



## Bioacoustics

The International Journal of Animal Sound and its Recording

ISSN: 0952-4622 (Print) 2165-0586 (Online) Journal homepage: <http://www.tandfonline.com/loi/tbio20>

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To cite this article: Laura M. Schaedler, Pedro H. L. Ribeiro, André C. Guaraldo & Lilian T. Manica (2019): Acoustic signals and repertoire complexity in Swallow-tailed Manakins (*Chiroxiphia caudata*, Aves: Pipridae), *Bioacoustics*

To link to this article: <https://doi.org/10.1080/09524622.2018.1563870>



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Published online: 08 Jan 2019.







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## Acoustic signals and repertoire complexity in Swallow-tailed Manakins (*Chiroxiphia caudata*, Aves: Pipridae)

Laura M. Schaedler <sup>a,b</sup>, Pedro H. L. Ribeiro <sup>b,c</sup>, André C. Guaraldo <sup>a,b</sup>  
and Lilian T. Manica <sup>b</sup>

<sup>a</sup>Programa de Pós-graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba, Brazil; <sup>b</sup>Laboratório de Ecologia Comportamental e Ornitologia, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil; <sup>c</sup>Programa de Pós-graduação em Zoologia, Universidade Federal do Paraná, Curitiba, Brazil

### ABSTRACT

Neotropical manakins (Pipridae) are well known for the male's multimodal courtship displays including acoustic and visual signals. In these birds, acoustic signals are important for attracting females to display arenas, often located at hidden perches within the forest. Here, we describe the acoustic repertoire of Swallow-tailed Manakins (*Chiroxiphia caudata*), a bird species well known for displaying cooperatively, but for which the acoustic repertoire has not been well-documented. We recorded calls and behaviour of Swallow-tailed Manakins on three display courts in the Atlantic Forest, Brazil. We classified calls to test our repertoire designations using linear discriminant analysis and asked how different sounds mapped onto components of the cooperative display. Prior to the display, males coordinate sounds either in duets, as has been shown in congeners, or in choruses, which we report for the first time in *Chiroxiphia*. Males also produce three mechanical sounds, so far undescribed in this species, and 11 calls associated with seven behaviours. Particularly prominent was the *wah* call produced while displaying, which becomes increasingly fast toward the *jump display's* end, possibly to stimulate females for copulation. Our study of the Swallow-tailed Manakin acoustic repertoire provides insights into specific signal categories females may assess as they attend male mating displays.

### ARTICLE HISTORY

Received 11 September 2018  
Accepted 15 December 2018

### KEYWORDS

Communication; birds;  
mechanical sound;  
multimodal signal; sexual  
selection

## Introduction

The songs and calls of birds are particularly important for communication in dense forests. In situations where vegetation obstructs visual contact over long distances, vocalizations may mediate territory defence and attract potential sexual partners to observe more complex, multimodal displays. Such displays often combine vocal and visual signals, as with Zebra Finches (*Taeniopygia guttata*, Williams 2001), Satin Bowerbirds (*Ptilonorhynchus violaceus*, Doucet and Montgomerie 2003), Lawes's Parotias (*Parotia lawesii*, Scholes 2008), Brown-headed Cowbirds (*Molothrus ater*,

**CONTACT** Laura M. Schaedler  [schaedler.laura@gmail.com](mailto:schaedler.laura@gmail.com)  
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O’Loughlen and Rothstein 2010) and Blue-back Grassquits (*Volatinia jacarina*, Manica et al. 2016). Particularly remarkable examples of species with multimodal display include polygynous lek species, such as New Guinean birds-of-paradise (Paradisaeidae) and neotropical manakins (Pipridae).

Multimodal displays likely have at least two benefits. First, they provide multiple channels over which signallers can convey and receivers can assess information about their quality (Møller and Pomiankowski 1993). Second, the degree to which display components are coordinated across different modalities may convey information about signaller quality (Briffa and Fortescue 2017; Manica et al. 2017). Our study focused on sounds produced during mating displays of Swallow-tailed Manakins (*Chiroxiphia caudata*; Aves: Pipridae), a bird of the Atlantic Forest. Acoustic signals of male Swallow-tailed Manakins produced prior to mating displays probably serve to attract females to display perches, while stereotypical cooperative (*cartwheel type jump display* or *jump display* and *jump display ending*) and solo displays (*solo precopulatory display*; Supplementary Video S1) may play an important role in female mate choice decisions (Foster 1981).

Descriptions of display behaviour and acoustic repertoires are available for many species in the genus *Chiroxiphia*. In general, Long-tailed (*C. linearis*), Lance-tailed (*C. lanceolata*) and Blue-backed (*C. pareola*) manakins have similar calls and cooperative displays, with similar repertoire sizes, phonetic resemblance of calls, motor resemblance of flight movements, and occurrence of male–male duetting and displaying (Trainer and McDonald 1993; DuVal 2007; Cárdenas-Posada et al. 2017; Villegas et al. 2018). On the other hand, although similar in many respects to those of other species in the genus, the displays of Swallow-tailed Manakins are distinguished by greater variation in the number of males present during displays (two to six males, Foster 1981). In addition, males in the family Pipridae are known to produce mechanical sounds during their displays (Prum 1998; Bostwick and Prum 2003, 2005), but such sounds have only been reported for one species in the genus *Chiroxiphia* (Lance-tailed Manakins, DuVal 2007).

