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ORIGINAL ARTICLE



Variation among vocalizations of *Taraba major* (Aves: *Thamnophilidae*) subspecies

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ABSTRACT

Geographical variation of bird vocalizations may be related to factors influencing sound production and sound propagation. If birds, e.g. the Great Antshrike (*Taraba major*), produce vocalizations that develop normally in the absence of learning, these variations may reflect evolutionary divergence within species. In this case, vocal variation could be influenced by habitat structure, since abiotic features and vegetal cover affect sound propagation through environment. Selective pressures may be acting on populations in different ways, which could culminate in a process of speciation. Thus, we searched for structural variation of Great Antshrike vocalizations between subspecies and sought for relationships between these vocal variation and environmental structure. We found variations in frequency and time features of vocalizations among subspecies, which are correlated to latitude, elevation and climate. We also observed an increase in vocal differences along with an increase in distances between individuals, which could reflect isolation of subspecies and the vocal adaptation to different environments.

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isolation-by-distance; vocal
variation; bioacoustics;
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Introduction

The current knowledge about vocal variation in birds is mostly restricted to oscine passerines (suborder Passeri). In this group, learning and auditory feedback exert great influence on vocal development (Marler & Tamura 1964; Marler 2000). Thus, vocal variation may be assigned to cultural differences that occur among different populations and it may be derived from learning deviations that occur over generations (Podos & Warren 2007). In contrast, suboscine passerines produce vocalizations in which learning exerts little or no influence on their ontogeny (Kroodsma 1984; Kroodsma & Konishi 1991; Touchton et al. 2014). These innate vocal signals tend to be relatively simple and stereotyped (Tobias et al. 2012), with little evidence of intraspecific variation (Lindell 1998; Bard et al. 2002; Seddon & Tobias 2006; Tobias et al. 2010). In this case, vocal variation may putatively reflect the genetic differences that occur among populations of the same species (Kroodsma 1984, 1989; Kroodsma & Konishi 1991). This paradigm regarding the development of suboscine vocalization is based on Tyrannidae (Kroodsma 1984, 1985, 1989) and

Thamnophilidae (Touchton et al. 2014), and many studies have shown that vocal variation occurs within suboscine species, as in Furnariidae (Lindell 1998), Tyrannidae (Sedgwick 2001; Lovell & Lein 2004; Ríos Chelén et al. 2005; Lein 2008) and Cotingidae (Fitzsimmons et al. 2008). In this case, vocal variation may be an indicator of allopatric divergence occurring within the species, which is an initial step in the process of speciation (Seddon 2005).

Since vocal divergence among populations could indicate evolutionary changes, the pattern of variation could be a reflection of the distance among populations (Koetz et al. 2007). Few studies have focused on the vocal variation of suboscine birds along geographical distances, whether in small parts of the species distribution (Payne & Budde 1979; Lein 2008) or across all of their areas of occurrence (Lovell & Lein 2013). Other studies correlated the vocal variation in suboscines to environmental structure (Ippi et al. 2011) and to different subspecies that varied morphologically and genetically (Paxton et al. 2008). The same kind of variation may occur in Great Antshrike subspecies, making them diagnosable through the acoustic features

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of their vocalizations. Isler et al. (1998) argued that even a small number of vocal characteristics could exhibit differences between pairs of species.

Suboscine birds have a high number of species in the Neotropics (Irestedt et al. 2004), and the Thamnophilidae are within this group of birds. The Great Antshrike (*Taraba major* (Vieillot 1816)) is a thamnophilid species that has a wide distribution, from northern Argentina to central Mexico (Ridgely & Tudor 1994). It inhabits the dense undergrowth of shrubs in riparian forests, savanna, and secondary forests, and also edges and clearings of tropical rain forests (Zimmer & Isler 2003). It is a sedentary bird that has shy habits and that moves discreetly in the environment, but it has a very conspicuous vocalization (Ridgely & Tudor 1994). Up to now, there are no reports on the vocal behavior of this species. Since vocalizations are related to several aspects of reproduction of thamnophilid birds, it is crucial to characterize these emissions and to understand factors that may shape the evolution of this behavior across the species.

Bioacoustics is an important tool for population studies, and it contributes to the resolution of issues in ornithology (Laiolo 2010), such as the existence of vocal variations within a species. Thus, the study of the vocalization of a species with a wide distribution, such as *T. major*, allows the recording of possible differences. If such differences are distinct enough, they might serve as a taxonomic tool where case birds have innate vocalizations. The understanding of the significance of these vocal variations is obstructed by the lack of quantitative analysis. We hypothesized that vocal variation occurs among Great Antshrike subspecies, and that it is related to differences in habitat structure, such as temperature, precipitation, vegetation cover and elevation. Therefore, our objective is to search for vocal variations in the acoustic structure of Great Antshrike vocalizations among subspecies of the complex and to seek for relationships between these possible variations and the environmental structure.

Material and methods

Definitions

Any vocal emission that was produced by birds in a specific vocal organ and was involved in the sound communication process among individuals was called a 'vocalization,' not a 'song.' The act of vocalizing should not be confused with the act of 'singing.' Bregman et al. (2016) demonstrated that the ability of pitch recognition is severely disrupted when the pitch is modulated. In this case, birds seem to rely on spectral envelope rather than harmonic pitch to recognize

patterns of sound. This mechanism of sound perception is distant from music since musical melody depends on fine spectral resolution while bird vocal signals seems to employ pitch as an auxiliary tool in the communication process (Shannon 2016).

For the same reason, we used the word 'element' to designate the smallest sound units that constituted the vocalization, instead of 'note.' All of these elements, grouped into a sound unit, were called a 'syllable' (Marler & Slabbekoorn 2004). The organization of these syllables in time sets was called a 'motif' (not 'phrase' or 'sentence') because this term included syntactical organizations at various levels of complexity (Berwick et al. 2011). Therefore, a vocalization was composed of sets of motifs arranged in a temporal sequence.

