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COMPARATIVE ANALYSIS OF VOCALIZATIONS OF GUANS (GALLIFORMES, CRACIDAE, PENELOPE) FROM BRAZIL (SOUTH AMERICA)

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ABSTRACT – The genus *Penelope* is a group of guans of the family Cracidae, Order Galliformes, which is widely distributed in Brazil, totaling seven species (*Penelope jacquacu*, *P. jacucaca*, *P. marail*, *P. pileata*, *P. obscura*, *P. ochrogaster* and *P. superciliaris*). Each guan species has a particular distribution, with the exception of the Rusty-margined Guan (*P. superciliaris*) that is found in almost all the national territory. The objective of this study involves analyzing the songs of the species of *Penelope* in different regions of Brazil, and comparing them to those of the species *P. superciliaris* to know if their singing patterns are modified when overlapping with other species of the genus, thus avoiding competition by acoustic interference. This comparative analysis involving several guan species is the first performed in cracids in the world, thus being highly relevant for future studies. Furthermore, we are providing the diagnostic characteristics, conservation status and ecological data of each species of the genus *Penelope* reported from Brazil.

KEY WORDS: ACOUSTIC INTERFERENCE; APOMORPHIES; COMPETITION; CONSERVATION STATUS; CRACIDS.

ANÁLISE COMPARATIVA DAS VOCALIZAÇÕES DOS JACUS (GALLIFORMES, CRACIDAE, PENELOPE) DO BRASIL (AMÉRICA DO SUL)

RESUMO – O gênero *Penelope* é um grupo de jacus da família Cracidae, Ordem Galliformes, que é amplamente distribuído no Brasil, totalizando sete espécies (*Penelope jacquacu*, *P. jacucaca*, *P. marail*, *P. pileata*, *P. obscura*, *P. ochrogaster* e *P. superciliaris*). Cada espécie de jacu tem uma distribuição particular, com exceção do jacupemba (*P. superciliaris*), o qual é encontrado em quase todo o território nacional. O objetivo deste estudo consiste em analisar os cantos das espécies de *Penelope* em diferentes regiões do Brasil, e comparando-os com os da espécie *P. superciliaris* para saber se os seus padrões de vocalização são modificados quando estão em sobreposição com outras espécies do gênero, evitando, desta forma, a competição por interferência acústica. Esta análise comparativa envolvendo várias espécies de jacus é a primeira realizada em cracídeos no mundo, sendo, portanto, altamente relevante para estudos futuros. Além disso, nós estamos fornecendo as características diagnósticas, estado de conservação e dados ecológicos de cada espécie do gênero *Penelope* reportada para o Brasil.

PALAVRAS CHAVE: INTERFERÊNCIA ACÚSTICA; APOMORFIAS; COMPETIÇÃO; ESTADO DE CONSERVAÇÃO; CRACÍDEOS.

ANÁLISIS COMPARATIVO DE LAS VOCALIZACIONES DE LOS GUANS (GALLIFORMES, CRACIDAE, PENELOPE) DEL BRASIL (AMÉRICA DEL SUR)

RESUMEN – El género *Penelope* es un grupo de pavas de familia Cracidae, Orden Galliformes, que es ampliamente distribuido en el Brasil, por un total de siete especies (*Penelope jacquacu*, *P. jacucaca*, *P. marail*, *P. pileata*, *P. obscura*, *P. ochrogaster* y *P. superciliaris*). Cada tipo de pava tiene una distribución particular, excepto por el yacupoí (*P. superciliaris*), que se encuentra en casi todo el territorio nacional. El objetivo de este estudio es examinar las vocalizaciones de las especies de *Penelope* en diferentes regiones de Brasil, y su comparación con la especie *P. superciliaris* para saber si sus patrones de vocalización se modifican cuando se superponen con otras especies del género evitando, de esta manera, la competición por interferencia acústica. Este análisis comparativo que involucra varias especies de pavas es el primero celebrado en crácidos en el mundo, por eso es muy relevante para futuros estudios. Además, estamos proporcionando las características de diagnóstico, estado de conservación y los datos ecológicos de cada especie del género *Penelope* reportados para Brasil.

