Vocal repertoire and group-specific signature in the Smooth-billed Ani, *Crotophaga ani* Linnaeus, 1758 (Cuculiformes, Aves)

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Abstract. Vocal plasticity reflects the ability of animals to vary vocalizations according to context (vocal repertoire) as well as to develop vocal convergence (vocal group signature) in the interaction of members in social groups. This feature has been largely reported for oscine, psittacine and trochilid birds, but little has been investigated in birds that present innate vocalization. The smooth-billed ani (Crotophaga ani) is a social bird that lives in groups between two and twenty individuals, and which presents innate vocalization. Here we analyzed the vocal repertoire of this species during group activities, and further investigated the existence of a vocal group signature. The study was conducted in the Southeast of Brazil between May 2017 and April 2018. Two groups of smooth-billed anis were followed, Guararema and Chargueada groups, and their vocalizations were recorded and contextualized as to the performed behavior. The vocal repertoire was analyzed for its composition, context and acoustic variables. The acoustic parameters maximum peak frequency, maximum fundamental frequency, minimum frequency, maximum frequency and duration were analyzed. To verify the vocal signature of the group, we tested whether there was variation in the acoustic parameters between the monitored groups. We recorded ten vocalizations that constituted the vocal repertoire of the Smooth-billed Ani, five of which ("Ahnee", "Whine", "Pre-flight", "Flight" and "Vigil") were issued by the two groups and five exclusive to the Chargueada group. There were significant differences in the acoustic parameters for "Flight" and "Vigil" vocalizations between the groups, suggesting vocal group signature for these sounds. We established that the Smooth-billed Ani has a diverse vocal repertoire, with variations also occurring between groups of the same population. Moreover, we found evidence of vocal group signature in vocalizations used in the context of cohesion, defense and territory maintenance.

Keywords. Vocal communication; Behavior; Vocal plasticity; Vocal group signature.

INTRODUCTION

Acoustic communication is generally used for recognition among individuals (Beecher, 1988; Berg *et al.*, 2011; Elie & Theunissen, 2018; Benti *et al.*, 2019); acquisition of information about populations (Salinas-Melgoza & Wright, 2012); and vocal labeling, especially among social birds (Wanker *et al.*, 2005). The use of a vocalization associated with a specific context is related to the bird's experience in using the respective signal (Janik & Slater, 2000). Thus, the study of vocal repertoire provides information on how an animal interacts with other species (*e.g.*, Hurd, 1996; Kort & Cate, 2001; Goodale & Kotagama, 2006), with members of its own species, and with the environment.

Pap. Avulsos Zool., 2021; v.61: e20216159 http://doi.org/10.11606/1807-0205/2021.61.59 http://www.revistas.usp.br/paz http://www.scielo.br/paz Edited by: Luís Fábio Silveira Received: 21/07/2020 Accepted: 17/06/2021 Published: 30/07/2021 The vocal plasticity of some bird species allows acoustic variations that can better adjust a vocalization to a specific environment noise profiles (Brumm *et al.*, 2009; Hardman *et al.*, 2017; Lazerte *et al.*, 2017), change some vocal characteristic of adult animals based on experience and context learned throughout life (James & Sakata, 2019), or to interact within a social system, resulting in vocal convergence or a vocal group signature (Mammen & Nowicki, 1981; Tyack, 2008; Martins *et al.*, 2018; Elie & Theunissen, 2018; Benti *et al.*, 2019).

Vocal group signatures are found in animal species that build stable social groups (Boughman, 1998; Sharp *et al.*, 2005; Benti *et al.*, 2019). Such signatures can have multiple impli-

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cations, including group cohesion during flight or foraging (Ford, 1991; Boughman, 1998; Hile & Striedter, 2000), interactions with social partners (Vehrencamp *et al.*, 2003; Radford, 2005), and even allows the inclusion or exclusion of non-group members (Tyack, 2008; Salinas-Melgoza & Wright, 2012). In the case of exclusion of non-group members, a vocal group signature acts as a password (Tyack, 2008) that allows, for instance, access to shared resources among group members. As a result, animals living in stable social groups may benefit from improved access to food resources, either through foraging or group defense (Krebs *et al.*, 1972; Rabenold, 1987; Brown, 1988; Wilkinson, 1992; Brown & Brown, 1996; Elie & Theunissen, 2018).