Our objective was to describe the acoustic repertoire of Swallow-tailed Manakins at their display arenas, assigning specific sounds to behavioural categories and associating them with different components of the display sequence. Specifically, we wanted to identify the sounds produced by males during duets and choruses, *jump displays*, and social interactions.

## Materials and methods

We studied Swallow-tailed Manakins during two breeding seasons (October–December 2014 and September 2015–January 2016) at Mananciais da Serra (25° 30’28”S 49°1’30”W), Piraquara, PR, Brazil. This region comprises a preserved area within the largest remnant of the Atlantic Forest biome, characterized by Mixed Ombrophilous Forests. We monitored three display courts (hereafter, C1, C2 and C3) that remained active throughout the breeding seasons and where males exhibited strong site fidelity. For analysing calling rate, we used data from an additional display court with only one perch and where males were not banded. In total, we monitored six display perches, including two in C1, three in C2 and one in C3.

## Data collection

We captured Swallow-tailed Manakins using mist-nets placed in areas surrounding courts. We banded individuals with unique combinations of colour bands and a numbered band provided by the Brazilian bird banding agency (CEMAVE/ICMBio). We sexed and aged individuals based on plumage colour, state of moult, and behaviour. We categorized males as either juvenile or adult based on plumage (Mallet-Rodrigues and Dutra 2012). Because juvenile males with completely green plumage are sometimes mistaken for females (Foster 1987; Doucet et al. 2007; Mallet-Rodrigues and Dutra 2012), we only considered birds with green plumage to be males when they were observed participating in displays and/or vocalizing intensely, and females when they attended *solo precopulatory displays* and copulated with adult males.

Behavioural observations, video and audio recordings were made from 06:00 to 12:00 and from 15:00 to 17:00 during a 4-day fieldwork trial in 2014, and at least three days per week during the 2015/2016 breeding season (September–January). We recorded sounds produced during observations at and near display arenas with a Marantz PMD 661 MKII recorder and a Sennheiser ME67 microphone mounted on a pistol grip and covered with a windshield to reduce handling and wind noise. We made all recordings in WAV format with 44.1-kHz sampling rate and 24-bit resolution. During observations and audio recordings, we noted the location (display perch and court), performance of any stereotypical display (*jump display*, *jump display ending* or *solo precopulatory displays*), presence of other individuals within the observer's sight or hearing distance (~50 m), copulations, aggressive chasing behaviour between males, and activities not related to the courtship display, such as foraging and preening. We also used videos from a Sony HDR-CX290 camera placed ~5 m from display perches to extract audio recordings and better identify individuals based on colour bands and the behaviours (as listed above) associated with each call.

## Acoustic analysis

We conducted spectrographic analysis using Raven Pro v1.4 software (Cornell Lab of Ornithology, Ithaca, NY; <http://www.birds.cornell.edu/raven>) and using Hann window type, discrete Fourier transform (DFT) of 512 samples and 50% overlap. For analysing modulation of *wah* calls, a call specific to *jump displays*, we used a DFT of 256 samples and a window size of 152 samples. All low-frequency background noise ( $\leq 500$  Hz) was filtered out.

For each call, we determined the following acoustic parameters: duration (time between the beginning and end of a call), peak frequency (frequency with the highest energy level), frequency 5% (robust measure of low frequency that excludes the lowest 5% of the total energy in the selection), frequency 95% (robust measure of high frequency that excludes the highest 5% of the total energy in the selection) and bandwidth 90% (robust measure of bandwidth or delta frequency, the difference between 5% and 95% frequencies). Studies of bird bioacoustics usually rely on these metrics because duration is intrinsically related to individual breathing capacity, since sounds are produced during the exhaling phase (Oberweger and Goller 2001), and

frequency parameters are a good proxy for the distribution of energy along calls (e.g. Charif et al. 2010).

We assigned calls into seven behavioural categories: 1) vocal coordination – antiphonal or overlapping calls by two or more males in display courts, presumably to attract females, 2) excitatory period – males vocalizing on display courts while others males performed either the *jump* or *solo precopulatory displays*, 3) *jump display* – sequential and rotational flight display of males, 4) *jump display ending* – when a male hovered facing the other males, turned his back to the female, and ended the display with a high-pitched call, 5) post-copulation – calls by females on display perches after copulation, 6) aggressive encounters – calls uttered during aggressive chasing male–male interactions and 7) casual/unclear – solitary males vocalizing on and off of display courts, presumably to announce their presence or to serve some undefined function, sometimes while foraging.

To quantify calling rates, we tallied the number of times each call was produced during the 5 min before each *jump display* for females started. We chose this period because males are more active due to the presence of females at the perch surroundings, thus providing a good sample of their calling behaviour. Calls produced during the *jump display* were not included in our measures of calling rates because males sing uninterruptedly and in superposition during displays, making it impossible to separate calls in discrete units.