File survey

We gathered vocalizations that were previously recorded by several persons. Due to the wide distribution of the species, recordings were obtained from the following bioacoustics libraries: Xeno-Canto website (www.xeno-canto.com), Wiki Aves website (www.wikiaves.com.br) and Macauley Library (Cornell Lab of Ornithology, Cornell University). We measured vocal features from one type of vocalization among the sound files, which is known as 'loudsong' (Willis 1967). The term 'loudsong' refers to antbirds' vocalizations since these vocal emissions differ from the traditional sense of song (Zimmer & Isler 2003). It is common in many antbirds that males and females produce loud vocalizations as solo or as duets. Generally, this vocalization consists of multiple elements or syllables emitted in a stereotypic sequence (Seddon & Tobias 2006).

The 'loudsong' vocalization of Great Antshrike has two different motifs, each one with a single type of syllable, which was classified according to the morphological structure that appeared on the spectrogram. We defined these syllables as 'syllable a' and 'syllable b.' The 'syllable a' has two harmonic elements and suffers gradual changes in morphology, frequency and duration over the course of the motif, becoming shorter in duration, higher in general frequency and wider in frequency bandwidth. 'Syllable a' is repeated several times and composes the first motif (A). 'Syllable b' is composed by trilled elements on multiple frequencies. These harmonics are very close to each other, and the juxtaposition of trilled elements makes the syllable sound harsh. The second motif (B) occurred at the end of motif A, being composed of one to three 'syllables b'. In a few cases, this motif was omitted (Figure 1).

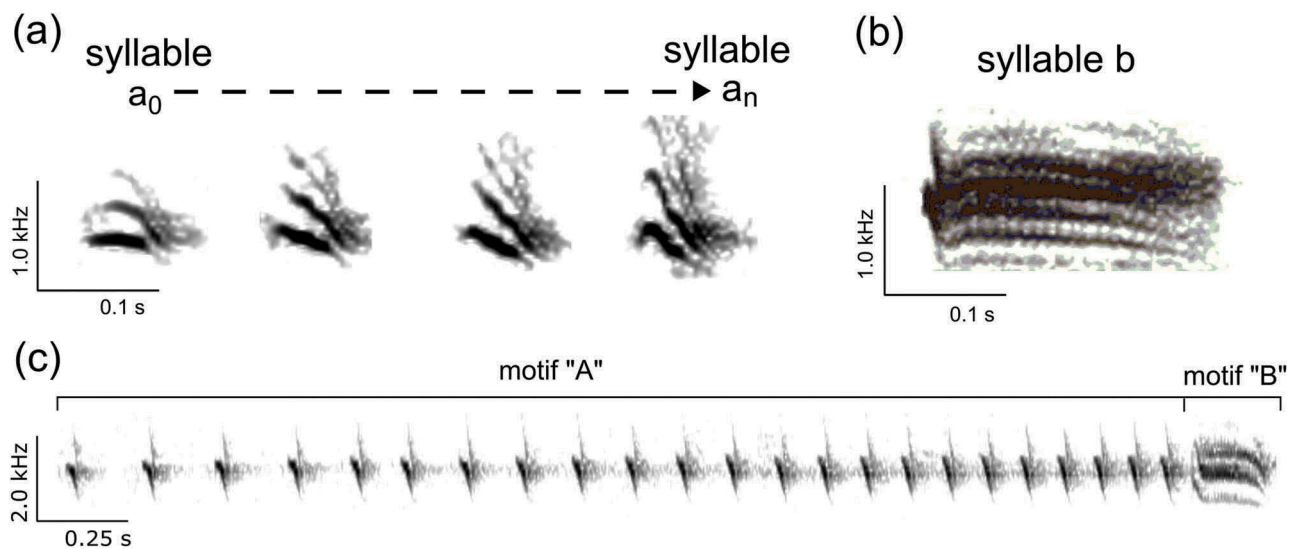


Figure 1. Spectrogram of Great Antshrike (*Taraba major*) vocalizations ('loudsongs'). (a) morphological structure of syllable 'a', showing the gradual changes that occurs on its temporal and spectral features during the bout. (b) morphological structure of syllable 'b'. (c) syntactic structure of the vocalization. Each bout is composed by two motifs, 'A' and 'B'. The motif 'A' is composed by syllables 'a' and the motif 'B' by syllables 'b'.

We sought to include recordings that covered the species' geographic range as much as possible. From the locations provided by the recorders, it was possible to assign each individual's vocalization to a subspecies assuming the distribution proposed by (Zimmer & Isler 2003) (Figure 2). The sound files recorded where subspecies occurrence overlapped were excluded from the sample to avoid confusion regarding classification. The files were further selected according to their quality. Those with excessive levels of noise (environmental noise amplitude greater than -42 dB on the power spectra), low quality of recording (signal amplitude at peak frequencies under -42 dB), overlapping vocalizations, or any other factor that could hamper the analysis of amplitude spectra, oscillograms and/or spectrograms were excluded from the sample. We also removed files with incomplete information, like the absence of coordinates, date and time of recording. If we found two or more files with the same features, we would select just one file. In total, we analyzed 289 vocalizations from 117 individuals belonging to six subspecies: *T. m. major* (42 files), *T. m. melanurus* (12 files), *T. m. obscurus* (9 files), *T. m. semifasciatus* (21 files), *T. m. staturus* (20 files) and *T. m. transandeanus* (13 files). For the other four subspecies (*T. m. borbae*, *T. m. duidae*, *T. m. granadensis* and *T. m. melanocrissus*) there were not enough vocalizations to be analyzed. Furthermore, we extracted geographic coordinates and height asl from the metadata of each file. We also collected climate data of each recording from <http://worldclim.org> (Hijmans et al. 2005), a

database that integrates climate data from 1950 to 2000. We extracted 19 climate variables (Table S1 in online supplementary material) for each point using DivaGIS 7.5 (Hijmans et al. 2001) at a resolution of 1 km^2 .