However, vocal convergence or development of a vocal group signature depends on vocal learning (Bradbury & Vehrencamp, 1998). Therefore, vocal signatures have been associated to birds that learn vocalizations, such as Songbirds (Nowicki, 1983, 1989; Camacho-Schlenker *et al.*, 2011), Psittaciformes (Hile & Striedter, 2000; Berg *et al.*, 2011; Martins *et al.*, 2018) and Trochilidae (Araya-Salas *et al.*, 2019. These birds have regions of the telencephalon that are responsible for vocal learning and that have morphological similarity between these groups (Jarvis *et al.*, 2000).

On the other hand, vocal group signature studies with bird groups of innate vocalization are scarce (Baker, 2004; Radford, 2005). Among these innate vocalizations birds, the Smooth-billed Ani (*Crotophaga ani* Linnaeus, 1758) can be highlighted.

The Smooth-billed Ani is a social bird, living in groups of two to more than twenty members, with an average of seven individuals. They use communal nests and cooperate to maximize the survival of the group (Davis, 1940), and are widely seen in cultivated regions and in open landscapes with shrubs. These animals present uniform black color, a high beak, and length of about 36 cm. They are poor fliers, with little wind resistance (Sick, 2001). This species occurs in the American continent, from Florida to Argentina and throughout Brazil and is mainly insectivorous, feeding largely on arthropods such as spiders, bedbugs and locusts (Sick, 2001).

The vocal repertoire of the Smooth-billed Ani has been studied in Cuba (Davis, 1940) and Puerto Rico (Grieves, 2014) by analysis of the bird's acoustic parameters, and associated with the bird's behavior. However, no study has been conducted in other localities of the American continent in order to identify how this repertoire occurs in different populations. Furthermore, the existence of vocal signature in this group has not yet been investigated.

Considering the limited number of studies on the vocal communication of the Smooth-billed Ani (Davis, 1940; Grieves, 2014; Grieves *et al.*, 2015), the present work had the following aims: (1) To describe the vocal repertoire of the species in the Southeast of Brazil and the context of its vocalizations; (2) to verify whether there are differences in its vocal repertoire with geographical variation; and (3) to assess the occurrence of a vocal group signature in this species.

MATERIAL AND METHODS

Study area

The data was collected in the municipality of Alegre, state of Espírito Santo, in the Southeast of Brazil. The predominant biome in this area is the Atlantic Forest, with tropical and humid Cwa climate characterized by hot and rainy summer and cool and dry winter. The mean annual temperature is 23.1°C, varying between 16.9°C and 29.0°C, and the total annual precipitation amounts to 1,341 mm (Lima *et al.*, 2008).

Two groups were sampled in different areas (one in Guararema and the other in Charqueada) (Fig. 1), apart by a distance of 3.5 km. These areas are characterized by the cultivation of eucalyptus, coffee, fruits and bamboo, with few farmhouses, dirt roads, and little traffic.

Acoustic data

Sampling was carried out between May 2017 and April 2018. Observations and data collection occurred twice a month for each Smooth-billed Ani group, being performed from 06.00 until 10.00 a.m. and from 04.00 p.m. until the return to the roost in the late afternoon. We recorded vocalizations from the two distinct groups, a group identified as Chargueada formed by 7 individuals, and the other group called Guararema with 10 individuals. Because Smooth-billed Anis are very territorial, occupying the same territory and roost tree for a long period, the groups in this study were accompanied when leaving as well as returning to the same roost, which allowed distinguishing the flocks. During data collection, the displacement areas of the groups were different, further suggesting that the two groups were distinct and did not meet during the field work.

For the collection of behavioral data, we adopted the *ad libitum* (Altmann, 1974) methodology, in which the observer freely records the behaviors of the individuals in a non-systematic way, from the moment of encountering them until the loss of visual contact, without time restrictions. A Celestron 8×21 binocular was used for the observations. If the birds vocalized, the vocalization was recorded and associated with the observed behavior. There were two observers, one for recording bird vocalizations and the other for observing and recording behaviors. Behavior collection was always performed by the same observer so as to avoid divergences in the behavior identification.