At display courts, we evaluated how males coordinated calls prior to *jump displays* by examining both the audio tracks of video-recordings and sound files captured with the digital audio recorder. We categorized coordination as overlapping (when calls overlapped), antiphonal (when calls did not overlap), and mixed (when calls were both overlapping and antiphonal). For antiphonal and mixed categories, we only considered non-overlapping calls separated by  $\leq 0.4$ -s. A 0.2-s interval has been used as the cut-off value for characterizing low and high precision of response times (Dahlin and Benedict 2014). Because there are not evaluations of response times in the genus *Chiroxiphia*, we adopted a conservative approach by doubling this value. We calculated the percentage of time males spent in coordination per recording, as the ratio of the duration of all coordinated calls over the total sampling period.

We documented the acoustic structure of *wah* calls during the initial, middle and final portions (hereafter, 1, 2 and 3, respectively) of the *jump display*. We divided the *jump display* into three portions because males tended to accelerate calls throughout the display (Foster 1981). This categorization enabled us to compare the acoustic parameters in three different moments of the display and to understand how males change their sounds accordingly. Each portion represented one-third of total display duration (i.e. from the first pulses to its end, excluding the *jump display ending*). We selected displays with a minimum duration of 3 s, and randomly selected 20 sequential pulses as an arbitrary sample size for an accurate average measure for each parameter, from the middle of each portion and measured the pulse period (i.e. the duration of intervals between pulses), the delta frequency (the difference between the upper and lower frequency limits of the selection), peak frequency, frequency 5% and frequency 95% of each. Identifying the male producing each pulse was not possible because they vocalized simultaneously, so the analysis reflects how the group progressed during displays. In some cases, sample sizes were less than 20 because other calls overlapped and masked the pulse segments of interest.

## Statistical analyses

To provide an objective assessment of our call classification based on visual inspection of their shape, we performed a linear discriminant analysis – LDA (function *lda*, R package MASS, R Core Team 2017; Venables and Ripley 2002) on the five extracted acoustic parameters and calculated the percentage of correct classifications (CC). We tested for data homogeneity (function *betadisper*, R package *vegan*; Oksanen et al. 2017) and used log transformation when necessary. Prior to LDA, we used MANOVA (Wilks' test) to test for differences between calls (function *manova*, R package *stats*, R Core Team 2017). We performed a stepwise variable selection to determine which acoustic parameters were more important in classifying calls (function *stepclass*, R package *klaR*, Weihs et al. 2005).

To test for variation in the pulse period of *wah* calls as displays progressed, we constructed a linear mixed model (function *lmer*, R package *lme4*; Bates et al. 2015) relating this variable with the following predictors: display portion (1, 2 and 3), total display duration, peak frequency and number of males participating in the display. Because we used repeated measures from a single display, we included the display identity as random effect in the model. We log-transformed pulse period and peak frequency and took the square root of display duration to achieve normal or approximate-normal distributions. We tested parameter significance using a likelihood ratio test (LRT) using an approximated chi-square distribution. To test for differences between each portion's pulse period, we ran Tukey *post hoc* pairwise comparisons (function *glht*, R package *multcomp*, Hothorn et al. 2008) and adopted a significance level of 0.017 after Bonferroni correction.

## Results

### Acoustic repertoire

Based on visual inspection of spectrograms of 498 sound samples from three courts (minimum number of individuals present during recordings was three in all courts), we identified 11 calls given in seven behavioural contexts (Table 1, Figure 1, Audios S2–10, Videos S1, S16–18). Males started duetting/chorusing producing *wews*, *pewas* and *ptuwaw*, phonetically similar calls with ascending and descending frequency modulations. When females arrived on display perches, males that did not engage in the *jump display* flew around the perch producing *wits* and *twos*, calls emitted together resembling a fast trill, and *pews* and *wips*, which also phonetically resemble the duets/choruses calls but are shorter in duration. Males displaying to females produced *wahs* throughout the *jump display* until the alpha male hovered in the air and called with loud *kes*, *teeecs* and *kees* during the *jump display ending*. All males may produce these calls during *jump display endings* in practice displays, but in displays for females only alphas do it. *Solo displays* and copulations were not accompanied by calls. After one copulation, a female stood on the display perch and uttered *wews*. Males also produced *wahs* during aggressive chasings on display courts. All calls were given by adults and juveniles and were uttered during interactions with conspecifics, whereas *wews*, *wits*, *twos* and *wips* were also given by solitary individuals (Table 1, Figure 1, Audios S2–10, Videos S1, S16–18).

**Table 1.** Acoustic repertoire of male and female Swallow-tailed Manakins, with the sex of individual producing the calls (M = male, F = female), behavioural context during which each call was produced, and mean ( $\pm$ SD) calling rate.