PALAVRAS CLAVE: INTERFERENCIA ACÚSTICA; APOMORFIAS; COMPETIÇÃO; ESTADO DE CONSERVAÇÃO; CRACÍDEOS.

INTRODUCTION

In Brazil, there are seven species of the genus *Penelope* (Cracidae: Galliformes). The Spix's Guan (*Penelope jacquacu*) is distributed in the Amazon region, south of the Solimões-Amazonas and west of the Negro river, in the States of Acre, Amazonas, Mato Grosso, Pará, Rondônia and

Roraima; in this same region Marail Guan (*P. marail*) occurs in the States of Amapá, Amazonas, Pará and Roraima, north of the Amazon river and east of the Negro river. The White-crested Guan (*P. pileata*) occurs in the east Amazonas, Maranhão, Mato Grosso and Pará States. Individuals of the White-browed Guan (*P. jacucaca*) are distributed among the States of the Northeast region to Minas Gerais. The Dusky-legged Guan (*P. obscura*) is from the States of Minas Gerais to Rio Grande do Sul. The Chestnut-bellied Guan (*P. ochrogaster*) occurs in Central Brazil, and in the States of Minas Gerais and Tocantins. Among all species, only the Rusty-margined Guan (*P. superciliaris*) occupies almost the entire Brazilian territory, with the exception of the States of Acre, Amapá, Amazonas and Roraima (Sibley & Monroe 1990, Stotz et al. 1996, Brooks 2006, Silveira & Straube 2008, BirdLife International 2015, WikiAves 2015). Possibly, their distribution over different geographic regions in the country may be responsible for the differentiation of singing among these individuals.

A phenomenon of sound that can be analyzed is “acoustic interference”, consisting of receiving sounds from two or more different sources. Same authors reported that the acoustic signals of different species communicating in the same habitat may suffer mutual interference and masking (Cody & Brown 1969, Littlejohn & Martin 1969, Ficken et al. 1974). Ficken et al. (1974) related evidence that bird species *Vireo olivaceus* and *Empidonax minimus*, which breed in similar habitats at similar times, adjust the temporal patterning of their singing with respect to the singing of another species in such a way as to avoid temporal overlap between the two kinds of songs (Ficken et al. 1974). Later, studies on comparative analysis of vocalizations of different species were performed by Winkler & Short (1978), involving acoustical signals in pied woodpeckers. Furthermore, Slabbekoorn et al. (1999) report on comparative analysis of birds, as the comparative analyses of “perch-coo” vocalizations in *Streptopelia* doves (Slabbekoorn et al. 1999). In assemblages of acoustically communicating animals, heterospecific sounds may constrain not only the evolution of signal traits but also the much less-studied signal-processing mechanisms, that define the recognition space of a signal, as observed in dendrobatid frogs (Amézquita et al. 2011). According to Florence’s Zoophonia, each species has a unique vocalization (Vielliard 1993). It is thus expected that the songs of the guan species will also corroborate this hypothesis. Due to the spatial distribution of the genus *Penelope* throughout the Brazilian territory, we intend to analyze if closer species tend to differ more pronouncedly in their vocalization. This study aims to test whether competition is acting as the main evolutionary force driving the species without interfering acoustically with each other.

The hypothesis of this research involves (1) analyzing the songs of the species of *Penelope* in different regions of Brazil, (2) and comparing these with the generalist species *P. superciliaris*. We are interested in discovering if singing is modified depending on the region where the species is located, as a result of competition with other species in the genus, thus avoiding competition by acoustic interference.