The recordings were always made from a distance of 10-15 meters so as not to interfere with the behavior of the observed population. Recordings were made with a Sony Icd-px240 digital voice recorder and a Sennheiser MKE600 (40-20,000 Hz) directional microphone. The vocalizations were recorded in MP3 and transformed to WAVE using the software Audacity version 2.4.0. After the transformation, the voices were analyzed in the WAVE format with 44.1-KHz, 16-bit sampling frequency. Considering that each flock comprised several individu-

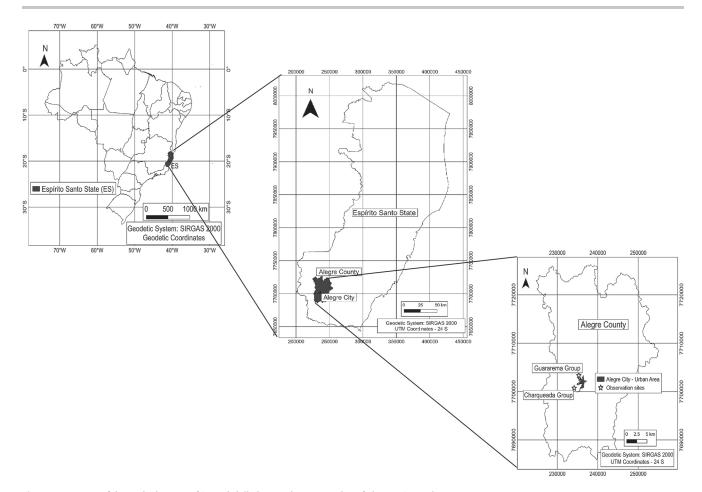


Figure 1. Location of the studied groups of Smooth-billed Ani in the municipality of Alegre, ES, Brazil.

als, and the recordings were made on different days and months, it is expected that the recordings of several individuals in the flock contribute to the group sampling as a whole, as well as to the identification of a vocal group signature.

Data analysis

To analyze Smooth-billed Ani's vocal repertoire, the vocalizations were categorized according to their structure and context. To define the context, the behavior was associated to the bird's vocalization. The nomenclature for vocalization was based on the context and followed the denominations proposed by Grieves (2014), who worked with this species in Puerto Rico. If no literature was available to designate the voicing, it was named according to the related behavior observed.

The vocalizations that are part of the vocal repertoire were also characterized in terms of the number of syllables, number of notes and the presence and absence of harmonics (Fig. 2). The recorded vocalizations with different structures, but same context were considered as the same voice, since the context was the same.

To compare the vocal repertoire we used the acoustic parameters "maximum peak frequency" (MPF), "maximum fundamental frequency" (MFF), "minimum frequency" (or low frequency) (MIF), "maximum frequency" (or high frequency) (MAF) and "duration" (DUR), obtained with the aid of the Avisoft-SASLab Lite software, version 5.1.22 (FFT lenght = 64; Frame = 100%; Window = Hamming; Bandwidth = 896 Hz; Resolution = 689 Hz). In Avisoft-SASLab software, after generating the spectogram, we use the option "activate rectangular cursor" to select the voice and in the tools tab, we click on "au-

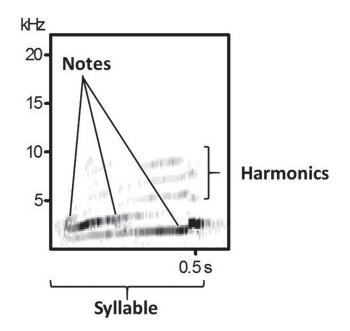


Figure 2. Song structure of the Smooth-billed Ani showing the notes, sillable and harmonic.

tomatic parameter measurements setup" to select the acoustic parameters.

The acoustic parameters used to compare the geographical variation between the data obtained in our work with those from Puerto Rico (Grieves, 2014) were MPF, MIF, MAF and Dur. To verify vocal group signature, we checked if there was a statistical difference between the parameters MPF, MFF, MIF, MAF and Dur of the voices of the groups Charqueada and Guararema. These acoustic variables were tested for normality using the Shapiro-Wilk test. We used the Mann-Whitney test for non-parametric data and analysis of variance (ANOVA) for parametric data. The analyses were performed in the R Studio software (RStudio Team, 2016).

