Taylor & Francis
Taylor & Francis Group

The vocal repertoire of *Myrmeciza loricata* (Lichtenstein, 1823) (Aves: Thamnophilidae)

T.O.S. Amorim[a]*, M.A. Manhães[b], A.F. Azevedo[c] and A. Andriolo[a,d]

[a]*Programa de Pós-graduação em Ecologia Aplicada ao Manejo e Conservação de Recursos Naturais, Universidade Federal de Juiz de Fora – ICB, Campus Universitário, Juiz de Fora, Minas Gerais, Brazil;* [b]*Universidade Federal de Juiz de Fora – ICB, Campus Universitário, Juiz de Fora, Minas Gerais, Brazil;* [c]*Pós-graduação em Oceanografia (PPGOCN), Faculdade de Oceanografia, Laboratório de Mamíferos Aquáticos e Bioindicadores (MAQUA), Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil;* [d]*Departamento de Zoologia, Universidade Federal de Juiz de Fora – ICB, Campus Universitário, Juiz de Fora, Minas Gerais, Brasil*

The vocal repertoire is a tool that can be used to support systematics, conservation, ecology and behavioural studies. We characterize the acoustic parameters of the vocal repertoire of the white-bibbed antbird (*Myrmeciza loricata*) and describe the possible functions of each vocalization. The male's song is related to territorial defence, and we found three calls in the repertoire. Call I is an alarm call, and call II is used for mutual recognition and remaining in contact with one another. Call III was emitted when the animals were foraging and when the individuals of the couple were very near to each other. Males and females sing as a duet, and their songs were individually distinct. The duet is possibly related to maintaining the pair bond, synchronizing breeding and warning potential intruders of the mated condition of the pair. This work is the first to describe the vocal repertoire of the white-bibbed antbird.

Keywords: alarm call; Atlantic Forest; contact call; duet; song

1. Introduction

The vocal repertoire of a species provides valuable information for understanding species behaviour, as a particular communication signal should correspond to a behaviour aimed at survival (Marler 2004; Vielliard and Silva 2007).

Data on the ontogeny and intra-specific sound communication of Passeriformes is primarily focused on oscine members (Scott and Lein 2004). However, the vocal characteristics of the Suboscines are generally used as an important taxonomic parameter, and studies on this group may elucidate the factors that contribute to their vocal behaviour (Johson et al. 1999; Helbig et al. 2002).

Thamnophilidae, which consists of mainly insectivorous species, is one of many bird families that inhabit the Atlantic Forest and is one of the most important families of the Neotropical avifauna (Skutch 1996). Therefore, Thamnophilidae is commonly included in inventories of the most important families of neotropical birds in forests that are closer to the equator (Bierregaard Jr and Lovejoy 1989; Stouffer and Bierregaard 1995).

---

*Corresponding author. Email: tosabio@gmail.com

The species *Myrmeciza loricata* is approximately 14.5 cm in length and inhabits the Atlantic Forest of Brazil in the states of Bahia, Minas Gerais, Espirito Santo, São Paulo and Rio de Janeiro (Ridgely et al. 1994; Sick 2001). *Myrmeciza loricata* couples walk on the forest floor searching for arthropods and apparently do not join mixed flocks (Sigrist 2006). Males have a wide and prominent white superciliary and buff spotting on the greater-coverts. The sides of the head and upper throat are black; they have a white bib with a band of black on their lower throat and white-tipped feathers across their chest. Females are similar in appearance to males, except they have an ochraceous throat and olivaceous mottling on the side of their breast (Ridgely et al. 1994). Studies on species of the family Thamnophilidae have investigated several aspects of Thamnophilidae vocalization, such as using vocalizations by eight syntopic species to establish limits between these species (Isler et al. 1998); determining the vocalizations, behaviour and distribution of *Cercomacra carbonaria* and possible relationships with other species within this group (Zimmer et al. 1997); comparing male and female *Hylophylax naevioides* songs to evaluate the differences between individuals (Bard et al. 2002); evaluating differences in the vocal features of *Myrmeciza laemosticta laemosticta* and *Myrmeciza laemosticta palliata* to determine whether these species are distinct (Chaves et al. 2010); describing the vocal repertoire of *Myrmeciza disjuncta* (Zimmer 1999); examining *Percnostola leucostigma saturata* vocalizations for studies of speciation (Braun et al. 2005); and examining *Myrmotherula brachyura ignota* vocalizations for taxonomic studies (Isler and Isler 2003). Vocal features are also used in studies of variation within and between groups in the same geographical region (Lovell and Lein 2004; Gonzáles and Ornelas 2005; Isler et al. 2005) and in sexual selection studies (Seddon et al. 2008).

Here, we describe the acoustic parameters of the vocal repertoire of the white-bibbed antbird (*Myrmeciza loricata*) and investigated the functions of its song and calls.

2. Material and methods

2.1. *Study area*

The white-bibbed antbird was studied at Poço D'Anta Biological Reserve (21°44′58.79″S, 43°19′7.09″W), located at the city of Juiz de Fora, Minas Gerais, Brazil. The reserve consists of approximately 277 ha of Atlantic Forest (Figure 1).

2.2. *Field methods*

The fieldwork was done from June 2010 to May 2011 and consisted of 1 day of sampling per week throughout the study period. The entirety of the forest was searched for individuals through an active search.

Vocalizations were recorded with a Zoom H4n digital portable recorder and a Yoga HT 81 unidirectional condenser microphone. Each vocal event was registered on a spreadsheet, and the geographical position associated with it was obtained using a Garmin eTrex H GPS device. When it was possible to see the individuals, we also registered their behaviour.

The sampling was carried out for 6 hours each sampling day, divided into the following periods: in the first and third weeks of the month, we recorded vocal events
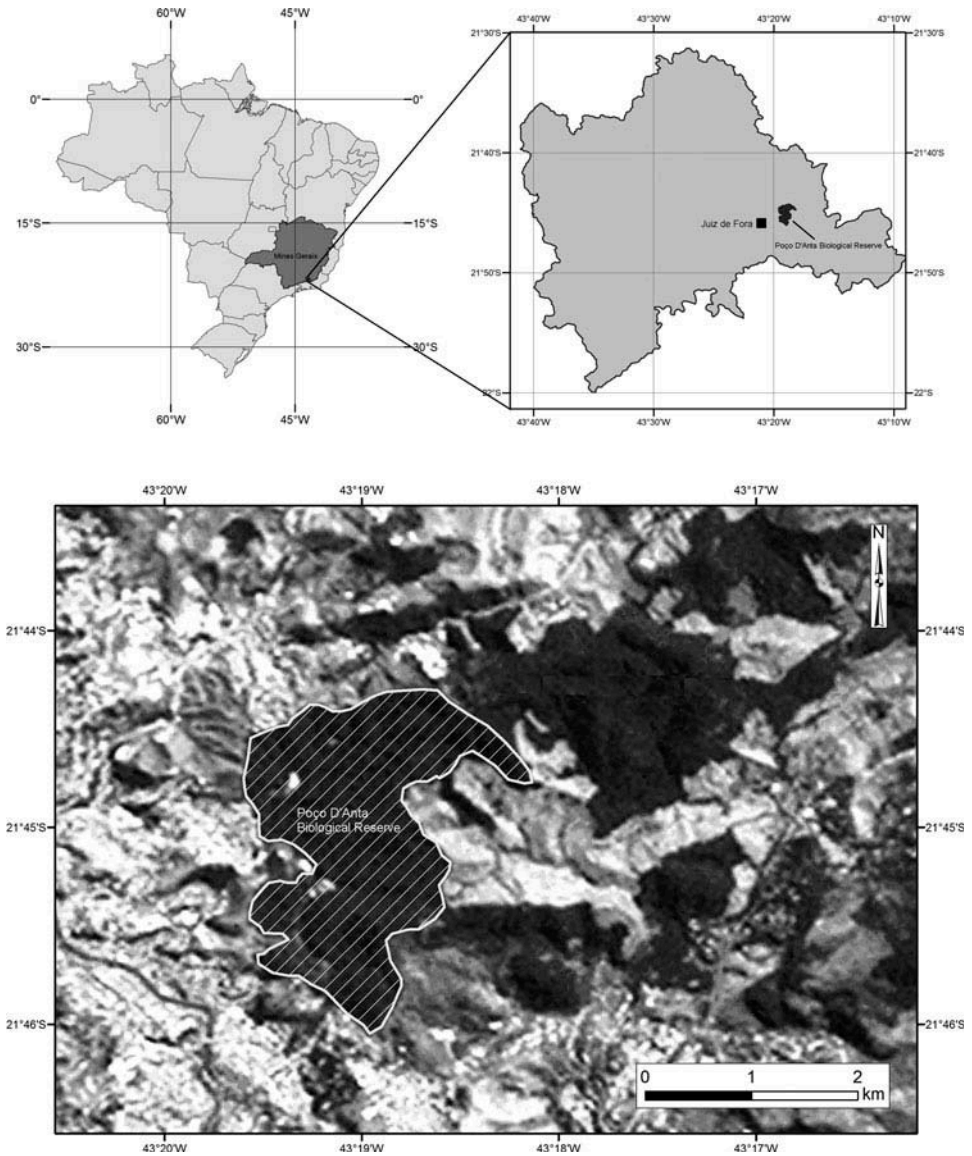
Figure 1. Study area – map and location of the Poço D'Anta Biological Reserve, Juiz de Fora, MG, Brazil.