Call categories	Sex	Behavioural context	Calling rate <sup>†</sup> (calls/min)	N (calls)
<i>wew</i>	M, F	M: Vocal coordination, casual F: post-copulation	M: $7.6 \pm 9.1$ F: Rare (<1)	229
<i>wit</i> *	M	Excitatory period, casual	Rare (<1)	5
<i>two</i>	M	Excitatory period, casual	Rare (<1)	7
<i>pew</i>	M	Vocal coordination, excitatory period	$2.3 \pm 3.6$	70
<i>pewa</i>	M	Vocal coordination	$21.5 \pm 21.9$	646
<i>ptuwa</i> <sup>x</sup>	M	Vocal coordination	$10.7 \pm 12.8$	322
<i>wip</i>	M	Vocal coordination, excitatory period, casual	Rare (<1)	1
<i>ke</i>	M	<i>Jump display ending</i>	- <sup>‡</sup>	- <sup>‡</sup>
<i>teec</i>	M	<i>Jump display ending</i>	- <sup>‡</sup>	- <sup>‡</sup>
<i>kee</i> <sup>+</sup>	M	<i>Jump display ending</i>	- <sup>‡</sup>	- <sup>‡</sup>
<i>wah</i> <sup>+</sup>	M	<i>Jump display, aggressive chasing</i>	- <sup>‡</sup>	- <sup>‡</sup>

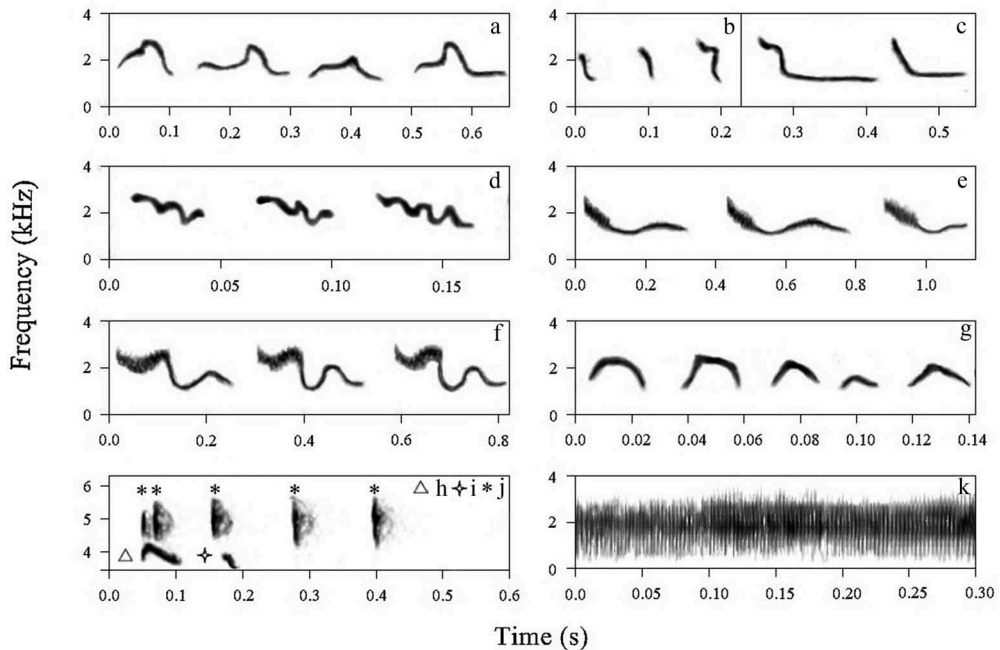
<sup>†</sup>Calling rate represents general activity of groups of males at four display courts and were tallied from six independent recordings.

<sup>‡</sup>Calls were not counted because the sampled period excluded the *jump display*.

\*Named after a similar call described by Trainer and McDonald (1993).

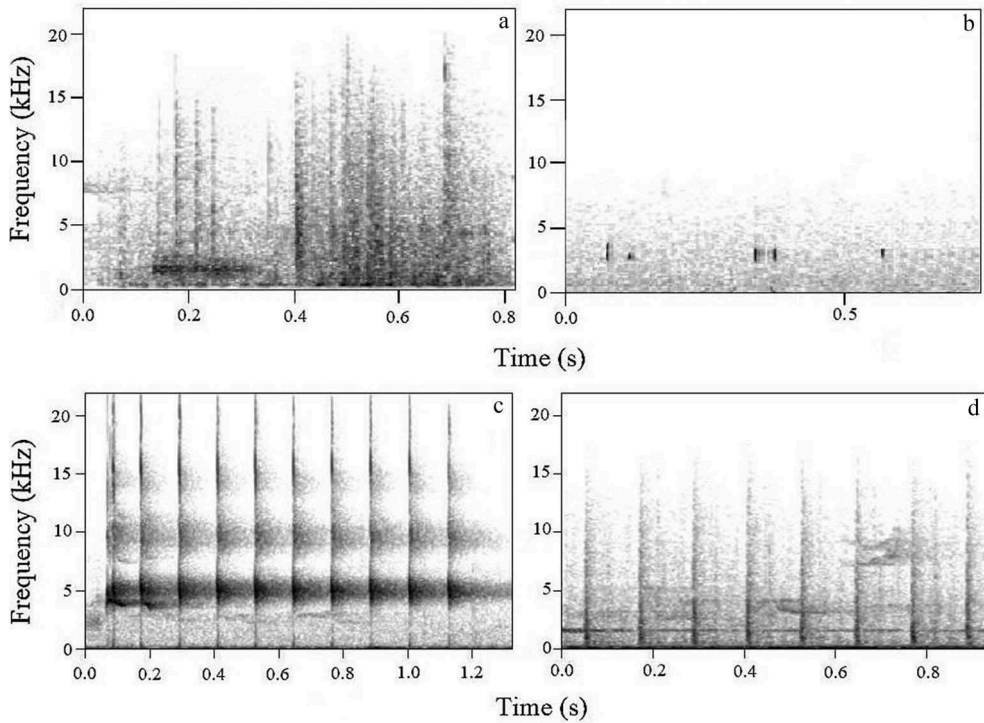
<sup>x</sup>Named after call described by Foster (1981).