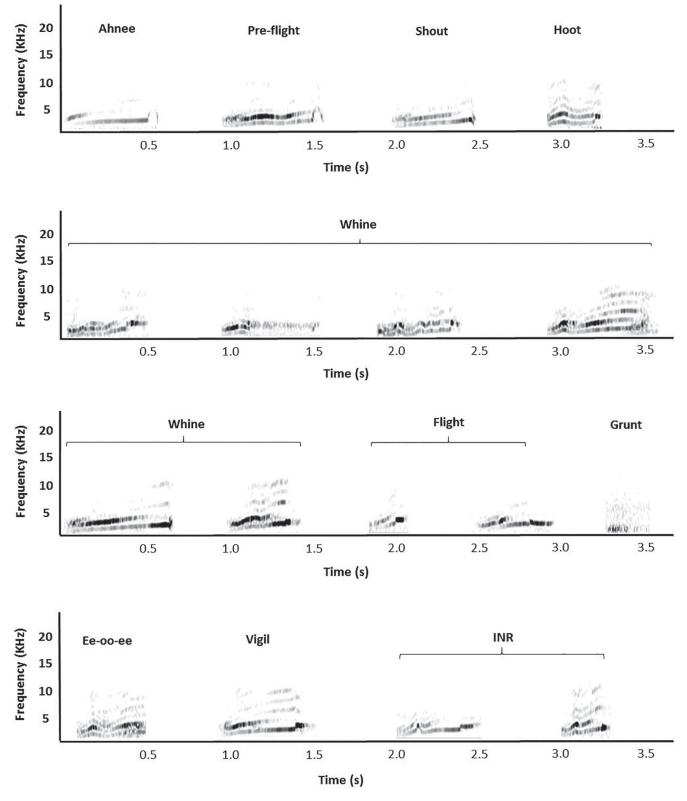


Figure 3. Spectrograms of the ten types of vocalizations of the Smooth-billed Ani: "Ahnee" (A), "Whine" (B, C, D, E, F and G), "Pre-flight" (H), "Shout" (I), "Flight" (J and K), "Hoot" (L), "Grunt" (M), "Ee-oo-ee" (N), "Vigil" (O), "INR" (P and Q).

RESULTS

A total of 207 vocalizations were obtained, of which 135 vocalizations were from the Charqueada group and 72 from the Guararema group. We identified ten vocal behaviors, constituting the vocal repertoire of the Smooth-billed Ani. Each vocalization was characterized in the context in which it was produced, and according to its structure (Table 1). Two vocalizations, "INR" and "Vigil", were only verified in the present population, of which "INR" was less frequent (n = 8) in the recordings and only for the Charqueada group. The "Vigil" vocalization was more frequent and in both Smooth-billed Ani groups (15 recordings for Guararema group and 29 for Charqueada group).

The vocalizations "Whine", "Flight" and "INR" presented different structures in the same context. The "Whine" vocalization had six different structures (Figs. 2B, C, D, E, F and G), varying between 2 and 3 notes and in the presence or absence of harmonics. The sounds "Flight" and "INR" showed variation in the number of notes, with 2 or 3 notes each (Table 1, Fig. 3).

"Ahnee", "Whine", "Pre-flight", "Flight", "Grunt", "Shout", "Hoot" and "Ee-oo-ee" were also recorded in the vocal repertoire of Smooth-billed Ani by other authors (Davis, 1940) and Grieves (2014). When comparing our data with those available by Grieves (2014), it we observed that the mean values for the parameter "maximum mean frequency" were higher for the present population in all similar vocalizations, while for the parameters "minimum frequency" and "maximum peak frequency" the means were higher for the population studied by Grieves (2014), except for "Hoot" sounds. The parameter "duration" had higher values in our study for the sounds "Ahnee", "Preflight", "Shout", "Hoot" and "Ee-oo-ee", while the other vocalizations had shorter duration by comparison (Table 2).

We also observed a variation in the vocal repertoire between the Guararema and Charqueada groups.