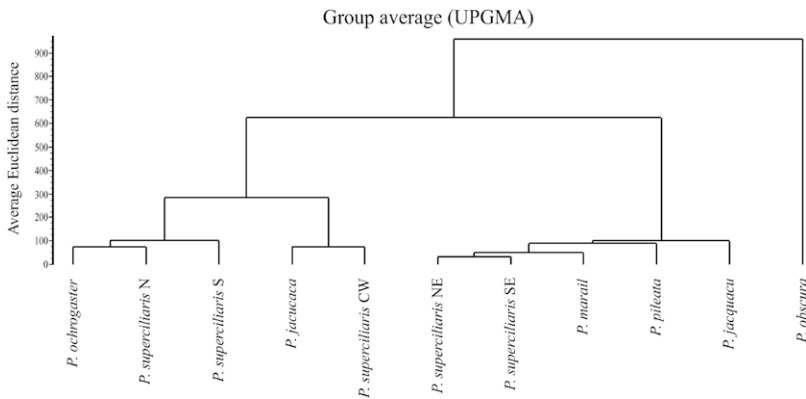
MATERIALS AND METHODS

Data collection and analyses of songs

The songs were obtained through Macaulay Library, WikiAves and xeno-canto websites, in wave format files (high-quality field recordings). The recording files were equalized and normalized

in software Audacity 2.1.1 (Audacity 2015). The program Sound Ruler 0.9.6.0 (Gridi-Papp 2007) produced the graphs (Cross Correlation): Oscillogram (Amplitude X Time) of the section and Oscillogram of the call, Spectrogram (Frequency X Time) and Power Spectrum (Amplitude X Frequency) (Appendix 1). Collected data were filled into the matrix, that includes note duration, period ($T=1/f$), dominant frequency, maximum frequency, minimum frequency, emission rate ($1/T$) and frequency band (MaxFreq minus MinFreq) (Table 1). The software Fitopac 2.1.2.85 (Shepherd 2010) elaborated the dendrogram (Figure 1) – average Euclidean distance, UPGMA (Unweighted Pair Group Method with Arithmetic Mean). Ten songs were used for each species. Rusty-Margined Guans from five localities that corresponds to five Brazilian regions – North, Northeast, Central-West, Southwest and South, resulted in 50 calls of *P. superciliaris*. Thus, in total 110 vocalizations calling type were analyzed. The best vocalizations of each guan, including the five localities of *P. superciliaris*, are in wave format (Appendix 2).

Figure 1 - Dendrogram of the vocalizations of the *Penelope* species from Brazil.



Data of Brazilian Species

The diagnostic characteristics, conservation status, ecological data and other information of the *Penelope* species from Brazil are based on same ornithologists authors and websites (e.g. Sick 2001, Grantsau 2010, BirdLife International, Handbook of the Birds of the World Alive, IUCN Red List of Threatened Species and WikiAves websites).

Table 1 - Collected data of the graphs of the *Penelope* species from Brazil (Cross Correlation).

Species	Note Duration	Period	Dominant frequency	Maximum frequency	Minimum frequency	Emission rate	Frequency band
<i>P. jacuacu</i>	0,4155	9,398	1031,25	1031,25	781,25	0,1064	250
<i>P. jacucaca</i>	0,1727	1,0452	1656,25	1656,25	1656,25	0,9568	0
<i>P. marail</i>	0,9197	4,4689	843,75	968,75	843,75	0,2238	125

<i>P. obscura</i>	0,0719	0,5035	2906,25	2968,25	2718,75	1,9861	250
<i>P. ochrogaster</i>	0,0959	0,4027	2093,75	2156,25	2031,25	2,4832	125
<i>P. pileata</i>	0,1007	0,8966	968,75	1093,75	968,75	1,1153	125
<i>P. superciliaris</i> N	0,1103	0,6233	2031,25	2031,25	2031,25	1,6044	0
<i>P. superciliaris</i> NE	0,0959	0,2461	906,25	906,25	843,75	4,0634	63
<i>P. superciliaris</i> CW	0,3612	0,6681	1593,75	1656,25	1531,25	1,4968	125
<i>P. superciliaris</i> S	0,1566	0,3964	2093,75	2093,75	1843,75	2,5227	250
<i>P. superciliaris</i> SE	0,0607	0,2685	906,25	906,25	906,25	3,7244	0

RESULTS

The dendrogram (Figure 1) showed two distinct groups, where the species *P. superciliaris* present in each group differs acoustically from other species grouped in each region. The vocalizations of *P. ochrogaster* (Central region) and *P. jacucaca* (Northeast region) do not suffer acoustic interference from vocalizations of *P. superciliaris*, which are regionally different. In the left tree, the pattern is reversed: the songs of *P. superciliaris* correspond to other regions of other species (North region). The vocalization of *P. obscura* differs completely from all other species, forming what we call an external group, inhabiting the Southeastern and Southern regions.