<sup>+</sup>Named after a similar call described by DuVal (2007).



**Figure 1.** Exemplars from the vocal repertoire categories of Swallow-tailed Manakins at our study sites. Calls are *wew* (A), *wit* (B), *two* (C), *pew* (D), *pewa* (E), *ptuwa* (F), *wip* (G), *ke* (H), *teec* (I) and *wah* (K). Each bar in the *wah* call produced during the *jump display* represents one pulse. Table 1 provides the behavioural contexts for each category.

We also documented three mechanical sounds, confirmed as such by records in the absence of calls and any beak movements and produced in synchrony with wing beats, likely representing wing snaps (Figure 2, Audios S9–13). The first, resembling a *frrr*, was produced by all individuals independent of sex and age, while flying rapidly around



**Figure 2.** Mechanical wing sounds produced by Swallow-tailed Manakins. *Frrrs* occurred when individuals fly rapidly around the display arena (a), *treecs* during the *solo display* (b), and *papapas* during the *jump display ending* in coordination (c) or not (d) with vocal sounds.

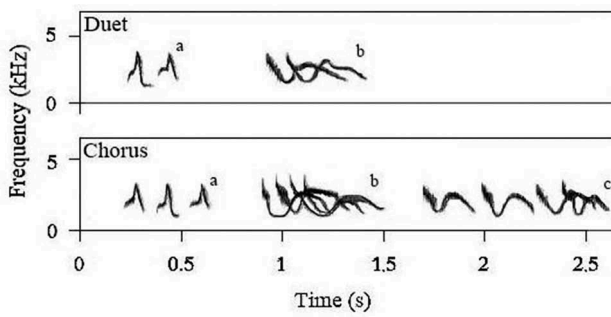
the display arena ( $N = 17$ , Figure 2(a), Audio S11, Video S14). The second, resembling a quick *treec* sound and similar in form to the *tick* mechanical sound produced by Club-winged Manakins (*Machaeropterus deliciosus*, Bostwick 2000), was produced only by males and recorded only twice, once during the *solo display* and once while a male was perched and rapidly beating his wings ( $N = 2$ , Figure 2(b), Audio S12 and Video S15). The third sound, resembling a muffled *papapa*, was produced only by males and is specific to the *jump display ending*, being made in synchrony or not with calls depending on male age ( $N = 27$ , Table 2, Figure 2(c,d), Audio S9–10, S13, Video S16). The *papapas* and *frrrs* ranged from a mean of  $0.8 \pm 0.9$  kHz up to more than 22.0 kHz (the threshold of recordings at a 44.1 kHz sampling rate) and from  $4.7 \pm 2.0$  kHz to  $14.0 \pm 2.0$  kHz, with similar durations of  $7 \pm 3$  ms ( $N = 129$  and 23; Figure 2(a,c,d)). *Treecs* ranged in frequency from  $3.0 \pm 0.2$  kHz to  $9.7 \pm 4.3$  kHz and averaged  $10 \pm 3$  ms in duration ( $N = 28$ ; Figure 2(b)).

Finally, in duets/choruses males vocalized for an average of  $0.92 \pm 0.63$  min ( $N = 9$ ), encompassing  $18\% \pm 13\%$  of the 5-min recording period. In these samples, we documented 531 cases of vocal coordination, including 183 (34%) duets (two coordinated calls, Audios S2, S8 and Video S17) and 348 (66%) choruses (three or more coordinated calls, Video S18, Figure 3). To coordinate calls during duets/choruses, different males within a group produced from two to 14 calls sequentially (mean =  $3.8 \pm 2.2$ ,  $N = 531$



**Table 2.** Minimum and maximum number of vocal and mechanical sounds produced by adult and juvenile males Swallow-tailed Manakins at the end of the *jump display*. Each line represents a different individual and they were recorded on different days and display perches. A = adult, J = juvenile.

Display court	Male age	Call <i>ke</i> (mean $\pm$ SD)	Call <i>teec</i> (mean $\pm$ SD)	Call <i>kee</i> (mean $\pm$ SD)	<i>Papapas</i> mechanical sounds (mean $\pm$ SD)	N (samples)
C1	J	0–1 (0.6 $\pm$ 0.5)	0–1 (0.2 $\pm$ 0.4)	0	1–12 (5.0 $\pm$ 4.2)	6
C2	J	1	0–1 (0.5 $\pm$ 0.7)	0–3 (1.5 $\pm$ 2.1)	3–10 (6.5 $\pm$ 4.9)	2
C2	J	1	1	0	2	1
C1	A	1	1	10–11 (10.5 $\pm$ 0.7)	10–11 (10.5 $\pm$ 0.7)	2
C2	A	1	1	11	11	1
C3	A	1–2 (1.1 $\pm$ 0.3)	0–1 (0.9 $\pm$ 0.3)	5–12 (10.4 $\pm$ 1.7)	5–12 (10.4 $\pm$ 1.7)	15

