire and a complex communication system, that suggests a high social complexity for this species (Freeberg et al., 2012; Peckre et al., 2019).

In comparison with other non-passerine birds, the vocal repertoire of the oilbird is larger than many species. For example, it is larger than the Bulwer’s Petrel (5) (Bretagnolle, 2019), the Common Ostrich (8) (Chiappone et al., 2023), the Yellow-faced Parrot (7) (de Araújo et al., 2011), the Eurasian Collared-dove (7) (de Kort & ten Cate, 2004), the African Penguin (4) (Favaro et al., 2014), the Common Coot (4) (Fu et al., 2021); Thick-billed Murre

(6) (Lefevre et al., 2001), the Yellow-breasted Barbet (4) (Mahamoud-Issa et al., 2024), the Greater Ani (3) (Riehl & Jara, 2009), the Kea (7) (Schwing et al., 2012), the Subdesert Mesite (5) (Seddon, 2002), and the Auklets (3-5) (Seneviratne et al., 2009). But it is also similar to some species like the Cactus Conure (9) (de Araújo & Araujo, 2020) and Orange-winged Parrots (9) (de Moura et al., 2011). This suggests that oilbirds have evolved a communication system more complex than a large proportion of species, which possibly supports the social life within the colonies and facilitates overcoming ecological deterrents.

Despite the considerably large size of the oilbird’s repertoire, it is still smaller than several other species such as the Australasian Swamphen (17) (Clapperton & Jenkins, 1984); the Eurasian Stone-curlew (11) (Dragonetti et al., 2013); the Smooth-billed Ani (11) (Grieves et al., 2015); the Eurasian Griffon Vulture (12) (Romani et al., 2022); the Pale-Winged Trumpeter (12) (Seddon et al., 2002); and the Palm Cockatoo (27) (Zdenek et al., 2015). A large repertoire indicates a wider form of communication and thus a more complex social system or different ecological aspects. Thus, the size of the oilbird’s vocal repertoire indicates that even though they have a complex communication system, the ecological conditions they live in, or the social system they have developed does not require a wider vocal repertoire to support it.

The oilbird vocal repertoire contained two categories of vocalization types: low frequency, low peak frequency, low amplitude, medium to short duration vocalization types (*growl, grunt, chuck, long chuck*); and high frequency, high peak frequency, high amplitude, long duration vocalization types (*one-part scream, complex scream, croak, short start scream*). This different categories may be due to ecological and functional reasons, low frequency, short, quiet vocalizations may be used to short distance communication and may be used for contact vocalizations between breeding pairs or close relatives (Luo et al., 2013);

while high frequency, long, loud vocalizations may be used as alarm (Digweed, 2019; Grieves et al., 2014) or aggressive (Klaas et al., 2015; Searcy & Beecher, 2009) vocalizations, or may serve as a group-level coordination in exiting the cave at night (Fichtel & Manser, 2010; Hollén et al., 2011; Radford, 2004), in particular *complex scream* which was the most common vocalization and was usually given in sequence or overlapped between multiple individuals specially at dusk. This suggests that oilbirds may use different vocalizations for specific ecological functions and that the vocal repertoire may be used in a wide range of ecological contexts. However, this warrants proper exploration.

Oilbirds have vocal repertoires comparable in size to species known for forming long-term pair bonds and of having year-round territoriality, as suggested by Leighton & Birmingham (2021). This tendency towards monogamy and pair bond formation in oilbirds has been suggested by Snow (1961) . Although the vocal repertoire of oilbirds may be related to their social organization, it seems that it is not associated to their breeding system. Species with large repertoires are often cooperative breeders (Leighton & Birmingham, 2021), however, oilbirds are not (Snow, 1961). Still the oilbird’s vocal repertoire is larger than some birds with a cooperative breeding system (e.g. Greig & Pruett-Jones, 2008; Riehl & Jara, 2009; Seddon, 2002; Warrington et al., 2014). Also, it has been suggested that birds with aerial foraging behavior tend to have smaller vocal repertoires overall (Leighton & Birmingham, 2021), however, although oilbirds are aerial foragers, they do not follow this trend, indicating that their colonial habits may be have a larger influence in their communication system. This shows evidence towards is a relationship between the social and ecological dynamics of the oilbirds and the size of their repertoire, especially in relation to social behavior, thus further supporting the social complexity hypothesis (Freeberg et al., 2012).

The vocal repertoire showed a high within-vocalization type acoustic variation. This may be a product of variations in vocal track anatomy (Suthers & Hector, 1988) that allow for individual or group identification (Benti et al., 2019; Elie & Theunissen, 2018; Lambrechts & Dhondt, 1995; Suthers & Hector, 1988). Alternatively, it may be a product of environmental degradation inside the caves (Barclay et al., 1979). Despite the high acoustic variation, oilbirds need to be able to communicate efficiently within the caves, thus they should be capable of distinguishing each vocalization type and its ecological function by other factors like contextual cues like time of day, behaviors related to each vocalization, relation with the transmitter, among others (Anderson et al., 2023; Freeberg, 2008).

Oilbirds face different challenges for communicating inside the caves, being the transmission of acoustic information an important one. Within the caves, where oilbirds spend most of the day, there are several signal deterrents. Mostly, caves with big chambers have high echoic surroundings, and the running water makes vocalizations easily masked (Barclay et al., 1979; Marimuthu & Chandrashekaran, 1985) thus making it difficult the communication between individuals. To solve this problem, oilbirds use low-frequency signals to reduce the directionality of their echolocation clicks (Konishi & Knudsen, 1979) but it is not known if they use the same strategy with other vocalizations. All of the vocalization types have a low peak frequency, close to or lower than 2 kHz, so they may use the same mechanism of echolocation clicks in the rest of the vocalizations to improve communication (Brinkløv et al., 2017). Also, this peak frequency matches the maximum hearing range of oilbirds (Konishi & Knudsen, 1979), which demonstrates that oilbirds have developed their vocal repertoire as a way to avoid and overcome ecological deterrents inside the caves and communicate efficiently.

The vocal repertoire of oilbirds was relatively large compared to other song-bird species and included structurally and functionally distinctive vocalization types, that allows for a high level of vocal complexity thus supporting the social complexity hypothesis for communication systems (Freeberg et al., 2012). These characteristics of the vocal repertoire, facilitates the formation of larger colonies, higher group density, and allows for a larger diversity in social roles or status of group members, and of social relationshios, that characterize bird species with complex social dynamics (Freeberg et al., 2012; Krause et al., 2007). The large repertoire and complex communication system of oilbirds most likely evolved from the unique characteristics of their colonial, nocturnal, and cave-dwelling ecology (Snow, 1961) but also allowed oilbirds to develop these unique way of living.

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