Table 1. Vocal repertoire of the Smooth-billed Ani. Char = Chargueada group, Guar = Guararema group.

Vocalization	Syllables	Number of notes	Harmonics	Context	Char	Guar
"Ahnee"	1	2	Present	Produced at dawn before leaving the communal roost and during foraging.	13	6
"Pre-flight"	1	3	Present	Produced one or more times before taking flight.	12	11
"Flight"	1	2-3	Present	Produced at the beginning or during the flight.	29	37
"Shout"	1	3	Present	Produced during periods of intense movement, either from predators or humans, near the communal roost site.	4	
"Hoot"	1	2	Present	Produced during the chase of intruders in the group's territory.	2	
"Grunt"	1	1	Absent	Produced inside the communal roost and also during the chase of intruders.	6	
"Whine"	1	2-3	Present or absent	Usually produced in the morning, before the birds leave the communal roost.	31	4
"Ee-oo-ee"	1	2	Present	Produced when the group is inside the communal roost, both in the morning and in the afternoon.	3	
"Vigil"	1	3	Present	Produced by the bird keeping vigil during the foraging period as well as when the flock was returning to the communal roost site.	27	14
"INR"	1	2-3	Present	Produced inside the communal roost in the morning and in the afternoon.	8	

Table 2. Mean values (\pm SD) for the acoustic parameters of similar vocalizations between the data by Grieves (2014) and those obtained in this work.

Vocalization type –	Maximum mean frequency (KHz)		Minimum mean frequency (KHz)		Maximum peak frequency (KHz)		Duration (s)	
	Present study	Grieves (2014)	Present study	Grieves (2014)	Present study	Grieves (2014)	Present study	Grieves (2014)
"Ahnee"	$\textbf{6.49} \pm \textbf{2.125}$	3.107 ± 0.672	0.131 ± 0.074	1.391 ± 0.276	2.278 ± 0.362	3.582 ± 1.394	0.6933 ± 0.0861	0.5001 ± 0.0701
"Pre-flight"	5.634 ± 2.093	3.120 ± 1.293	0.160 ± 0.126	1.397 ± 0.189	2.539 ± 0.236	3.550 ± 1.880	0.555 ± 0.0579	0.3494 ± 0.0665
"Flight"	$\textbf{6.245} \pm \textbf{1.903}$	$\textbf{3.250} \pm \textbf{1.086}$	$\textbf{0.187} \pm \textbf{0.196}$	1.320 ± 0.170	2.739 ± 0.565	3.487 ± 1.273	0.343 ± 0.0758	0.3835 ± 0.0487
"Grunt"	4.766 ± 1.229	2.035 ± 0.583	0.100 ± 0.0	1.327 ± 0.442	1.283 ± 0.194	2.224 ± 0.624	0.0786 ± 0.0111	0.1362 ± 0.0285
"Shout"	5.550 ± 2.193	3.515 ± 0.592	$\textbf{0.200} \pm \textbf{0.115}$	1.552 ± 0.222	$\textbf{2.125} \pm \textbf{0.298}$	3.301 ± 0.107	0.460 ± 0.0255	0.373 ± 0.0331
"Hoot"	9.650 ± 2.050	1.854 ± 0.943	0.100 ± 0.0	$\textbf{0.839} \pm \textbf{0.117}$	2.400 ± 0.0	2.028 ± 1.583	0.411 ± 0.0275	0.1502 ± 0.037
"Ee-oo-ee"	6.466 ± 2.542	5.302 ± 2.680	$\textbf{0.166} \pm \textbf{0.115}$	$\textbf{0.866} \pm \textbf{0.0}$	$\textbf{2.433} \pm \textbf{0.450}$	4.779 ± 2.971	0.411 ± 0.0275	0.3925 ± 0.0795
"Whine"	$\textbf{7.091} \pm \textbf{2.839}$	$\textbf{2.888} \pm \textbf{0.295}$	0.117 ± 0.074	1.218 ± 0.049	$\textbf{2.408} \pm \textbf{0.559}$	3.130 ± 0.353	0.5311 ± 0.1655	0.6486 ± 0.1987

Table 3. Mean values $(\pm$ SD) for the acoustic parameters of similar vocalizations between the Smooth-billed Ani groups, Guararema (Guar) and Charqueada (Char). DUR = Duration; MAF = Maximum frequency; MIF = Minimum frequency; MFF = Maximum fundamental frequency; MPF = Maximum peak frequency. * Statistical difference between areas.