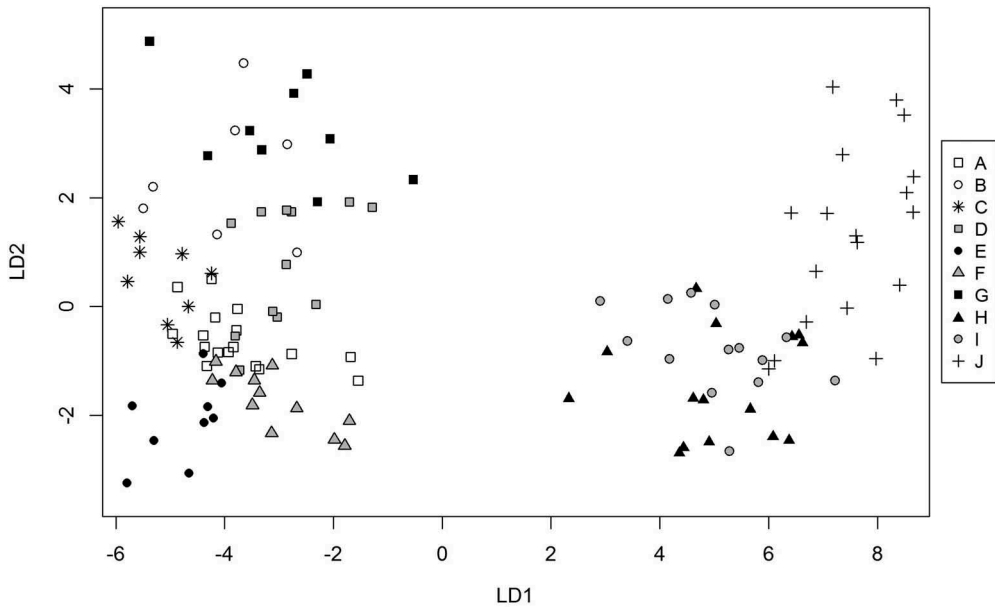


**Figure 3.** Duets and choruses of *wews* and *pewas* produced in antiphonic coordination (a), overlapped (b) and mixed (c).

vocal coordinations), using *ptuwas* (34%), *pews* (26%), *pewas* (23%), *wews* (13%) and *wips* (4%). Coordinations occurred on average  $11.8 \pm 7$  times/min and were most commonly mixed (43%), followed by antiphonal (41%) and overlapped (16%, Figure 3).

### Statistical categorization of calls

We found homogeneity among variances ( $F = 1.04$ ,  $df = 9$ ,  $p = 0.4$ ) and differences among calls (MANOVA: Wilks = 0.003,  $df = 9$ ,  $p < 0.001$ ). The LDA generated five linear discriminant functions (LDs); the first two explained 95% of the total variance (Figure 4). The first LD accounted for 86% of the total variance and separated calls by frequency 95% and bandwidth 90% (standardized coefficients: 3.56 and  $-1.65$ , respectively). The second LD accounted for 9% of the total variance and separated calls by delta time, frequencies 5% and 95% and bandwidth 90% (standardized coefficients =  $-2.34$ , 1.54,  $-2.70$ , and 1.59, respectively). Ninety-two samples (75%) were correctly assigned to the groups of calls defined a priori by visual inspection (Table 3). Eight of the pre-assigned groups showed  $>65\%$  classification accuracy (Table 3). Among all acoustic parameters, duration and frequency 5% weighted most heavily in assigning calls to each group (Table 4).



**Figure 4.** Distribution of the linear discriminant scores (LD) of all calls, except *wah*, in the axis 1 and 2 (LD1 and LD2, respectively). Calls are as in Figure 1: *wew* (A), *wit* (B), *two* (C), *pew* (D), *pewa* (E), *ptuwa* (F), *wip* (G), *ke* (H), *teec* (I) and *kee* (J).

**Table 3.** Number of samples assigned by a linear discriminant analysis (LDA) to each call group and the percentage of correct classifications (CC). *Jump display wah* call was not included because it is composed of several pulses which prevents individual analysis. Correct classifications are read in rows for each call because they represent samples visually classified *a priori* in call groups and columns represent re-assignments by the LDA based on acoustical parameters. Bold numbers represent correctly assigned samples.

Groups	<i>wew</i>	<i>wit</i>	<i>two</i>	<i>pew</i>	<i>pewa</i>	<i>ptuwa</i>	<i>wip</i>	<i>ke</i>	<i>teec</i>	<i>kee</i>	CC (%)
<i>wew</i>	<b>13</b>	0	1	0	0	4	0	0	0	0	72
<i>wit</i>	0	<b>3</b>	1	1	0	0	2	0	0	0	42
<i>two</i>	0	0	<b>9</b>	0	0	0	0	0	0	0	100
<i>pew</i>	2	0	0	<b>10</b>	0	0	0	0	0	0	83
<i>pewa</i>	2	0	0	0	<b>6</b>	1	0	0	0	0	66
<i>ptuwa</i>	4	0	0	0	0	<b>8</b>	0	0	0	0	66
<i>wip</i>	0	1	0	0	0	0	<b>8</b>	0	0	0	88
<i>ke</i>	0	0	0	0	0	0	0	<b>6</b>	6	3	40
<i>teec</i>	0	0	0	0	0	0	0	3	<b>11</b>	0	78
<i>kee</i>	0	0	0	0	0	0	0	0	0	<b>18</b>	100