Analysis of vocalizations

To prevent biased measurements, we extracted the variables on identity and location of each vocalization blind. The assigned subspecies of each individual was identified after we did the measurements. The syllables of vocalizations were visually classified according to the morphology of the elements on the spectrogram (fast Fourier transform (FFT) = 512 bits, overlap = 93.75%, range = dB^2 , Hanning window) generated by Sonic Visualizer 2.4 software (Cannam et al. 2010). For each digital sound file (44,100 Hz, 16-bit resolution and '. wave' format), we selected from one to three vocalizations. We used the oscillogram to measure time variables and the amplitude spectra (-42 dB limit, Hanning Window, resolution = 2048 points) to measure frequency variables. This limit was set to avoid the frequency bands of environmental noise.

The measured variables were: T1: number of syllables of motif A (units); T2: duration of motif A (s); T3: trill rate of the motif A ($T1/T2$) (units s^{-1}); T4: trill rate of the first half of motif A, dividing the number of syllables in the first half of motif A by half of T2 (units s^{-1}); T5: trill rate of the second half of motif A,

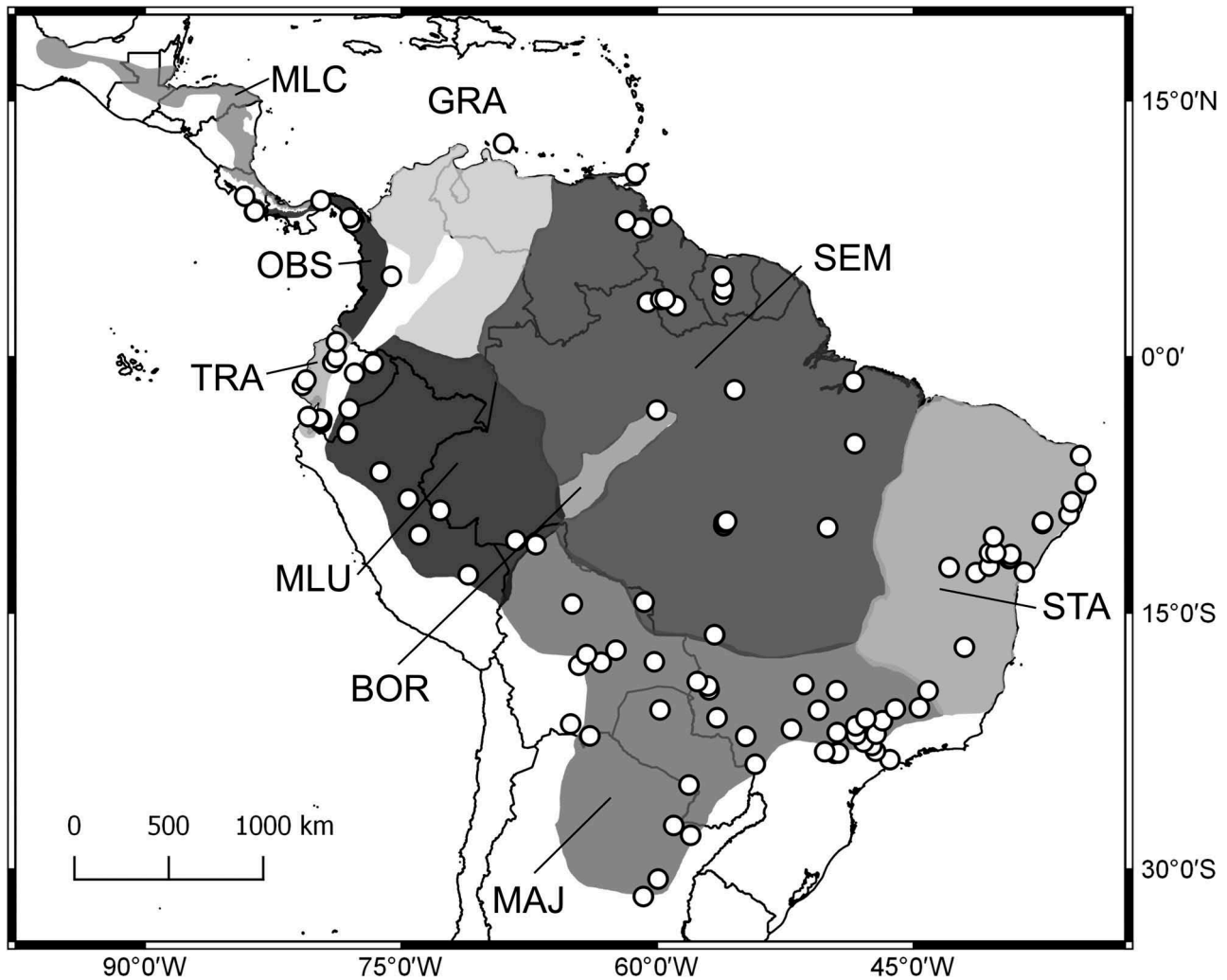


Figure 2. Distribution of *T. major* subspecies: *T. m. borbae* (bor), *T. m. major* (maj), *T. m. melanocrissus* (mlc), *T. m. melanurus* (mlu), *T. m. granadensis* (gra), *T. m. obscurus* (obs), *T. m. semifasciatus* (sem), *T. m. stagurus* (sta), and *T. m. transandeanus* (tra). The subspecies *T. m. borbae*, *T. m. melanocrissus* and *T. m. granadensis* were not analyzed due to the low number of samples. White circles indicate the location of sound files used.

dividing the number of syllables in the second half of motif A by half of T2 (units s^{-1}); T6: change in trill rate, dividing T5 by T6 (dimensionless); T7: duration of the largest syllable of motif B (s); F1: maximum frequency of motif A (kHz); F2: minimum frequency of motif A (kHz); F3 – frequency bandwidth of the motif A (F1 – F2) (kHz); F4 – peak frequency of motif A (kHz); F5 – maximum frequency of motif B (kHz); F6 – minimum frequency of motif A (kHz); F7 – frequency bandwidth of the motif B (F6 – F5) (kHz); and F8 – peak frequency of motif B (kHz).