from 06:00 to 12:00. In the second and fourth weeks of the month, we recorded vocal events from 12:00 to 18:00. Hence, we sampled the area for 24 hours each month.

2.3. *Acoustical procedures*

The recordings were digitized at a sampling rate of 44.1 KHz at 16-bit resolution. We used Raven Pro. 1.3 (Cornell Laboratory of Ornithology, New York, NY) to produce

the sonograms (window size: 512 samples; window type: Hann; overlap: 60%; hop size: 205 samples). The following acoustical parameters were used to describe the vocal repertoire:

(1) Minimum frequency (Hz): lower frequency bound of the selection.
(2) Maximum frequency (Hz): upper frequency bound of the selection. The selection was made from the beginning of the first note to the end of the last note in each phrase. For vocalizations that did not form phrases, the selection was made from the beginning of the note to its end. The maximum and minimum frequencies were respectively measured in the upper and lower bounds in the selection (Figure 2).
(3) Bandwidth (Hz): the difference between the maximum and minimum frequencies.
(4) Centre frequency (Hz): the frequency that divides the selection into two frequency intervals of equal energy.
(5) Dominant frequency (Hz): the frequency with the highest energy within the selection.
(6) First quartile frequency (Hz): the frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection.
(7) Third quartile frequency (Hz): the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection.
(8) Number of notes: the number of notes in the selection. A note was defined as an unbroken trace on a spectrogram (Slabbekoorn 2004).
(9) Phrase/note duration (s): the time from the start of first note to the end of last note. A phrase was defined as a sequence of notes. We measured the note duration when the vocalizations did not form phrases.
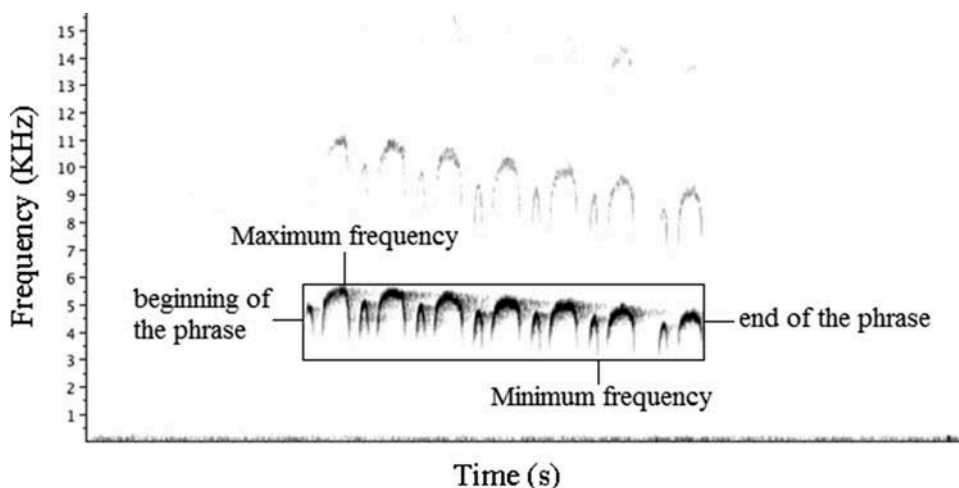(10) Note rate (note/s): number of notes per time duration.

Figure 2. Bounds of the selection to determine the beginning and end of the phrase and the maximum and minimum frequencies.

(11) Inter-phrase/note duration (s): the time elapsed from the end of the last note of a phrase to the beginning of the first note of the following phrase, also known as the silent interval. In vocalizations in which notes did not form phrases, the measure used was the inter-note duration.

2.4. *Statistical procedures*

We calculated the minimum, maximum and mean values of all acoustic parameters for each recording (vocal event). Vocal events of the same vocalization from the same individual were measured together when the vocal events were emitted consecutively. The mean and standard deviations of the minimum, maximum and mean for each type of vocalization recorded were calculated.

3. Results

We obtained 32.50 h of audio recordings. We found three types of calls and one song in the vocal repertoire of *M. loricata*. Individuals were observed walking on the forest floor and often perched on shrubs and fallen trunks.

3.1. *Songs*

We analysed 2816 song phrases, of which 2801 were produced by males (*n* = 96) and 15 were produced by females (*n* = 6). The male songs comprised two different notes emitted alternately with two harmonics. Both note structures presented an upward–downward modulation (Figure 3A). We observed males singing in an undefined context, while foraging and when other males sang. Often, the male song caused a response from other males in the neighbourhood.

We observed females singing with males, indicating duets. We found that male and female songs were individually distinct and sex specific. The female song comprised two different notes with harmonics (first harmonic) and exhibited an upward–downward modulation. The female song notes were sung in two different ways: the notes were emitted alternately or the female emitted a trill at the beginning of the phrase (Armstrong 1963; Ritchison 1988). The trill notes varied, with a mean of 4.66 ± 0.58 notes. The song phrases of males and females also overlapped (Figure 3B–D). All duets were initiated by males; the females did not produce loud songs in isolation from their partners. Females produced songs in response to their partners when they were near or far from the male and if the couple approached one another. At the time of the meeting, the male ruffled his feathers, remained in front of the female and moved his tail upward.