### **Wah calls modulation rate**

The *wah* call produced during the *jump display* (*wah* in Figure 1, Audios S8, S9, Videos S15, S18) consisted of a rapid series of pulsed signals of ~380 Hz, with pulse periods (duration of interval between pulses) varying from 2.7 to 3.9 ms. We confirmed the vocal origin of this sound by behavioural observations in the field and by 500 h of video recordings; males produced *wahs* while perched during all field observations and 25 times in video recordings. We found displays varying from 3.4 to 72.1 s (mean  $28.6 \pm 19.3$  s), 1464.3 to 3703.7 Hz (mean  $2160.5 \pm 462.1$  Hz) of

**Table 4.** Mean ( $\pm$ SD) of acoustic parameters of each Swallow-tailed Manakin call.  $N$  = number of calls. DT = delta time (s), F5 = frequency 5% (kHz), F95 = frequency 95% (kHz), BW90 = bandwidth 90% (kHz), PF = peak frequency (kHz). Only DT and F5 were significantly important parameters to classify calls according to a linear discriminant analysis (LDA). *Jump display wah* call was not included because it consisted of several pulses that prevented extraction of these parameters.

Calls	$N$ calls	$N$ males*	DT	F5	F95	BW90	PF
<i>wew</i>	18	6	0.13 $\pm$ 0.03	1567.3 $\pm$ 205	2610.9 $\pm$ 168	1043.5 $\pm$ 367	2331.7 $\pm$ 233
<i>wit</i>	7	4	0.04 $\pm$ 0.01	1475.5 $\pm$ 158	2418.6 $\pm$ 305	943.1 $\pm$ 258	2106.3 $\pm$ 236
<i>two</i>	9	4	0.1 $\pm$ 0.03	1264.5 $\pm$ 83	2611.7 $\pm$ 361	1347.2 $\pm$ 373	1939.5 $\pm$ 434
<i>pew</i>	12	4	0.07 $\pm$ 0.04	1710.4 $\pm$ 149	2731.8 $\pm$ 117	1021.4 $\pm$ 177	2244.5 $\pm$ 211
<i>pewa</i>	9	4	0.31 $\pm$ 0.11	1441.6 $\pm$ 97	2512.5 $\pm$ 181	1070.9 $\pm$ 190	2207.6 $\pm$ 173
<i>ptuwa</i>	12	4	0.19 $\pm$ 0.02	1757.8 $\pm$ 196	2625.0 $\pm$ 97	867.1 $\pm$ 212	2328.1 $\pm$ 111
<i>wip</i>	9	5	0.02 $\pm$ 0.01	1667.5 $\pm$ 219	2306.5 $\pm$ 208	639.0 $\pm$ 145	2098.8 $\pm$ 204
<i>ke</i>	15	5	0.04 $\pm$ 0.01	3440.6 $\pm$ 486	4012.1 $\pm$ 831	571.5 $\pm$ 376	3775.7 $\pm$ 641
<i>teec</i>	14	5	0.03 $\pm$ 0.01	3268.0 $\pm$ 288	3677.3 $\pm$ 385	409.3 $\pm$ 194	3570.5 $\pm$ 377
<i>kee</i>	18	4	0.01 $\pm$ 0.01	4251.0 $\pm$ 147	5227.8 $\pm$ 236	976.7 $\pm$ 262	4771.2 $\pm$ 256

\*This refers to the minimum number of males, since unbanded males recorded on different days could be different individuals.

**Table 5.** Results of the linear mixed models of the *wah* call pulse period in relation to the display portion (1: initial; 2: middle; 3: final), total display duration (s), peak frequency (Hz) and number of males participating in the display. The random effect term was the display identity, with variance = 0.5. Post-hoc Tukey pairwise comparison results include Bonferroni correction of the significance level.  $b$  = angular coefficient, LRT = Likelihood ratio test,  $df$  = degree of freedom.

Predictor	$b \pm SE$	LRT	$df$	$P$ value	Tukey <i>post hoc</i>		
					pairwise comparisons	$z$ value	$P$ value
Display portion		8.5	2	0.01			
1	0.07 $\pm$ 0.53				1 versus 2	1.3	0.52
2	0.27 $\pm$ 0.21				2 versus 3	-3.0	0.007
3	-0.45 $\pm$ 0.25				3 versus 1	-1.8	0.20
Display duration	-0.02 $\pm$ 0.18	0.009	1	0.92			
Peak frequency	0.11 $\pm$ 0.11	0.9	1	0.31			
Number of males	-0.005 $\pm$ 0.24	0.0006	1	0.98			

peak frequency and 1 to 3 males (mean  $2 \pm 0.72$ ). When controlling for display identity as random effect, we found a significant relationship between pulse period and display portion, but not with display duration, peak frequency or number of males displaying (Table 5). Pulse periods were similar between portions 1 ( $3.18 \pm 0.25$  ms) and 2 ( $3.24 \pm 0.22$  ms) and 1 and 3 ( $3.11 \pm 0.18$  ms, Table 5), but decreased significantly from portion 2 to 3 (Table 5).