Statistical analysis

We conducted principal component analysis (PCA) on the vocal variables to reduce the redundancy and collinearity of the data, and reduce its number to a small set of

independent variables. It generated five principal components (VPCs) with absolute eigenvalues greater than 1.0 (Table 1) that explained 84.46% of the variance among data. The PCA was also performed on the 19 climatic variables for the same reasons mentioned before, which generated four climatic principal components (CPCs) that summarize 89.70% of the climatic variation among samples (Table S1). We compared the VPC residuals of variation among subspecies using a multivariate analysis of variance (MANOVA). The VPC that presented eigenvalues greater than $|1.0|$ were used in discriminant function analysis (DFA). This analysis allowed the reduction of variables for grouping the samples into a number of sets that were already known. Through the DFA, we classified the samples in groups and compared them with the different subspecies, checking the percentage of correct jackknifed classifications.

Table 1. Principal components of vocal variables extracted from vocalizations of *T. major*. Each VPC is predominantly related to some vocal variables (bold values), with the exception of VPC4. Also shown are eigenvalues (Eigen.) of each VPC and percentage of variance (% of Var.) among variables that is explained by these VPCs.

Vocal Variable	VPC1	VPC2	VPC3	VPC4	VPC5
T1	0.184	0.329	0.688	0.356	-0.485
T2	-0.177	0.723	0.430	0.257	-0.412
T3	0.408	-0.840	0.317	0.137	-0.060
T4	0.398	-0.825	0.034	0.286	-0.156
T5	0.358	-0.778	0.485	0.040	0.023
T6	-0.094	0.124	0.668	-0.354	0.277
T7	-0.469	0.097	0.438	-0.269	0.062
F1	0.841	0.310	-0.082	0.320	0.194
F2	0.801	0.312	-0.183	0.155	-0.081
F3	0.390	0.118	0.131	0.392	0.520
F4	0.843	0.298	-0.128	0.218	0.025
F5	0.755	0.212	0.218	-0.360	0.229
F6	0.824	0.073	0.005	-0.474	-0.195
F7	-0.326	0.175	0.298	0.293	0.653
F8	0.832	0.124	0.121	-0.404	0.035
Eigen.	5.005	3.038	1.857	1.423	1.346
% of Var.	33.4	20.5	12.4	9.5	9.0

We tested the correlation between vocal features and environmental variables using the Spearman correlation on VPCs, CPCs, elevation and latitude. We used the same approach to seek for relationship between VPCs and year of recording. A Mantel test was used to determine whether the matrix geographical distances were related to the distance matrix among vocalizations. The geographical distances were obtained from the latitude and longitude data of the sound files, and we calculated them on Geographic Distance Matrix Generator 1.2.3 software (Ersts 2014). The vocal distance was obtained from the Euclidean distances between the scores of the principal components for each pair of vocalizations. The analyses were performed using SPSS Statistics 22.0 software (IBM SPSS Inc. 2012), except for the Mantel test, which was performed in Past 3.0 software (Hammer 2011).

Results

We show the means \pm SD of each variable in Table 2. Principal component analysis on vocal features showed that VPC1 varied positively with mean frequency values (F1, F2, F4, F5, F6, F8); VPC2 was correlated positively to length of motif A (T2) and negatively to trill rate (T3, T4 and T5); VPC3 corresponded positively to number of syllables (T1) and pace (T6); VPC4 was negatively correlated to frequency values of motif B (F6 and F8); and VPC5 was positively correlated to frequency bandwidth of motif B (F5). There was a statistically significant difference ($p < 0.05$) among VPCs of different subspecies ($F_{25,399} = 12.297$, $p < 0.001$; Wilks' Lambda = 0.120, partial $\eta^2 = 0.346$).

The univariate ANOVAs conducted as part of MANOVA showed that VPC1 ($F_{5,111} = 33.495$, $p < 0.001$, partial $\eta^2 = 0.601$), VPC2 ($F_{5,111} = 11.033$, $p < 0.001$, partial $\eta^2 = 0.332$), VPC3 ($F_{5,111} = 8.405$, $p < 0.001$, partial $\eta^2 = 0.275$), VPC4 ($F_{5,111} = 3.222$, $p = 0.009$, partial $\eta^2 = 0.127$) and VPC5 ($F_{5,111} = 2.868$, $p = 0.018$, partial $\eta^2 = 0.114$) were statistically different among subspecies. The differences on VPCs among subspecies are displayed in Figure 3. *Taraba m. major* and *T. m. stagusurus* exhibited higher values for VPC1 and VPC2 than other subspecies. Regarding VPC3, only *T. m. stagusurus* displayed lower values than the others. VPC4 seemed to assume lower values only to *T. m. melanurus* and *T. m. obscurus*. Lastly, the values of VPC5 were higher in *T. m. obscurus* and lower in *T. m. melanurus*, whereas the other subspecies exhibited intermediate values.