3.2. *Call I – alarm*

We analysed 3005 call I – alarm phrases (*n* = 61 individuals). This call was produced when the observer approached places where other individuals were located. The call I – alarm can be described as a series of pulses (Figure 4).
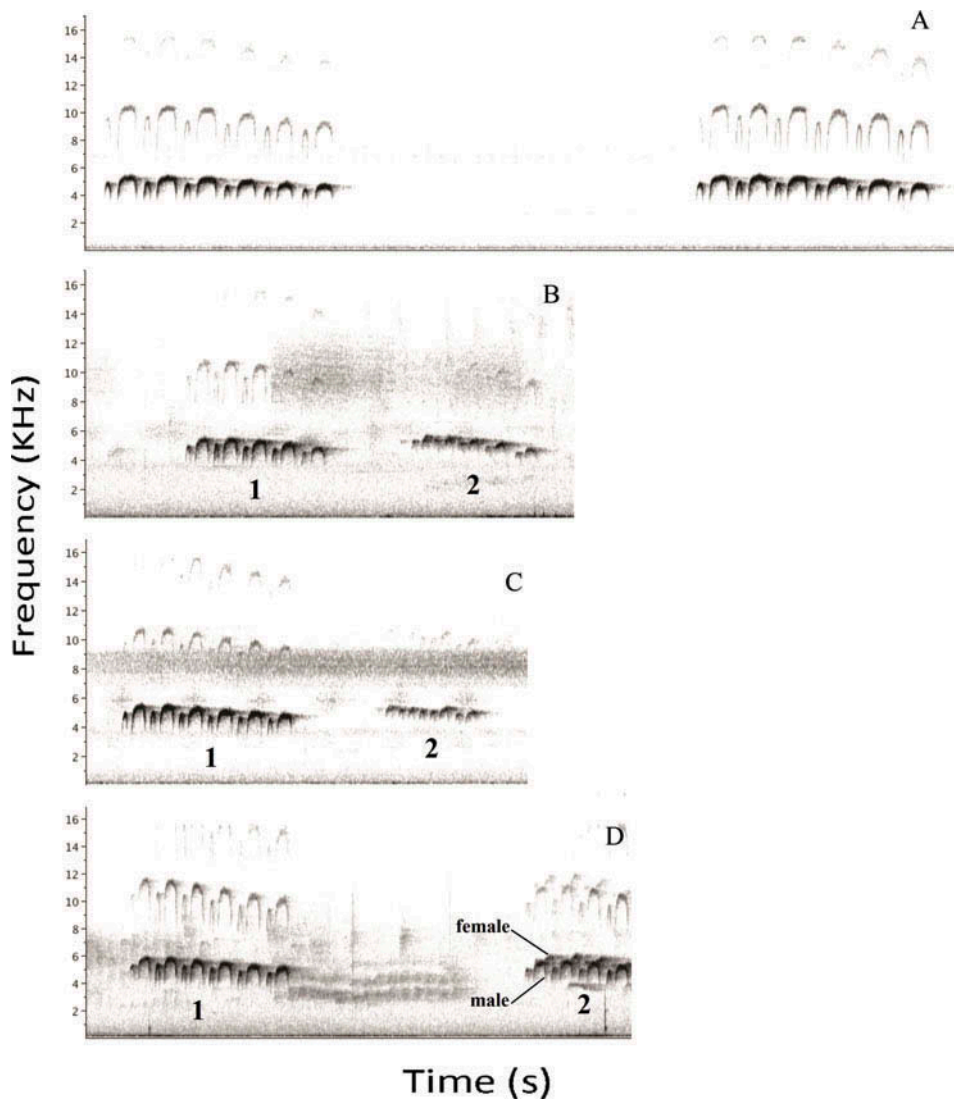
Figure 3. Sonograms of the songs and duet of *Myrmeciza loricata*. (A) Male song. (B) 1-male phrase song, 2-female phrase song with alternated notes. (C) 1-male phrase song, 2-female phrase song with initial trill followed by alternated notes. (D) 1-male phrase song, 2-male and female overlapped phrases song.

3.3. *Call II*

This call can be described as notes produced singly or in phrases. We analysed 2189 notes and 53 phrases (*n* = 40 individuals). This call was produced by males and females and was not individually distinct or sex specific. The birds produced this call when they were near each other (e.g. when the couple was walking on the forest floor together) or when they were distant from each other, in which case the couple approached one another or maintained their distance but continued vocalizing. This
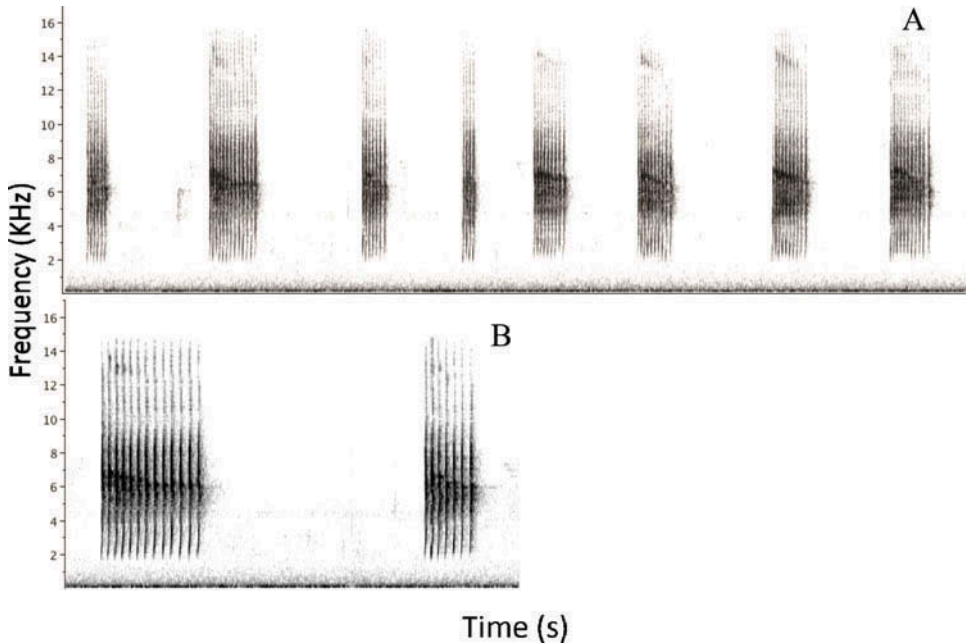
Figure 4. Sonograms of the call I (alarm) of *Myrmeciza loricata*. (A) Rattle phrases sequence. (B) Zoom showing the series of vertical tick notes.

call was also observed during flight, in which case it was produced in phrases. The note can be described as one modulation, upward and strongly downward with rapid modulations (wheezing quality) and harmonics (first harmonic and second harmonic) (Figure 5).

3.4. *Call III*

This call can be described as several kinds of notes produced singly or in phrases. We analysed 114 notes and 21 phrases ($n = 15$ individuals). We observed this call to be produced when males foraged and when males approached females.

The different patterns of notes are described as follows:

(1) Note "C" ($n = 43$) consisted of an upward–downward inflection with harmonics (first harmonic). This note was produced singly or between songs, call I (alarm) or call II phrases (Figure 6).
(2) Notes "D + E" ($n = 10$) consisted of one inflection with no harmonic. These notes were always produced together, but they were isolated from other types of vocalizations (Figure 7A).
(3) Note "F" ($n = 11$) consisted of three inflections and no harmonic. This note was produced singly or in phrases (Figure 7B).
(4) Note "G" ($n = 22$) consisted of two inflections and harmonics (first harmonic, second harmonic and third harmonic) and was produced singly (Figure 7D).
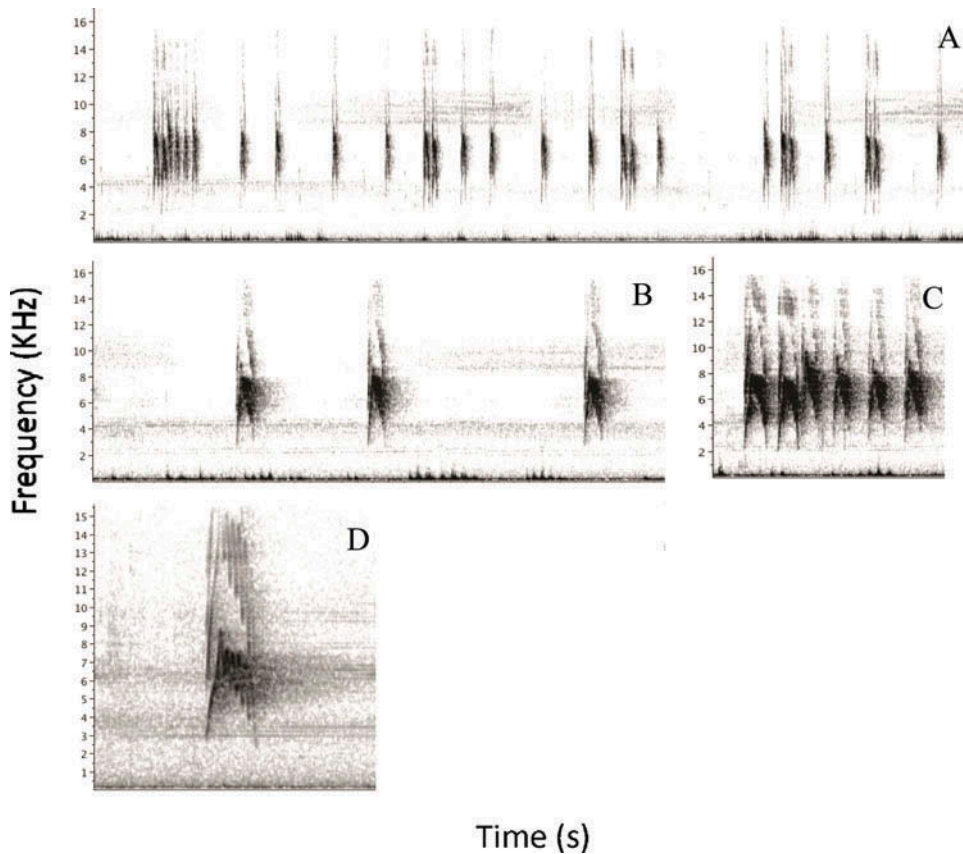
Figure 5. Sonograms of the call II of *Myrmeciza loricata*. (A) Sequences of phrases and notes. (B) Notes emitted singly. (C) Notes emitted in phrase during the flight. (D) Note showing strongly down-slurred rapid modulations (wheezing quality).