Vocalization type	MAF (KHz)		MIF (KHz)		MPF (KHz)		MFF (KHz)		DUR (s)	
	Guar	Char	Guar	Char	Guar	Char	Guar	Char	Guar	Char
"Ahnee"	5.450 ± 0.84	6.976 ± 2.38	0.166 ± 0.10	0.115 ± 0.05	2.366 ± 0.61	2.238 ± 1.89	2.333 ± 0.64	2.138 ± 0.20	$\textbf{0.722} \pm \textbf{0.09}$	0.67 ± 0.08
"Whine"	4.95 ± 0.94	7.36 ± 2.89	0.100 ± 0.0	0.119 ± 0.79	2.25 ± 0.10	2.42 ± 0.59	2.25 ± 0.10	2.11 ± 0.43	0.44 ± 0.05	0.54 ± 0.17
"Pre-flight"	6.53 ± 2.47	4.80 ± 1.28	0.136 ± 0.12	$\textbf{0.183} \pm \textbf{0.13}$	2.58 ± 0.18	2.50 ± 0.27	2.40 ± 0.44	2.34 ± 0.28	0.54 ± 0.05	0.56 ± 0.06
"Flight"	6.31 ± 1.56	6.15 ± 2.29	$0.154^{*} \pm 0.17$	$0.231^{*} \pm 0.21$	2.71 ± 0.49	2.77 ± 0.64	2.40 ± 0.58	2.41 ± 0.45	0.33 ± 0.08	0.34 ± 0.06
"Vigil"	7.26* ± 1.71	$6.04^{*} \pm 2.04$	0.1000 ± 0.0	0.151 ± 0.11	$2.85^{\ast}\pm0.91$	$2.38^{\ast}\pm0.28$	2.36 ± 0.47	2.24 ± 0.36	0.53 ± 0.05	0.56 ± 0.06

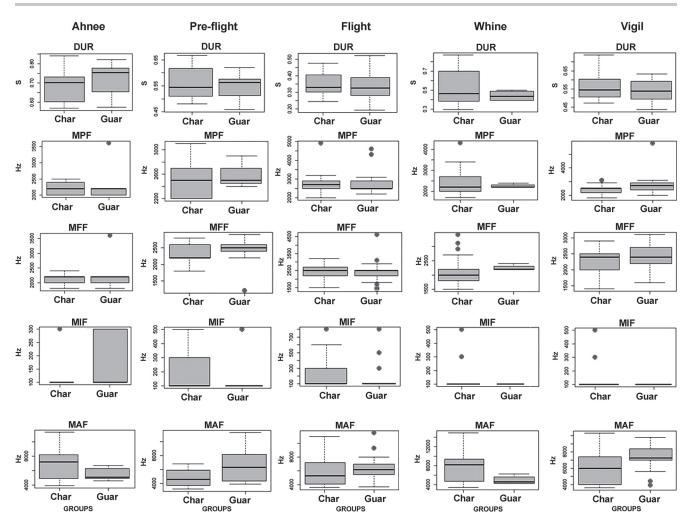


Figure 4. Boxplots (median and quartiles) of acoustic parameters of the similar vocalizations of Charqueada and Guararema groups of Smooth-billed Ani. Vocalizations: "Ahnee", "Whine", "Pre-flight", "Flight" and "Vigil". Acoustic parameters: DUR = duration; MPF = maximum peak frequency; MFF = maximum fundamental frequency; MIF = minimum frequency; MAF = maximum frequency.

Table 4. T test and Mann-Whitney values comparing similar vocalizations between the Smooth-billed Ani groups, Charqueada and Guararema. df = Degrees of freedom; DUR = Duration; MAF = Maximum frequency; MIF = Minimum frequency; MFF = Maximum fundamental frequency; MPF = Maximum peak frequency. * Statistical difference.