We found correlation ($p < 0.05$) between vocal and environmental features: CPC1 and VPC1 ($r = -0.681$, $p < 0.001$); CPC2 and VPC2 ($r = 0.441$, $p < 0.001$); CPC3 and VPC1 ($r = 0.265$, $p = 0.004$); elevation and VPC2 ($r = -0.319$, $p < 0.001$); and latitude and VPC1 ($r = -0.801$, $p < 0.001$). However, we did not find significant correlations between VPCs and year of recording ($r = 0.113$, $p = 0.093$). Regarding climatic variables, we found that temperature and humidity were related mainly to temporal structure. Warmer and humid environments, with little temperature variation (CPC1) were correlated with vocalizations with lower frequency (VPC1). On the other hand, warmer and dryer environments (CPC2) were correlated with vocalizations in which motif A had longer duration and slower trill rate (VPC2). The patterns of isothermality and variance of precipitation (CPC3) were correlated with vocal frequency patterns (VPC1), since vocalizations had higher frequency with the decrease of precipitation variation and with the increase of temperature variation. Latitude had a strong negative correlation with VPC1, which means that the increase in latitude was associated to decrease in frequencies (both means and bandwidths). Elevation was negatively correlated to VPC2, showing that its increase was associated to shorter duration and faster trill rate of vocalizations. There was a positive correlation between the vocal and geographical distances (Mantel test: $n = 9999$ permutations, $r = 0.2156$, $p < 0.001$).

DFA employed the five VPCs and generated five discriminant functions (DFs) (Table 3). Approximately 69.2% of the original samples were correctly classified by DFA (Table 4). Only the samples assigned to *T. m. transandeanus* received a low rating of correct classification (less than 60%). The distribution of samples in the discriminant space demonstrated that the distinction

Table 2. Vocal features (mean \pm SD) of *Taraba major* subspecies.

Vocal feature	Subspecies					
	maj	mel	obs	sem	sta	tra
T1 (unit)	44.77 \pm 9.33	43.23 \pm 9.05	30.41 \pm 8.54	42.23 \pm 7.49	32.83 \pm 8.89	31.14 \pm 5.93
T2 (s)	7.08 \pm 1.45	7.83 \pm 1.28	5.07 \pm 1.28	8.56 \pm 2.06	6.07 \pm 1.61	4.09 \pm 0.72
T3 (units s ⁻¹)	6.36 \pm 0.80	5.50 \pm 0.69	6.00 \pm 0.53	5.04 \pm 0.79	5.44 \pm 0.55	7.64 \pm 0.88
T4 (units s ⁻¹)	4.88 \pm 0.89	4.33 \pm 0.52	4.18 \pm 0.44	3.85 \pm 0.69	4.37 \pm 0.50	6.03 \pm 0.70
T5 (units s ⁻¹)	7.79 \pm 1.02	6.74 \pm 0.89	7.79 \pm 0.95	6.24 \pm 1.07	6.46 \pm 0.86	9.24 \pm 1.31
T6	1.61 \pm 0.21	1.56 \pm 0.12	1.88 \pm 0.28	1.64 \pm 0.23	1.48 \pm 0.19	1.54 \pm 0.13
T7 (s)	0.68 \pm 0.19	0.88 \pm 0.25	0.91 \pm 0.17	0.88 \pm 0.35	0.48 \pm 0.11	0.70 \pm 0.21
F1 (kHz)	1.79 \pm 0.14	1.39 \pm 0.15	1.25 \pm 0.08	1.44 \pm 0.16	1.70 \pm 0.11	1.33 \pm 0.08
F2 (kHz)	1.38 \pm 0.12	1.10 \pm 0.08	1.00 \pm 0.10	1.15 \pm 0.15	1.33 \pm 0.14	1.01 \pm 0.06
F3 (kHz)	0.40 \pm 0.13	0.28 \pm 0.09	0.26 \pm 0.09	0.28 \pm 0.11	0.36 \pm 0.09	0.33 \pm 0.05
F4 (kHz)	1.58 \pm 0.12	1.26 \pm 0.10	1.14 \pm 0.06	1.31 \pm 0.14	1.51 \pm 0.11	1.23 \pm 0.09
F5 (kHz)	2.11 \pm 0.10	1.93 \pm 0.16	1.99 \pm 0.21	1.92 \pm 0.21	2.05 \pm 0.18	1.87 \pm 0.18
F6 (kHz)	1.73 \pm 0.18	1.55 \pm 0.18	1.53 \pm 0.23	1.39 \pm 0.22	1.68 \pm 0.16	1.47 \pm 0.20
F7 (kHz)	0.41 \pm 0.14	0.38 \pm 0.09	0.45 \pm 0.09	0.53 \pm 0.17	0.37 \pm 0.09	0.40 \pm 0.10
F8 (kHz)	1.93 \pm 0.14	1.69 \pm 0.22	1.75 \pm 0.18	1.61 \pm 0.23	1.81 \pm 0.16	1.62 \pm 9.21

Abbreviations: maj, *T. m. major*; mel, *T. m. melanurus*; obs, *T. m. obscurus*; sem, *T. m. semifasciatus*; sta, *T. m. stagusurus*; tra, *T. m. transandeanus*.