(5) Note "H" ($n = 17$) consisted of three inflections and no harmonics. This note was produced singly (Figure 7E).

(6) Note "I" ($n = 23$) consisted of three inflections and harmonics (first harmonic), and it was produced after call II (Figure 7C).

(7) Note "J" ($n = 9$) is a downward note with no harmonic. This note was produced between call II notes (Figure 7F).

Table 1 presents data describing the acoustical parameters of all of the vocalizations, and Table 2 presents data describing the acoustical parameters of each kind of call III note.

4.   Discussion

This is the first work to describe the vocal repertoire and duets of *M. loricata*. The vocal repertoire of *M. loricata* described in this paper consists of simple songs and calls. Several studies with other species of the family Thamnophilidae have also
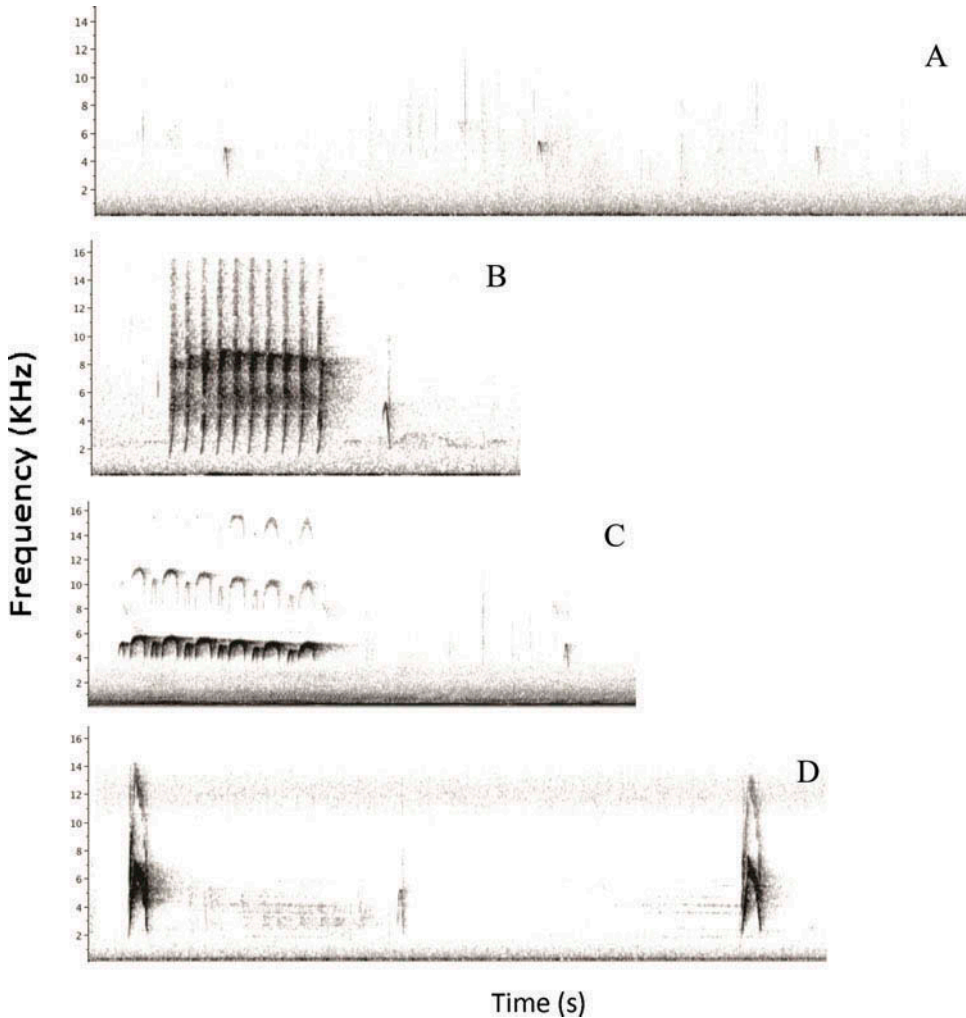
Figure 6. Sonograms of the note "C" (call III) of *Myrmeciza loricata*. (A) Note "C" emitted singly. (B) Note "C" emitted with call I (alarm). (C) Note "C" emitted with male song. (D) Note "C" emitted with call II.

described repertoires with the same design (Willis 1968, 1972, 1982; Willis and Oniki 1972, 1981).

The song of the white-bibbed antbird is simple and most often triggered by other individuals in the neighbourhood, which suggests that this vocalization carries a specific message of territorial defence. We found that the notes of the white-bibbed antbird song consist of one modulation, as was previously found by Willis (1972) in his study of the repertoire of Spotted antbirds (*Hylophylax naevioides*). The call I – alarm consists of a rattle and was emitted when the observer approached the place where the individuals were located. In *H. naevioides*, Willis (1972) also described the same rattle design in this kind of call; in accordance with the results obtained by this author, this call was
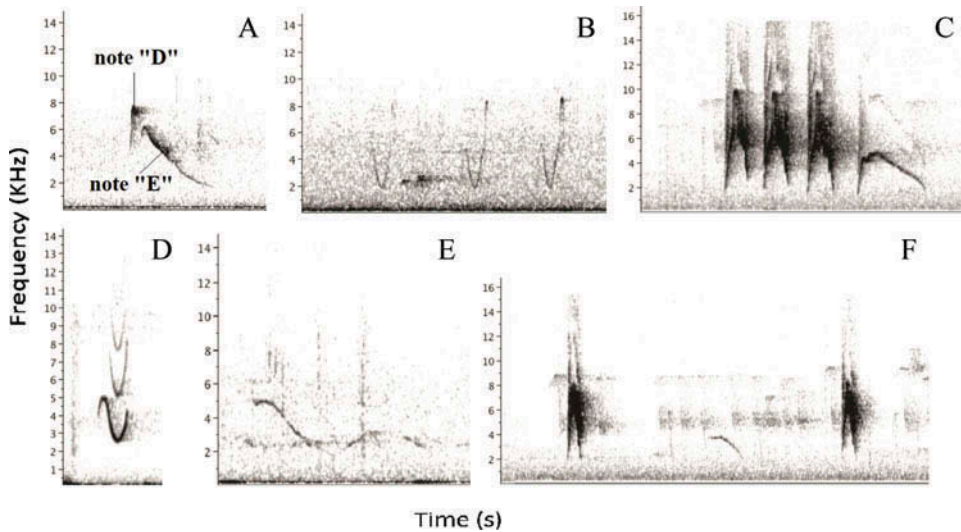
Figure 7. Sonograms of other notes (call III) of *Myrmeciza loricata*. (A) Notes "D + E". (B) Note "F". (C) Note "I" emitted with call II. (D) Note "G". (E) Note "H". (F) Note "J" emitted with call II.

produced when large animals and humans were seen and when the observer walked through the woods.