Data of the genus Penelope Merrem, 1786 reported from Brazil

Penelope jacquacu Spix, 1825

Spix's Guan

Jacu de Spix

Apomorphy. Ventral side of body dark reddish-brown.

Description. 66-76 cm; male 1242-1360 g, female 1142 g. With bronze olive green upperparts and bright rufescent underparts from lower foreneck to undertail-coverts. *Penelope jacquacu* is a large species with dark plumage, but with clear bottoms and superciliary band intensely brownish; reddish legs and eyes of blue color with naked around the area.

Habitat. Humid rain and cloud forest, including both solid ground and seasonally flooded forest. Also in forest borders, slashed clearing with scattered trees and gallery forest. In tropical zone and locally in lower subtropical zone.

Distribution. Occurs in the upper Amazon to the river Tapajós (Mato Grosso), Bolivia, Colombia, Guyana and to the left the Negro river bank.

Food and feeding. Small fruits (e.g. of palms) and seeds have been found in gizzards of collected birds; apparently prefers ripe, soft fruit. Forages singly, in pairs or in small family groups, mainly in middle and top strata of trees; seldom descends to ground.

Conservation status (IUCN). Least Concern (LC).

Penelope jacucaca Spix, 1825

White-browed Guan

Jacucaca

Apomorphy. This species has different part of the naked neck separate on the sides of the head by a black and a white band.

Description. 65-70 cm. Conspicuous white supercilium with a narrow black line below, separating it from bare skin of sides of face. *Penelope jacucaca* is a large very dark kind, cinnamon colored, with white streaks and black tuft. Broad white superciliary areas unite the forehead.

Habitat. Inhabits dry areas of stunted forest and Caatinga. In lowlands.

Distribution. Occurs in the States of Maranhão, Piauí, Ceará, Paraíba, Alagoas and Bahia.

Food and feeding. Sometimes individuals come to ground to feed, and they can visit the Rhamnaceae *Ziziphus juazeiro* trees to feed.

Conservation status (IUCN). Vulnerable (VU).

Penelope marail Müller, 1776

Marail Guan

Jacumirim

Apomorphy. Ventral side of the body is dark brown. Tarsus 65 mm or less. Bright olivaceous green on dorsal side.

Description. 63-68 cm; 770-1015 g. It has greenish olive gloss on back, wings and central tail feathers, and bluish black lateral tail feathers. *Penelope marail* has a plumage with crisp green reflections. The tarsus is short, an adaptation to arboreal life.

Habitat. Heavy tropical forest, especially near water, near the coast or inland; less often in secondary growth.

Distribution. Amapá, Amazonas, Pará, Roraima, French Guyana, Surinam, Guyana and Venezuela.

Food and feeding. Almost exclusively fruit, especially berries and Dupas. It is a large seed disperser.

Conservation status (IUCN). Least Concern (LC).

Penelope obscura Temminck, 1815

Dusky-legged Guan

Jacuaçu

Apomorphy. Black feet.

Description. 68-75 cm; 960-1200 g. Only member of genus with dark legs; overall plumage and bare facial skin also dark. *Penelope obscura* is a southern representative of large size. Very dark

bronze-green, almost whitish superciliary band and without any rufousness on the wing; mantle, neck and chest finely striated with white. The male has a red iris. Female brown.

Habitat. Tall forest, gallery forest, small river islands with forest surrounded by grassland, woodland patches and secondary growth in lowlands and foothills of tropical and upper tropical zones; sometimes ventures into scrub and agricultural land.

Distribution. In São Paulo and in the Serra do Mar on the coast, having become very scarce; sometimes side of by side the jacutinga. They live in the Southeast and South regions of Brazil, Minas Gerais and Rio de Janeiro to Rio Grande do Sul, Uruguay, Paraguay, Argentina and Bolivia.