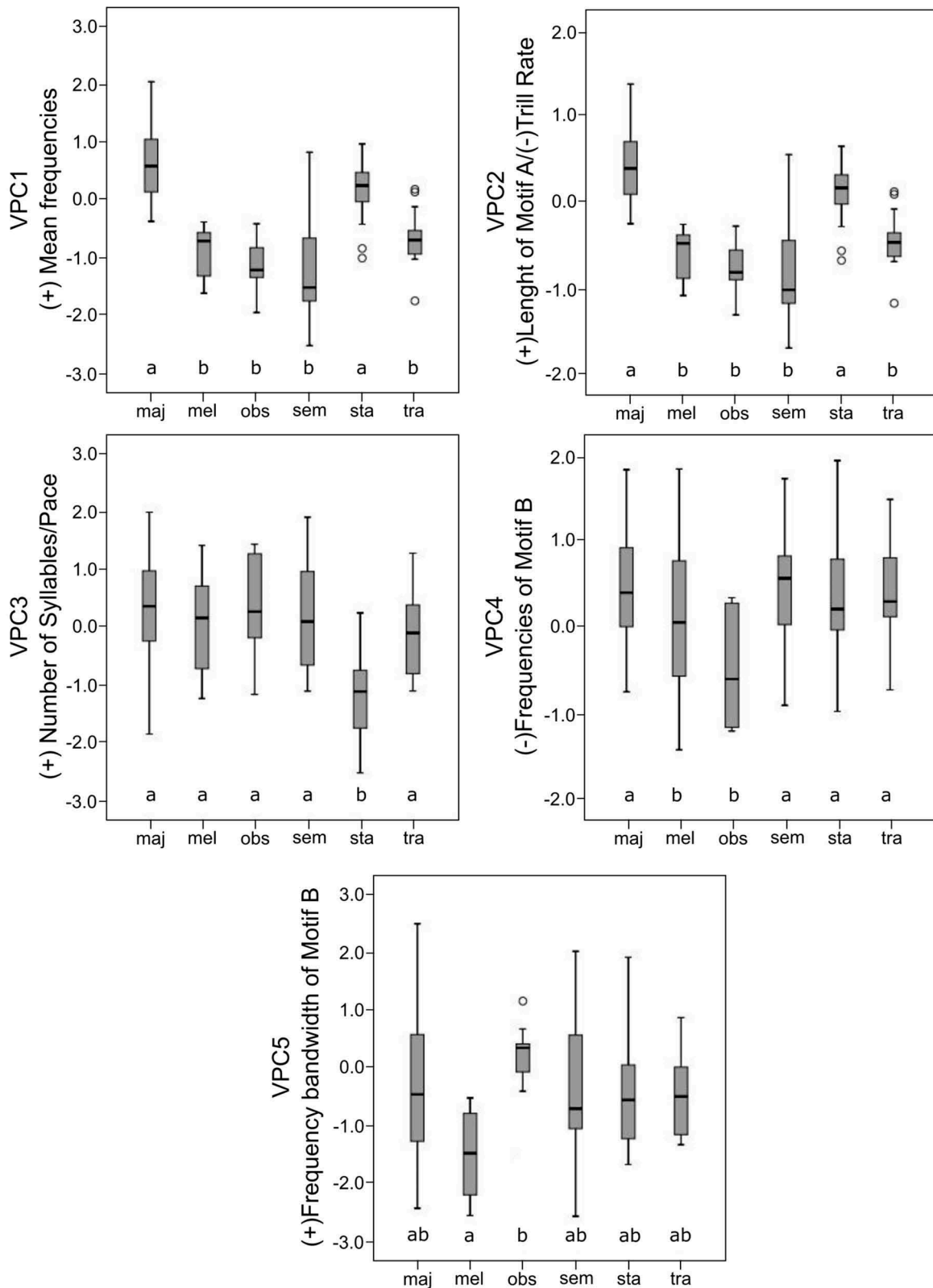


Figure 3. Values of vocal principal components (VPC1-5) among subspecies. The '+' and '-' symbols represent positive or negative prevalence of the variables that are summarized by the designated VPC. The letters ('a' and 'b') represent the homogeneous subsets of subspecies for one VPC proposed by Tukey *post hoc* test (*T. m. major*: maj, *T. m. melanurus*: mel, *T. m. obscurus* – obs, *T. m. semifasciatus*: sem, *T. m. stagurus*: sta and *T. m. transandeanus*: tra).

Table 3. Correlations among vocal principal components (VPCs) and standardized canonical discriminant functions (DF) of vocalizations of *Taraba major*. Also shown are eigenvalues (Eigen.) of each DF and percentage of variance (% of Var.) among VPCs. Each DF is associated to a different VPC, showing that some variables (like frequencies summarized by VPC1 and trill rates summarized by VPC2) have more importance in discriminating subspecies. Greatest absolute correlation between vocal component and discriminant functions is indicated in bold.

	DF1	DF2	DF3	DF4	DF5
VPC1	0.770	0.488	-0.100	-0.314	-0.245
VPC2	0.169	-0.771	0.456	0.272	-0.309
VPC3	-0.084	0.377	0.884	0.070	-0.252
VPC4	0.150	-0.103	0.235	0.201	0.933
VPC5	0.016	0.163	-0.160	0.943	-0.243
Eigen.	2.280	0.578	0.352	0.112	0.073
% of Var	67.2	17.0	10.4	3.3	2.2

Table 4. Jackknifed classification matrix between assigned and predicted subspecies of *Taraba major* by discriminant analysis. Percentage of correct classification is indicated in bold.

		Predicted ssp					
		maj	mel	sem	sta	obs	tra
Assigned ssp	maj	69.0	2.4	0.0	2.4	23.8	2.4
	mel	0.0	75.0	0.0	8.3	8.3	8.3
	sem	0.0	0.0	77.8	0.0	11.1	11.1
	sta	4.8	4.8	9.5	66.7	9.5	4.8
	obs	20.0	0.0	0.0	0.0	75.0	5.0
	tra	0.0	7.7	7.7	30.8	0.0	53.8

Abbreviations: maj, *T. m. major*; mel, *T. m. melanurus*; obs, *T. m. obscurus*; sem, *T. m. semifasciatus*; sta, *T. m. staturus*; tra, *T. m. transandeanus*

between the samples assigned to the subspecies was not perfect. We plotted DF1 and DF2 to explore the data since they summarized 90.9% of the variance of the discriminant space. We observed the formation of clusters between pairs of subspecies: *T. m. major*–*T. m. staturus*, *T. m. melanurus*–*T. m. semifasciatus* and *T. m. obscurus*–*T. m. transandeanus* (Figure 4).