Call II consists of first and second harmonics and was produced singly or in phrases. Willis (1972) described call notes with a design similar to that which we found for call II, in terms of the note shape, the number of harmonics and being produced singly or in phrases. *Myrmeciza loricata* emit call II in two behavioural contexts. In the first context, a couple is near to each other or distant from each other (in which case the couple may approach one another) indicating that this vocalization may be related to communication and contact within the pair. In the second context, the male white-bibbed antbird emits call II during flight. In contrast, *H. naevioides* emits this call during imminent danger such as when a hawk approaches, and during flight.

We observed that call III – C was emitted when a couple approached one another and during foraging. Willis (1972) described similar notes that were also emitted when males and females approached each other and during copulation. Moreover, the same behaviour that we observed in the white-bibbed antbird was observed in *H. naevioides*: the male ruffled his feathers and kept singing while remaining in front of the female. In the same work, the author reported that the male could alternate this call with song, which we also observed in the white-bibbed antbird as a way of maintaining the bond between the couple.

Willis (1968), in his behavioural study of Lunulated and Salvin's antbirds (*Gymnopithys lunulatus* and *Gymnopithys salvini*), described calls similar to call I of the white-bibbed antbird, which were also emitted when the animal was disturbed by the observer or by other animals. Similar notes to call III – C were found in the same work. These notes were also emitted when the couple approached each other and during feeding. In addition, the author described for both species a similar

Table 1. Descriptive data of the acoustical parameters of white-bibbed antbird (*Myrmeciza loricata*) vocalizations.

Acoustical parameters		Song		Call I – alarm	Call II	Call III
		Male	Female			
Minimum frequency (Hz)	min.	3420.8 ± 357.6	3767 ± 187.9	1395.4 ± 778.5	2599.6 ± 921.4	1914.6 ± 517.9
	max.	4089.6 ± 297.6	4144.9 ± 162.5	2997.2 ± 866.4	4326.2 ± 622.1	2511.1 ± 385.1
	mean	3749.7 ± 291.9	3934.1 ± 107.3	2153 ± 741.1	3506.4 ± 722.4	2175.9 ± 471.3
Maximum frequency (Hz)	min.	5525.1 ± 374	5963 ± 323.1	10,996.4 ± 2235.9	7373.7 ± 1150.5	4655.4 ± 763.6
	max.	5927.4 ± 346.7	6193.4 ± 331	13,081.8 ± 694.7	9255.8 ± 945.3	5465.7 ± 620.6
	mean	5733.6 ± 295.2	6091.2 ± 299.8	12,101.8 ± 2260.1	8238.9 ± 664.3	5037.9 ± 559.5
Bandwidth (Hz)	min.	1632.2 ± 306.1	1851 ± 306.6	8489.5 ± 2626	3642.8 ± 1061.2	2666.8 ± 915.1
	max.	2391.9 ± 406.9	2344.5 ± 458.8	11,266.8 ± 2892.9	6119.4 ± 1428.6	3519.8 ± 843.9
	mean	2030.1 ± 330.1	2157.1 ± 350.4	9955 ± 2721.9	4742.9 ± 1030.8	3089.5 ± 809.9
Centre frequency (Hz)	min.	4848.3 ± 121.8	5236.9 ± 231.1	5506.9 ± 1652.6	5206.4 ± 1385.8	3319.8 ± 871
	max.	5203.5 ± 142.7	5340.2 ± 243.6	7407.4 ± 805.5	20,100.1 ± 43333.6	4461.2 ± 683.2
	mean	5025.2 ± 118.6	5288.5 ± 224.6	6684.4 ± 828.5	12,531.3 ± 21361.3	3927.1 ± 620.6
Dominant frequency (Hz)	min.	4613.9 ± 400.2	5236.8 ± 231.1	4490.2 ± 2017.7	4743.9 ± 969.5	3115.2 ± 842.2
	max.	5405.2 ± 168.9	5615.6 ± 377.2	8065.4 ± 738.6	7703.4 ± 632.3	4593.8 ± 575.2
	mean	5085.7 ± 122.5	5431 ± 281.5	6911.1 ± 982.8	6474.3 ± 662	3799 ± 510.4
First quartile frequency (Hz)	min.	4638.6 ± 145.5	5030.2 ± 188.7	4269.9 ± 1449.9	4739.5 ± 1046.2	2545.3 ± 988
	max.	5011.7 ± 163.2	5168 ± 243.6	6517.9 ± 936.8	6136.5 ± 1155.3	3450.3 ± 1192
	mean	4809.2 ± 116.8	5092.2 ± 201.5	5567.2 ± 855.1	5404.2 ± 947.2	2939.7 ± 990.9
Third quartile frequency (Hz)	min.	5061.3 ± 139.4	5340.2 ± 322.3	6647.8 ± 1376.8	5958.6 ± 1050.9	3406.6 ± 1245.4
	max.	5390.1 ± 144.9	5581.4 ± 261.2	8037.2 ± 721.9	7505.5 ± 1322	4412.2 ± 1448.6
	mean	5222.5 ± 135	5483.8 ± 273.1	7435.7 ± 666.2	6813.3 ± 1234.7	3968.7 ± 1309
Phrase/note duration (s)	min.	1.287 ± 0.317	1.250 ± 0.266	0.297 ± 0.148	0.15 ± 0.045	0.053 ± 0.018
	max.	2.378 ± 0.286	1.841 ± 0.173	0.886 ± 0.251	0.378 ± 0.242	0.203 ± 0.232
	mean	1.911 ± 0.161	1.549 ± 0.159	0.547 ± 0.132	0.557 ± 2.157	0.1 ± 0.093
Number of notes	min.	7.29 ± 2.13	7.8 ± 1.79	4.03 ± 2.17	1	1
	max.	13.38 ± 1.81	10.6 ± 1.14	12.77 ± 4.72	1.59 ± 0.97	1.08 ± 0.29
	mean	10.91 ± 0.99	9.63 ± 0.87	7.59 ± 2.47	1.03 ± 0.04	1.06 ± 0.22
Note rate (note/s)	min.	0.005 ± 0.001	0.006 ± 0.001	8.199 ± 5.318	3.669 ± 1.206	12.556 ± 7.900
	max.	0.712 ± 1.904	1.098 ± 2.441	16.625 ± 2.599	7.133 ± 1.581	21.839 ± 8.485
	mean	0.044 ± 0.128	0.225 ± 0.488	13.401 ± 1.972	5.147 ± 1.043	17.003 ± 7.073
Inter-phrase/note duration (s)	min.	3.154 ± 1.062	9.879 ± 4.749	1.964 ± 1.775	2.038 ± 1.775	7.328 ± 10.459
	max.	16.226 ± 15.741	34.544 ± 34.469	13.807 ± 32.637	19.522 ± 31.861	27.212 ± 24.505
	mean	5.457 ± 1.523	20.379 ± 17.523	3.381 ± 1.780	6.388 ± 14.402	14.286 ± 15.935

Note: Values are mean ± SD (range). Min. (minimum value), max. (maximum value).

Table 2. Descriptive data of the acoustical parameters of each kind of call III notes of the white-bibbed antbird (*Myrmeciza loricata*).