		Acoustic variables						
		MAF	MIF	MPF	MFF	DUR		
"Ahnee"	Test value	2.268	29	44.5	38	1.027		
	df	1	1	1	1	1		
	Р	0.150	0.187	0.647	0.963	0.325		
"Whine"	Test value	89.5	66	63	32.5	71		
	df	1	1	1	1	1		
	Р	0.161	0.652	0.979	0.1255	0.6592		
"Pre-flight"	Test value	36.5	80.5	0.674	46.5	0.266		
	df	1	1	1	1	1		
	Р	0.0738	0.2316	0.421	0.2327	0.611		
"Flight"	Test value	450.5	657.5	563	570	0.299		
	df	1	1	1	1	1		
	Р	0.2688	0.0292*	0.7326	0.6668	0.586		
"Vigil"	Test value	117	224	110.5	0.751	1.578		
	df	1	1	1	1	1		
	Р	0.0489*	0.095	0.0281*	0.392	0.217		

Although the field sampling effort was similar between Smooth-billed Ani groups (Charqueada = 1,271 minutes and Guararema = 1,129 minutes), the number of vocal records was different, with 135 vocalizations recorded for the Charqueada group and 72 for the Guararema group. The Charqueada group also had a greater number of vocal behaviors (n = 10) than the Guararema group (n = 5) (Table 1). "Whine" (n = 31), "Flight" (n = 29) and "Vigil" (n = 27) were the most recorded vocalizations in the Charqueada group, while in the Guararema group "Flight" was the most frequent (n = 37).

The vocalizations "Ahnee", "Whine", "Pre-flight", "Flight" and "Vigil" were recorded for both groups (Charqueada and Guararema) (Fig. 4), while "INR", "Ee-oo-ee", "Hoot", "Grunt" and "Shout" were only verified for the Charqueada group. There were no vocalizations exclusive to the Guararema group (Table 1).

The vocal group signature were verified to "Flight" and "Vigil" vocalizations, in which there were statistical differences between the groups (Tables 3 and 4). For "Flight", the variation occurred in the parameter MIF (Wilcox-test = 657.5, degrees of freedom [df] = 1, p = 0.0292), whereas for "Vigil", variation was detected in MAF (Wilcox-test = 117, df = 1, p = 0.0489) and MPF (Wilcox-test = 110.5, df = 1, p = 0.0281), suggesting a vocal group signature for these vocalizations.

DISCUSSION

Here ten vocalizations were recorded in the observed Smooth-billed Ani population, compared to 13 vocalizations reported by Grieves (2014) in Puerto Rico and 11 by Davis (1940) in Cuba.

Such difference in the vocal repertoire of these birds may be related to the period of data sampling. The vocalizations that were recorded only by Davis (1940) and Grieves (2014), were associated to defense and protection of the nests. They recorded voices associated with defense of the nests and danger behavior, as "Alarm call", "Quack", "Whew" (Davis, 1940) and "Ahnee alarm", "Chlurps", "Chucks" (Grieves, 2014), and related to the presence of birds in the nests, as "Complaint", "Objecting", "Chuckle" in Davis (1940) and "Growls" and "Whistle" in Grieves (2014).

The recording of these vocalizations by these authors but not by us could be because the sampling effort of the work of these authors was all during the breeding season, which may have increased the chances of recording these types of vocal behaviors. On the other hand, we distribute our sampling effort in the two phases of the animal's life, reproductive and non-reproductive period, which may have decreased our chances of recording vocalizations associated with reproductive behavior, but favored the possibility of recording the vocalization of "Vigil", associated with the vigilance behavior during group foraging.

The vocalizations recorded only in this study were "Vigil" and "INR". The first voice was frequent in our study, while the second one ("INR") was less frequent, and only in one of the groups. The "INR" sound was considered as a different vocalization from "Whine" because, despite having the same context of the bird within the roost, it does not precede the bird's departure from the roost, but rather its remaining in it. This different voices recorded in this study and by others authors demonstrating a variation in the vocal repertoire of the Smooth-billed Ani populations.