Food and feeding. Fruits, including those of *Eugenia uruguayensis*, *Citharexylum montevidense*, *Rapanea lorentziana*, *Didymopanax* sp., *Calypttranthes* sp. and *Croton* sp., also those of certain palms, which are apparently favorite food in Paraguay; recorded invading poultry yards to feed on corn in Rio Grande do Sul; study in São Paulo suggests species is rather specialized as frugivorous.

Conservation status (IUCN). Least Concern (LC).

Penelope ochrogaster Pelzeln, 1870

Chestnut-bellied Guan

Jacu de Barriga Castanha

Apomorphy. Ventral side of body bright reddish-brown.

Description. 67-75 cm. Plumage less contrasted, mainly because upperparts are paler; hindneck of same general color as rest of upperparts; browner ear-coverts. Black band bordering bare facial skin and throat, and richer rufous underparts. *Penelope ochrogaster* is a very large species of reddish-brown crest and contrasting whitish superciliary stripe with black eyebrow which extends in a stripe around the ear and throat region.

Habitat. Typically occurs in swampy woods of deciduous trees and also savannas, in low-lands. Probably prefers heavily wooded areas along rivers or in swamps; also inhabits mixed areas of forest interspersed with savanna or campo. Preferred habitat in Poconé region, Mato Grosso, is semi-deciduous gallery forest growing on higher terrain that is rarely flooded; during the dry season these areas generally have a heavy covering of leaf litter on the ground.

Distribution. Occurs in the “cerrado” (tropical savanna), northern Pantanal and along the São Francisco River, in the States of Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais and Tocantins.

Food and feeding. Recorded feeding on the flowers of a *Tabebuia* sp. tree.

Conservation status (IUCN). Vulnerable (VU).

Penelope pileata Wagler, 1830

White-crested Guan

Jacupiranga

Apomorphy. Dorsal side of the neck reddish-brown, blackish green back.

Description. 75-82 cm, 1100-1600g. Most colourful member of genus, with marked contrast between glossy dark greenish olive on most of upperparts and rich chestnut rufous areas on underparts. Rufous hindneck and upper mantle, contrasting with rest of mantle, back, wings and tail, clearly distinguish this species. *Penelope pileata* is a great unmistakable species recognized by the white and tousled tuft and charged by the brown color of the neck and lower part; green mantle.

Habitat. Forest in lowlands; seems to occur exclusively in rather dense forest, although general ecology still poorly known.

Distribution. It is restricted to the southern bank of the Amazon. Occurs from the lower Xingu Wood to eastern Pará, Maranhão and Mato Grosso.

Food and feeding. It is mostly arboreal, but sometimes also forages in the soil.

Conservation status (IUCN). Vulnerable (VU).

Penelope superciliaris Temminck, 1815

Rusty-margined Guan

Jacupemba

Apomorphy. It has a conspicuous secondary margined brown-reddish color.

Description. 55 cm; 750-880g. *Penelope superciliaris* is the smallest representative of this genus. Possesses more prominently in males a triangular nude area and red dewlap displays a rudimentary tuft, wide wings with ferruginous edges distinct, whitish breast with design, red iris in both sexes.

Habitat. Heavy forest, forest borders, gallery forest, capoeira, forest groves in cerrado woodlands, caatinga, river and lake edge, usually in lowlands: recorded at 1100 m at Serra do Japi (São Paulo).

Distribution. It occurs south of the Amazon and Madeira River, in Central region, Northeast and Meridio-eastern Brazil, to States of Rio Grande do Sul and Paraguay.

Food and feeding. Mainly fruits, including those of bicuiba (*Virola* sp.), sapacaia (*Lecythis* sp.) murici (*Byrsonima* sp.) and guarumo (*Cecropia* sp.).

Conservation status (IUCN). Least Concern (LC).

DISCUSSION

The results corroborate the hypothesis presented in this paper, since species probably differ acoustically when they have very similar distributions, so that acoustic interference does not happen between these species. In addition, the vocalizations of *P. superciliaris* in several locations in Brazil differ when they are in coexistence with other species of its genus, avoiding competition among the two co-occurring species. In this regard, the concept of acoustic niche can be used to specify the regions where each species inhabits. From one generalized song (*P. superciliaris*), species in sympatry (overlapping distributions) evolve different vocalizations.

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