Acoustical parameters		"C"	"D + E"	"F"	"G"	"H"	"I"	"J"
					Notes			
Minimum frequency (Hz)	min.	1609.2 ± 490.6	1726.1 ± 33.9	1667.1 ± 91.3	1239.7 ± 204	1665.5 ± 183	1659 ± 102	3007 ± 94.5
	max.	2555.1 ± 376.6	2332 ± 6.9	1886 ± 90.5	1805.1 ± 211	1794.9 ± 149.4	2159 ± 278.7	3118.4 ± 112.1
	mean	2029.6 ± 400.7	2045.8 ± 86.9	1776.5 ± 89.1	1527.1 ± 193	1708.6 ± 149.4	1945.8 ± 140.5	3084.9 ± 96.6
Maximum frequency (Hz)	min.	4531 ± 111.8	3558.2 ± 68.2	3829.2 ± 305.6	3772.1 ± 502.1	4628.7 ± 104.4	3418.9 ± 387.6	5256.7 ± 189
	max.	5936.2 ± 270.3	3962.1 ± 54.3	4310.8 ± 292.3	5829.5 ± 511.5	4534 ± 169	3962.1 ± 217.5	5434.9 ± 185.5
	mean	5236.3 ± 152.5	3768 ± 2.6	4070 ± 291.4	4568.3 ± 476.3	4540.9 ± 169	3729.8 ± 29.5	5368 ± 166.7
Bandwidth (Hz)	min.	602.9 ± 298.4	1356 ± 163.2	2162.1 ± 299	2057.5 ± 630.9	861.4 ± 487.3	1644.5 ± 122.3	2249.7 ± 94.5
	max.	1851.9 ± 294.2	2106.1 ± 165.2	1550.4 ± 266.8	4561.7 ± 647.7	1033.6 ± 344.6	1918.6 ± 224.4	2316.5 ± 77.1
	mean	1325 ± 207.5	1722.2 ± 89.5	1302.8 ± 285.9	3041.2 ± 597.8	861.3 ± 344.6	1783.9 ± 170	2283.1 ± 73.2
Centre frequency (Hz)	min.	2670.2 ± 652.2	3100.8 ± 243.6	2907 ± 286.4	2584 ± 331.2	3445.3 ± 487.2	2756.3 ± 243.6	4737.3 ± 121.8
	max.	4478.9 ± 372.1	3531.5 ± 121.8	3273 ± 281.3	3962.1 ± 342.5	3359.2 ± 455.7	3359.2 ± 121.8	4909.6 ± 172.3
	mean	3816.2 ± 253	3251.5 ± 30.4	3090 ± 276.1	3326.9 ± 315.7	3273 ± 455.7	3100.8	4866.5 ± 144.1
Dominant frequency (Hz)	min.	2454.8 ± 494.8	2584 ± 487.2	2605.5 ± 684.7	1894.9 ± 786.2	3703.7 ± 852.6	3014.7 ± 609	4909.6 ± 121.8
	max.	4823.4 ± 140.6	3617.6 ± 121.8	3789.8 ± 680.4	4478.9 ± 793.3	3789.8 ± 652.2	3531.5 ± 121.8	5081.9 ± 172.3
	mean	3697.9 ± 254	3246.7 ± 98.1	3197.7 ± 682.5	3413 ± 768.1	3560.1 ± 652.2	3359.2 ± 121.8	5038.8 ± 144.2
First quartile frequency (Hz)	min.	2411.7 ± 579.9	2670.1 ± 121.8	2347.1 ± 221.6	2067.2 ± 411.1	2928.5 ± 243.7	2411.8 ± 243.6	4134.4 ± 198.9
	max.	3746.8 ± 294.2	3186.9 ± 121.8	2584 ± 218.7	3445.3 ± 425.3	2842.4 ± 263.1	2842.4 ± 121.8	4306.7 ± 198.9
	mean	3138.9 ± 331.4	2879.4 ± 38.9	2465.6 ± 213.6	2637.8 ± 388.2	2813.7 ± 263.1	2684.5 ± 20.3	4306.7 ± 154.1
Third quartile frequency (Hz)	min.	3445.3 ± 344.5	3273 ± 487.3	3402.2 ± 296.6	3100.8 ± 347.4	3789.8 ± 730.9	3100.8 ± 487.3	4909.6 ± 121.8
	max.	5038.8 ± 165	3703.7 ± 121.8	3789.8 ± 292.8	4306.6 ± 349.8	3876 ± 553.8	3703.7 ± 121.8	5081.9 ± 172.3
	mean	4463.9 ± 166.8	3506.3 ± 5.1	3596 ± 282.9	3832.9 ± 336.7	3675 ± 553.8	3459.7 ± 101.5	5038.8 ± 144.2
Phrase/note duration (s)	min.	0.031 ± 0.008	0.285 ± 0.037	0.106 ± 0.015	0.079 ± 0.018	0.454 ± 0.115	0.053 ± 0.004	0.069 ± 0.013
	max.	0.068 ± 0.006	0.536 ± 0.033	0.121 ± 0.015	0.171 ± 0.019	0.483 ± 0.115	0.069 ± 0.015	0.069 ± 0.019
	mean	0.049 ± 0.005	0.41 ± 0.012	0.113 ± 0.015	0.122 ± 0.02	0.5 ± 0.115	0.059 ± 0.006	0.078 ± 0.016
Number of notes	min.	1	2	1	1	1	1	1
	max.	1	2	1	1	1	1	1
	mean	1	2	1	1	1	1	1
Note rate (note/s)	min.	14.895 ± 1.246	3.742 ± 0.232	9.768 ± 1.763	5.848 ± 1.216	2.279 ± 0.579	14.950 ± 3.241	11.565 ± 1.776
	max.	33.832 ± 7.052	7.076 ± 0.913	14.493 ± 1.807	12.864 ± 1.235	2.186 ± 0.535	18.868 ± 3.220	16.949 ± 3.353
	mean	21.918 ± 3.154	5.128 ± 0.115	12.131 ± 1.691	8.338 ± 1.569	2.080 ± 0.535	17.155 ± 1.272	13.225 ± 2.716
Inter phrase/note duration (s)	min.	6.087 ± 4.491	3.304 ± 4.672	0.097 ± 0.015	0.109 ± 0.032	0.915 ± 0.105	6.059 ± 0.776	0.104 ± 0.025
	max.	30.199 ± 48.203	21.414 ± 7.601	6.663 ± 2.126	3.414 ± 2.469	4.963 ± 6.989	18.503 ± 11.717	3.169 ± 2.814
	Mean	18.707 ± 21.041	11.200 ± 0.27	1.245 ± 1.053	0.761 ± 0.266	3.545 ± 6.199	12.717 ± 5.668	0.663 ± 0.104

Note: Values are mean ± SD (range). Min (minimum value), max. (maximum value).

vocalization to call II of the white-bibbed antbird, which was emitted when the animal was alert. Willis (1982) described other alarm calls that Scale-backed antbirds (*Willisornis poecilonotus*) used in response to the presence of large animals and humans. We found that *M. loricata* sometimes emitted call III – C and songs together. Willis and Oniki (1972) described a similar call in the Chestnut-backed antbird (*Myrmeciza exsul*), which was emitted by males after singing or when he approached a female or fed her. The same authors, in 1981, described a similar alarm call in the slender antbird (*Rhopornis ardesiaca*), which is used to alert other individuals to the presence of potential predators.

It is therefore likely that the alarm calls and calls with notes equivalent in design to call III – C of *M. loricata* are an ancestral feature or have converged in the family Thamnophilidae in response to the presence of large animals and humans and during courtship behaviours, respectively. Vocal properties have a genetic basis, and vocal similarities between species may depend upon their phylogenetic relatedness (Price and Lanyon 2002; Päckert et al. 2003; Miller and Baker 2009). The physical environment shapes the properties of vocal signals (McCracken and Sheldon 1997), and similarities may result from convergence (Seddon 2005; Nicholls and Goldizen 2006). Additionally, the properties of vocal signals vary with their signalling context as well, resulting in homoplasy in vocal traits that serve specific functions in specific acoustic environments (Marler 1955).