The vocal repertoire of the species is composed by at least ten different types of vocalizations, eight ("Ahnee", "Pre-flight", "Flight", "Grunt", "Shout", "Hooot", "Ee-oo-ee" and "Whine") were also mentioned by Grieves (2014), and five ("Ahnee", "Grunt", "Hoot", "Shout" and "Whine") by Davis (1940). Despite this variation in vocal repertoire in relation to the observations of Davis (1940) and Grieves (2014), it can be said that Smooth-billed Anis have a well-defined repertoire, characterized by vocalizations like "Ahnee", "Whine", "Pre-flight", "Flight", "Grunt", "Shout", "Hoot" and "Eo-e-ee", as they occur in more than one population. Moreover, the fact that one or more vocalizations have not been detected in all studies does not necessarily mean that they do not integrate the repertoire, but rather that they may just not have been recorded in a specific sampling period.

Vocal repertoire variations have been studied in other birds with less or more elaborate repertoires. For instance, the great curassow (*Crax rubra*) has been reported to exhibit only five vocalization types, of which two are sex-specific (Baldo & Mennill, 2011), whereas the Niceforo's wren (*Thryophilus nicefori*) displays 21 sound types, with sexual variation in the vocal repertoire, ranging from 12 to 21 sound types in males and 7 to 9 in females (Valderrama *et al.*, 2008). Compared with variation of these extremes, Smooth-billed Anis have a well-diversified repertoire.

Another important aspect in the bioacoustics of the Smooth-billed Ani is its ability to modify the vocalization structure for the same context. For instance, it uses the vocalizations "Whine", "Flight" and "INR", which differ in number of notes and the presence or not of harmonics, all in the same context, as shown in Table 1 and Fig. 3.

In the case of the two groups of Smooth-billed Ani that we followed, we found that there were differences between the groups for some similar voices, specifically for "Flight" and "Vigil" voices. This difference was interpreted as a vocal group signature, detected by significant differences in some acoustic parameters of these vocalizations. This is consistent with the circumstances of these vocalizations, since "Flight" is used in the context of group cohesion during flight, as also observed in budgerigars (Hile & Striedter, 2000), whereas "Vigil" is used in territory surveillance and monitoring, alerting the other members of the group about any imminent danger. This type of vocal signature is related to various mammal groups, such as bats (Boughman, 1998; Wenrickboughman & Swilkinson, 1998; Gillam & Chaverri, 2012; Knörnschild et al., 2012), wolves (Zaccaroni et al., 2012), gazelles (Volodin et al., 2014), meerkats (Townsend et al., 2010), whales (Vester et al., 2016), as well as for birds that exhibit vocalization learning (Mammen & Nowicki, 1981; Nowicki, 1983, 1989; Baker, 2004; Elie & Theunissen, 2018; Martins et al., 2018; Araya-Salas et al., 2019; Benti et al., 2019). However, as previously mentioned, studies in birds with innate vocalization are scarce (Baker, 2004; Radford, 2005).

Considering all the above, the present study represents a relevant contribution of acoustic information for the Smooth-billed Anis, a group of birds with innate vocalization and elaborate vocal repertoire, including interpopulation variation. In addition, it provides evidence of vocal group signature in the species, serving as basis for further research to increase the knowledge about this bird group.

CONCLUSION

The Smooth-billed Ani has an elaborate vocal repertoire, presenting voicings that are common across populations (*e.g., "Ahnee", "Pre-flight", "Flight", "Shout", "Hoot",* "Grunt", "Whine", "Ee-oo-ee"). Variations were observed in the vocal repertoire and in the acoustic parameters of vocalizations between different populations, or even between groups of the same population, but further studies in other populations should be performed to better clarify these variations. In addition, we found an evidence of a vocal group signature in vocalizations used in the context of cohesion, defense and territory maintenance, in which there is a need to identify the group itself and not the individuals.

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AUTHORS' CONTRIBUTIONS

Ronan de Azevedo Monteiro: Conceptualization, Methodology, Field work, Data collect, Formal analysis, Writing – original draft. **Carolina Demetrio Ferreira:** Supervision, Conceptualization, Data analysis, Writing – original draft, review & editing. **Gilmar Perbiche-Neves:** Data analysis, Writing – review & editing. All the authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

CONFLICT OF INTEREST

Authors declare there are no conflicts of interest.

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