Discussion

Variation among subspecies

From our results, we demonstrate the acoustic variation among vocalizations of *T. major*, and its relationship with subspecies of the complex. Such variation among groups, populations or subspecies was also observed in other species, like *Henicorhina leucophrys* (Troglodytidae, Dingle et al. 2008; *Campylorhynchus rufinucha* (Troglodytidae, Sosa-López et al. 2013) and even in non-Passerine species, like *Cuculus canorus* (Cuculidae, Wei et al. 2015). Because there is evidence that learning has little influence on the development of vocalizations of suboscine birds (Touchton et al. 2014), vocal variation among Great Antshrike populations could not be attributed to learning deviations or any cultural factor among populations.

In this case, it seems that some genetic component could be influencing vocal variation. Individuals of the same subspecies that inhabit the same geographical region tend to share the same gene pool. The effect of isolation-by-distance might happen in *T. major* vocalizations because an increase in geographic distance implies an increase in acoustic differences between vocalizations. However, we could not assume that the population structure was uniform. *Taraba major* is a species that has a wide distribution (a mean of 2441.71 ± 1317.41 km of distance among samples), but at the same time, it is resident and it presents little evidence of movement through the environment (Zimmer & Isler 2003). This behavior could be a barrier to gene flow through the whole distribution of the species. Although we did not test the variations in Great Antshrike genetic structure, some studies demonstrate concordance between genetic and vocal divergence in tracheophone suboscine species (Isler et al. 2005; Irwin et al. 2008; Chaves et al. 2010). Therefore, the ‘isolation-by-distance’ model seems plausible since geographic distance between individuals is correlated to vocal differences, which was also found in other suboscine birds (Sedgwick 2001). These vocal changes may be a reflection of genetic differentiation that arose from geographic distances. The vocal variation associated with geographic isolation was observed in *Empidonax traillii* (Sedgwick 2001), a tyrannid bird. Lovell and Lein (2013), in spite of finding significant differences between *E. alnorum* (Tyrannidae) vocalizations in different regions of North America, failed to correlate these differences to the distances between individuals.

Environmental influence on vocal variation

The pattern of variation may be related to the adaptation processes, which optimize sound transmission in different environments (Boncoraglio & Saino 2007) as stated by Morton (1975) in the acoustic adaptation hypothesis. According to his work, vocalization of closed environment species (i.e. forest species) had more pure tones and included fewer trills than those of open habitat species (i.e. grassland species). This finding is supported by posterior studies, which showed that transmission of pure tone vocalizations may be enhanced by reverberation (Nemeth et al. 2006). Adaptation to environmental acoustic features seems to be a strong selective force acting upon bird songs, and one should expect this kind of variation within populations (Brumm & Naguib 2009). Several studies suggest this has within-species effects, with vocalizations having lower trill rates and lower frequencies in closed habitats (Hunter &