The structure of the acoustic call is crucial for the optimal performance of the call's function. Calls with a wide bandwidth that are produced faster and in series are easier to locate than are those with narrow bandwidth and fewer repetitions. Likewise, high frequencies reach smaller distances and present a reduced active space (Marler 2004). In view of these features, call II, in contrast to the other calls we observed, appears well adapted to perform the function of communication and contact within a pair. The narrow bandwidth and lower frequency emission of this call is difficult to locate and enlarges the active space to ensure effective information exchange between the mates, especially when they are distant from each other (Marler 2004).

Call I – alarm consisted of a wide bandwidth rattle, so presenting a signal with a smaller active space that is easier to locate. In accordance with Marler (2004), the design of this call allows the call to fulfil its role well by providing clear information quickly. After the alarm call is emitted, predators may be discouraged because the signaller reduces the probability of the attack by showing that the predator has been detected and its attack is no longer unexpected. In addition to informing individuals of the presence of danger, this type of call can indicate the exact location of danger, thereby encouraging escape or notifying the signaller's mate to remain hidden and so increasing the chances of protecting the individual's family group.

Call III consisted of a narrow bandwidth and low-intensity emission, which may be favourable during foraging and interactions between the couple because the individuals could be very susceptible to attack by predators in both of these situations.

Contact calls are used by species that live in denser habitats and identify the individuals of a social group or a couple during the breeding season (Marler 2004). As mentioned previously, it is possible that call II provides specific recognition between males and females because the couple responded to each other even when far from one another. We found that call II was also emitted during flight, but in this case, the

notes were produced in phrases. In accordance with Constantine and The Sound Approach (2006), different acoustic features in the structure of a call can be used to discriminate between different functions in different behavioural contexts. Moreover, many species use contact calls during flight, modifying the temporal structure. Many finches do not present a call dedicated primarily to maintaining contact, but they often use forms of the flight call, differing in tempo and loudness, for both contact and separation (Marler 1956). Therefore, the emission of the notes of call II in phrases constitutes a flight call.

Call III consisted of different notes emitted at low intensity during foraging and courtship behaviours. Sounds that can be described by a variable structure are simple variations of the same signal with the same biological function (Smith 1996; Vielliard and Silva 2007). Low intensity emissions could minimize the detection of individuals (Nunes and Betini 2002), and therefore, this feature appears advantageous during foraging and courtship behaviours, as we observed for the white-bibbed antbird. Calls with multiple functions were observed in other studies. Brown (1964) and Hope (1980) described an alarm call of Steller's jay of North America that is given when an intruder approaches on the ground or for other sudden alarming events. This call also serves as a short-range flight call, a distance contact signal and an agonistic call used in close range interactions between two jays.

Sometimes calls used as separation signals (a call used to separate members of a flock, a family or a mated pair) are borrowed from another context, such as flight or alarm. Marler (1956) studied crossbills that give a burst of loud flight calls when they drift apart while foraging, attracting companions and eliciting replies. Chaffinches separated from the winter flock give another call that also has other functions, for example, predator mobbing.

In general, we found a relationship between the structure and function of calls. The type of call given in a particular situation obviously varies with the degree of danger and the vulnerability of the caller and its companions (Klump and Shalter 1984). It is important to take account of what an actual listener can hear because the active space of a call varies, depending on who is listening. The acoustic structure of a call itself is critical; generally, the lower the pitch is, the further a sound travels (Wiley and Richards 1982; Larom et al. 1997).

There are many factors that contribute to call design (Morton 1975; Wiley and Richards 1978, 1982; Hope 1980; Bradbury and Vehrencamp 1998; Morton et al. 1998; Marler 2004). Such a "perfect alarm call" would be a narrowband, pure tone, pitched high enough so that it does not travel far, so limiting the active space. Jurisevic and Sanderson (1994) described the alarm calls of Australian passerines in response to flying predators as being narrower, relatively higher-pitched, shorter, louder and often more repetitive than the hawk calls of North American and European species. What is ideal for one species may be less so for another, even a close relative, if it has a different lifestyle. Sometimes two phylogenetically more distant species have alarm calls that are structurally more similar than those of two closely related species if the former share a similar environment and the latter do not (Marler 2004).

Another highly specialized signal is the distress call given when a bird is held in the grip of a predator. These calls are often piercingly loud, with a harsh tone and with the frequency adjusted for long-range transmission (Matheoven et al. 1997). The structure of this call appears to be rather narrowly constrained by the function it serves (Conover 1994; Wise et al. 1999). Additionally, Rowley and Russel (1997)

correlated a contact call of Australian fairy-wrens with its structure: narrow-band, high-pitched, short duration and short-range calls are likely to be audible only over short distances so are less likely to betray a bird's location to a predator. The acoustic structure of bird calls is due to natural selection and is often highly adapted to their function. Selection to maximize the active space is reflected in adjustments of acoustic structure and calling behaviour. Adaptations to facilitate or hinder call localization are frequent. There are selection pressures that favour species specificity in a bird call; specifically distinctive signals provide a particular facilitation of communication between members of the same species and group (Marler 2004; Slabbekoorn 2004).

We found that males and females sang in duets, often with overlapping phrases. Farabaugh (1982) defined a duet as a union of acoustic displays in which two birds coordinate their songs with some degree of temporal precision. Hall (2004), based on this concept, defined a duet as a linking of vocalizations emitted by paired individuals. This author presents some hypotheses that are most likely to provide broadly applicable explanations of the function of duets: avoiding being usurped from partnership (advertising own mated status to same-sex outsiders), preventing partner being usurped from partnership (advertising partner's mated status to opposite-sex outsiders), initiating a joint resource defence (collaboratively displaying to outsiders in defence of territory or other resources) and signalling commitment (singing in a duet to indicate willingness to invest and elicit reciprocal investment from partner, which may be used deceptively if partners are in conflict over relative levels of investment).

White-bibbed antbird males always initiate the duet and sing more frequently. This observation is in agreement with many studies of other species of the family Thamnophilidae. For example, a study by Seddon and Tobias (2005) determined that warbling antbird (*Hypocnemis cantator*) females rarely sing in isolation and primarily sing in response to males. Zimmer et al. (1997) found that the Rio Branco antbird (*Cercomacra carbonaria*) duet is initiated by one or more male phrases; only after the initial male phrases does the female vocalize. Willis (1972) described males and females of the Spotted antbird (*Hylophylax naevioides*) singing in duet; when far from each other, the female sang in response to a male.

As we found in *M. loricata*, Bard et al. (2002) noted differences between the songs of male and female *Hylophylax naevioides*. These differences may indicate the sex of the intruder to the couple, and this information will probably be crucial in strategies involving territorial defence.

The vocal repertoire of *M. loricata* is similar to the repertoire of other species of the family Thamnophilidae, especially when considering the design of the calls.

Acknowledgements

References

Armstrong EA. 1963. The structure and components of bird song: a study of bird song. New York: Oxford University Press.

Bard SC, Hau M, Wikelski M, Wingfield JC. 2002. Vocal distinctiveness and response to conspecific playback in the Spotted Antbird, a neotropical suboscine. Condor. 104:387–394.

Birregard RO Jr, Lovejoy TE. 1989. Effects of forest fragmentation on amazonian understory bird communities. Acta Amaz. 19:215–241.

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland, MA: Sinauser Associates.

Braun MJ, Isler ML, Isler PR, Bates JM, Robbins MB. 2005. Avian speciation in the Pantepui: the case of the Roraiman Antbird (*Percnostola* [*Schistocichla*] "*leucostigma*" *saturata*). Condor. 107:327–341.

Brown JL. 1964. The integration of agonistic behavior in the Steller's jay *Cyanocitta stelleri* (Gmelin). UC Publ Zool. 60:223–328.

Chaves JC, Cuervo AM, Miller MJ, Cadena CD. 2010. Revising species limits in a group of *Myrmeciza* Antbirds reveals a cryptic species within *M. laemosticta* (Thamnophilidae). Condor. 112:718–730.

Conover MR. 1994. Stimuli eliciting distress calls in adult passerines and response of predators and birds to their broadcast. Behaviour. 131:19–37.

Constantine M, The Sound Approach. 2006. The sound approach to birding: a guide to understanding bird sound. UK: The sound approach. Poole.

Farabaugh SM. 1982. The ecological and social significance of duetting. In: Kroodsma DE and Miller EH, editors. Acoustic communication in birds. New York: Academic Press; p. 85–124.

Gonzáles C, Ornelas JF. 2005. Song structure and microgeographic song variation in Wedge-tailed Sabrewings (*Campylopterus curvipennis*) in Veracruz, Mexico. Auk. 122:593–607.

Hall ML. 2004. A review of hypotheses for the functions of avian duetting. Behav Ecol Sociobiol. 55:415–430.

Helbig AJ, Kox AG, Parkin DT, Sangster G, Collinson M. 2002. Guidelines for assigning species rank. Ibis. 144:518–525.

Hope S. 1980. Call form in relation to function in the Steller's jay. Am Nat. 116:788–820.

Isler ML, Isler PR. 2003. Species limits in the Pygmy Antwren (*Myrmotherula brachyura*) complex (Aves: Passeriformes: Thamnophilidae): 1. The taxonomic status of *Myrmotherula brachyura ignota*. Proc Biol Soc Wash. 116:23–28.

Isler ML, Isler PR, Brumfield RT. 2005. Clinal variation in vocalizations of an antbird (Thamnophilidae) and implications for defining species limits. Auk. 122:433–444.

Isler ML, Isler PR, Whitney BM. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). Auk. 115:577–590.

Johson NK, Remsen JV Jr, Cicero C. 1999. Acta XXII Congressus Internationalis Ornithologici: Bird Life South Africa. Ottawa: National Museull of Natural Sciences (University of Ottawa Press). Resolution of the debate over species concepts in ornithology: a new comprehensive biological species concept; p. 1470–1482.

Jurisevic MA, Sanderson KJ. 1994. Alarm vocalizations in Australian birds: convergent characteristics and phylogenetic differences. Emu. 94:69–77.

Klump GM, Shalter MD. 1984. Acoustic behavior of birds and mammals in the predator context. Z Tierpsychol. 66:189–226.

Larom D, Garstang M, Payne K, Raspet R, Lindeque M. 1997. The influence of surface atmospheric condictions on the range and area reached by animal vocalizations. J Exp Biol. 200:421–431.

Lovell SF, Lein MR. 2004. Song variation in a population of Alder Flycatchers. J Field Ornithol. 75:146–151.

Marler P. 1955. Characteristics of some animal calls. Nature. 176:6–7.

Marler P. 1956. The voice of the chaffinch and its function as a language. Ibis. 98:231–261.

Marler P. 2004. Birds call: a cornucopia for communication. In: Marler P and Slabbekoorn H, editors. Nature's music: the science of birdsong. San Diego: Elsevier Academic Press; p. 132–177.

Matheoven NT, Aubin T, Dabelsteen T. 1997. Propagation of bird acoustic signals: comparativestudy of atarling and blackbird distress calls. Life Sci. 320:869–876.

McCracken KG, Sheldon FH. 1997. Avian vocalizations and phylogenetic signal. Proc Nat Acad Sci U S A. 94:3833–3836.

Miller EH, Baker AJ. 2009. Antiquity of shorebird acoustic displays. Auk. 122:6–11.

Morton ES. 1975. Ecological sources of selection on avian sounds. Am Nat. 109:17–34.

Morton ES, Naguib M, Wiley RH. 1998. Degradation and signal ranging in birds: memory matters (and replies). Behav Ecol Sociobiol. 42:135–148.

Nicholls JA, Goldizen AW. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. J Anim Ecol. 75:549–558.

Nunes EG, Betini S. 2002. Métodos de estimativa de abundância de psitacídeos. In: Galetti and Pizo MA, editors. Ecologia e conservação de psitacídeos no Brasil. Belo Horizonte: Melopsittacus Publicações Científicas.; p. 99–112.

Päckert M, Martens J, Kosuch J, Nazarenko AA, Veith M. 2003. Phylogenetic signal in the song of crests and kinglets (Aves: Regulus). Evolution. 57:616–629.

Price JJ, Lanyon SM. 2002. Reconstructing the evolution of complex bird song in the oropendolas. Evolution. 56:1514–1529.

Raven Pro. 2010. Interactive sound analysis software. Cornell Lab of Ornithology. Version 1.3. Ithaca (NY). Available from: http://www.birds.cornell.edu/raven

Ridgely RS, Tudor G, Brown WL. 1994. The birds of South America: The suboscine passerines. Austin (TX): University of Texas Press.

Ritchison G. 1988. Song repertoire and the singing behavior of male northern cardinals. Wilson Bull. 100:583–603.

Rowley I, Russel E. 1997. Fairy-wrens and Grasswrens: Maluridae. Oxford: Oxford University Press.

Scott FL, Lein MR. 2004. Song variation in a population of Alder Flycatchers. J Field Ornithol. 75:146–151.

Seddon N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. Evolution. 59:200–215.

Seddon N, Merril RM, Tobias JA. 2008. Sexually selected triats predict patterns of species richness in a diverse clade of Suboscine birds. Am Nat. 171:620–631.

Seddon N, Tobias JA. 2005. Duets defend mates in a Suboscine Passerine, the Warbling Antbird (*Hypocnemis cantator*). Behav Ecol. 10:73–83.

Sick H. 2001. Ornitologia brasileira. Rio de Janeiro: Nova fronteira.

Sigrist T. 2006. Aves do Brasil – uma visão artística. São Paulo: Avis Brasilis.

Skutch AF. 1996. Antbirds and ovenbirds: their lives and homes. Austin: University of Texas Press.

Slabbekoorn H. 2004. Singing in the wild: the ecology of birdsong. In: Marler P and Slabbekoorn H, editors. Nature's music: the science of birdsong. San Diego (CA): Elsevier Academic Press; p. 178–205.

Smith WJ. 1996. Using interactive playback to study how songs and singing contribute to communication about behavior. In: Kroodsma DE and Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press; p. 377–397.

Stouffer PC, Birregard RO Jr. 1995. Use of amazonian forest fragments by understory insectivorous birds. Ecology. 76:2429–2445.

Vielliard JME, Silva ML. 2007. A Bioacustica como ferramenta de pesquisa em Comportamento animal. In: Assis G, Brito R and Martin WL, editors. Estudos do Comportamento II. Belém: Editora UFPA; p. 141–156.

Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds sound transmission and signal detection. In: Kroodsma DE and Miller EH, editors. Acoustic communication in birds. New York: Academic Press; p. 132–181.

Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds sound transmission and signal detection. In: Acoustic communication in birds. New York: Academic Press; p. 132–181.

Willis ED. 1968. Studies of the behavior of Lunulated and Salvin's Antbirds. Condor. 70:128–148.

Willis ED. 1972. The behavior of Spotted Antbirds. Am Ornithol Union. 10:1–162.

Willis ED. 1982. The behavior of Scale-backed Antbirds. Wilson Bull. 94:447–462.

Willis ED, Oniki Y. 1972. Ecology and nesting behavior of the Chestnut-backed Antbird (*Myrmeciza exsul*). Condor. 74:87–98.

Willis ED, Oniki Y. 1981. Notes on the Slender Antbird. Wilson Bull. 93:103–107.

Wise KK, Conover MR, Knowlton FF. 1999. Responses of coyotes to avian distress calls: testing the startle-predator and predator-attraction hypotheses. Behavior. 136:935–949.

Zimmer K. 1999. Behavior and vocalizations of the Caura and the Yapacana Antbirds. Wilson Bull. 111:195–209.

Zimmer KJ, Whittaker A, Stotz DF. 1997. Vocalizations, behavior and distribution of the Rio Branco Antbird. Wilson Bull. 109:663–678.