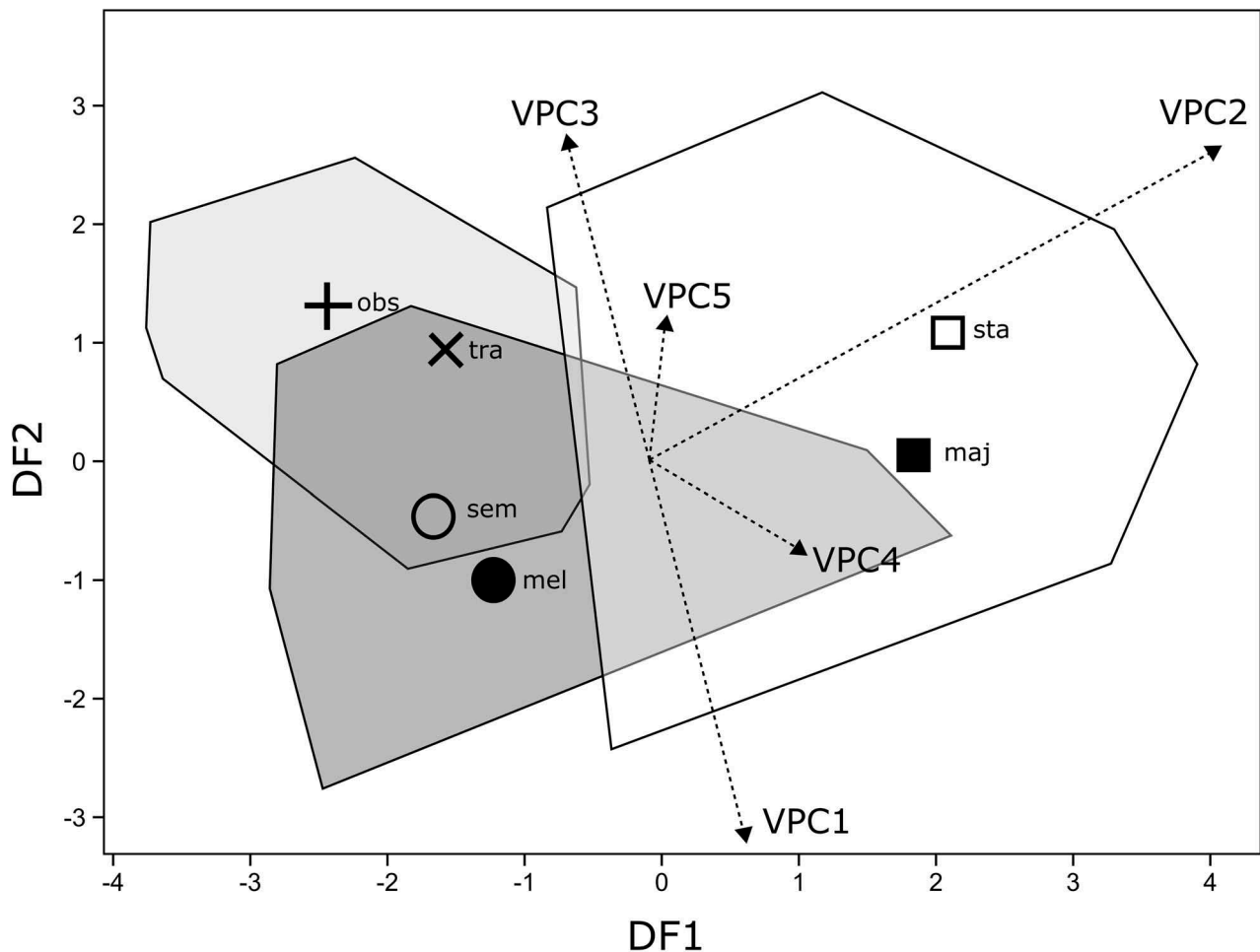


Figure 4. Distribution of samples in the discriminant space, employing the DF1 and DF2 as main axis. The dotted lines represent the convex hull delimited by pairs of subspecies (maj-sta, mel-sem, obs-tra). The symbols represent the distribution of centroid functions for each subspecies. The dotted arrows represent the prevalence of each VPC on discriminant space (*T. m. major*: maj, *T. m. melanurus*: mel, *T. m. obscurus*: obs, *T. m. semifasciatus*: sem, *T. m. stagus*: sta and *T. m. transandeanus*: tra).

Krebs 1979; Handford 1981; Handford & Loughheed 1991; Nicholls & Goldizen 2006).

Differences in the vegetal structure between habitats could impose different selective pressures on the acoustic signals produced by birds (Wiley & Richards 1978; Tubaro & Segura 1994; Brown & Handford 2000; Boncoraglio & Saino 2007; Ey & Fischer 2009; Ippi et al. 2011). Thus, the vegetal and atmospheric absorption of a particular environment may favor the transmission of certain temporal and spectral features of bird vocalizations (Slabbekoorn et al. 2007). Absorption, scattering and reverberation are also related to temperature and humidity, but they occur in a complex way. In general, signals with frequencies around 2 kHz (like Great Antshrike vocalization) suffer the greatest attenuation as temperature increases and humidity decreases (Wiley & Richards 1982). Differences on gradients of temperature and humidity between populations could affect the way that vocal sound is transmitted, since velocity, degradation and attenuation of sound

depends on these features. This could imply that environment exerts selective pressures on Great Antshrike vocalizations. Morphological variation could also be a product of habitat divergence. In this case, any correlation between habitat structure and body size could also reflect on animal vocal structure (Ziegler et al. 2011). Other environmental factors, like biotic and abiotic noise, might influence vocal structure (Kirschel et al. 2009).

The latitude plays an important role on vocal variation since individuals of Great Antshrike vocalize with lower frequencies in lower latitudes, which could be related to morphological characteristics of birds. The structure of vocalization may be influenced by this variation and several authors observed a negative tradeoff between body size and frequency of vocalizations (Podos 2001; Podos & Nowicki 2004; Seddon 2005; Caro et al. 2013). As predicted by Bergmann's rule, individuals situated at higher latitudes tend to have larger body size (Zink & Remsen 1986; Ashton 2002; Olson et al. 2009) and several studies have

Table 5. Comparison of body mass of individuals of different *Taraba major* subspecies. We assigned subspecies based on the coordinates provided.

Reference	Location	Latitude	Mass (g)	Assigned subspecies
Alderete & Capllonch 2010	N Argentina	32°S–23°S	56.2	<i>T. m. major</i>
Smith et al. 2012	NE Paraguay	23°S	52.5	<i>T. m. major</i>
Salvador 1990	N Argentina	23°S	58.2	<i>T. m. major</i>
Piratelli et al. 2001	W of Brazil	21°S–20°S	53.6	<i>T. m. major</i>
Piratelli 2003	W of Brazil	21°S–20°S	52.6	<i>T. m. major</i>
Oniki & Willis 1991	W of Brazil	15°S	45.9	<i>T. m. major</i>
Yabe et al. 2010	W of Brazil	19°S	55.0	<i>T. m. major</i>
Roos et al. 2006	NE Brazil	10°S–9°S	52.3	<i>T. m. stagurus</i>
Novaes & Lima 1990	N of Brazil	10°S	61.2	<i>T. m. semifasciatus</i>
Silva et al. 1990	N of Brazil	5°S–3°S	58.0	<i>T. m. semifasciatus</i>
Dunning 2008	Suriname	1°N–5°N	59.3	<i>T. m. semifasciatus</i>
Haverschmidt 1948	Suriname	1°N–5°N	59.1	<i>T. m. semifasciatus</i>
Hartman 1955	Panama	8°N–9°N	67.3	<i>T. m. obscurus</i>
Stiles & Skutch 1989	Costa Rica	8°N–11°N	75.0	<i>T. m. obscurus</i>

found evidences of this pattern occurring in birds (94 species, see Meiri & Dayan 2003) including Neotropical ones, like *Henicorhina leucophrys* (Tubaro & Segura 1995), *Diglossa carbonaria* (Graves 1991) and *Amblycercus holosericeus* (Kratler 1993). However, although we did not perform morphometric measurements on birds, we think that Bergmann's rule does not apply to the Great Antshrike. Some morphometric studies of different populations of these birds revealed a tendency for larger individuals to occur near to the Equator (Table 5). In this case, morphological variation could affect vocal production, and might explain why individuals at lower latitudes produce vocalization with lower frequencies. Thus, connection between latitude and vocal features could arise as a by-product of morphological difference among populations. For the same reasons, elevation seems to influence vocal structure through morphological adaptations. Birds at higher elevations tend to have smaller bills and smaller body size (Caro et al. 2013), which may constrain the acoustic features of vocal emissions based on biomechanical limitations (Podos 2001; Seddon 2005). If the differences across vocal structure observed in *T. major* subspecies are associated with distances and environmental features, they might reflect the differential selective pressures and geographic isolation that could be occurring within species. However, taxonomic and molecular evidence is needed to understand the real significance of geographical variations in suboscines.


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