## Discussion

Male Swallow-tailed Manakins in our study produced 11 distinct acoustic elements, with one also produced by females. Despite the greater complexity of the social interactions of Swallow-tailed Manakins, the size of their vocal repertoire is within the range previously reported for males in other species in the genus (Trainer and McDonald 1993; DuVal 2007; Cárdenas-Posada et al. 2017).

Our visual inspection and categorization of calls was generally supported by LDA, despite its modest classification accuracy for four calls. Acoustic parameters of *wits*, *pewas*, *ptuwas* and *kes* overlapped those of other calls and were accordingly assigned to

those with subpar accuracy (respectively in 58%, 34%, 34% and 60% of the LDA classifications). However, we still consider these calls to be unique because they can be easily distinguished through visual patterns (Figure 1).

Our data confirm, for the second time across the entire *Chiroxiphia* genus, the production of stereotyped mechanical sounds, previously described only in Lance-tailed Manakins (DuVal 2007). We hypothesize that these sounds may stimulate females for copulation, as calls produced during displays, but this remains an open question. As Lance-tailed Manakins, Swallow-tailed Manakins may produce mechanical sounds via wing clicks. In both species they are multiple broad-frequency spectrum pulses (Prum 1998), similar in structure and behavioural contexts, occurring during solo displays in Lance-tailed Manakins *slow flights* and Swallow-tailed Manakins *butterfly flights* (DuVal 2007; Ribeiro and Manica, unpubl. data). Further, we also confirmed the production of ‘a mechanical whirring noise’ (Figure 2) made when flying between branches as originally described by Foster (1981). However, we do not know if it is produced intentionally or if it is an artefact of the hovering flight. Manakins, such as those in the genera *Manacus* and *Pipra*, are well known for producing mechanical sounds (Bostwick and Prum 2003), sometimes having morphological specializations like the enlarged and solid ulnae and modified secondary feathers of Club-winged Manakins (*Machaeropterus deliciosus*, Bostwick and Prum 2005; Bostwick et al. 2012). Although the sound mechanisms of several species in the family Pipridae have been well documented, we still lack a comprehensive description for Swallow-tailed Manakins, thus we expect future high-speed video recordings will allow us to reveal mechanisms underlying the sound production.

Acoustic sounds of juvenile males differed from those of adults. During the *jump display ending*, second-year males produced wing clicks that were uncoupled from vocal signals and were narrower in frequency range with fewer repetitions than those of adult males (Figure 2, Table 2). Young males of other manakin species also produce incomplete displays. For example, immature male Band-tailed Manakins (*Pipra fasciicauda*) rarely produce the final call during *swoop-in* flight displays (Robbins 1983). The fact that juveniles produce incomplete *jump displays* in the absence of females either solitarily or while paired with other males, reinforce the hypothesis that practice during cooperative displays may help birds improve their performance, which may improve chances of copulation in the future (Foster 1981; DuVal 2007).

For the first time in this genus, we detected choruses in Swallow-tailed Manakins. Chorusing is clearly related to the large number of males that participate in *jump displays* (2–8; Ihering 1936) and studies of other *Chiroxiphia* species have shown that duets are important for attracting females. For Long-tailed Manakins, duets with greater frequency matching are positively correlated with female visitation rate (Trainer and McDonald 1995). This species usually displays in fixed partnerships of two males and frequency matching improves after years of interactions (Trainer et al. 2002). In contrast, the way male Swallow-tailed Manakins choose display partners is unclear, but the existence of coordination in duets/choruses, as in Long-tailed Manakins, suggests that it could be a key factor for female attraction. Given the variability in number and type of calls produced in duets/choruses, as well as number of males attending courts, forming alliances within courts may be more complex for Swallow-tailed Manakins than for other manakin species where displays are made by fewer

males. They may choose to display cooperatively with partners that sing similar songs, or adjust calls according to the available partners (Trainer et al. 2002). By knowing beforehand that choruses occur, studies can be further designed to address the dynamics of such behaviour and understand its influence on cooperative displays.

We observed that the *wah* call produced during the *jump display* is distinct from the species' other vocal elements due to its differential production mechanism, which involves rapid amplitude modulations. Apparently, similar sounds are also produced by other species in the genus *Chiroxiphia*, as indicated by descriptions of phonetically similar calls in cooperative displays (Slud 1957; Gilliard 1959; Foster 1977; Trainer and McDonald 1993; DuVal 2007; Cárdenas-Posada et al. 2017). In other *Chiroxiphia*, the pulsed nature of this call was not explored. Nevertheless, sonograms usually display *wah* calls as sounds presenting sidebands (as in DuVal 2007), which are indicative of amplitude modulated calls. Increasing window size in spectrogram parameters will allow visualization of sidebands as the tapered pulses presented here.

We suggest two reasons why *wah* calls may be important for female choice in Swallow-tailed Manakins. First, *wahs* are fundamental elements of the *jump display* because all cooperative displays included these sounds. Second, *jump displays* play a role in mate choice probably with attractive and excitatory functions, enhancing a male's chances of copulation as opposed to events when alpha males only produce *solo precopulatory displays* (Foster 1981). Thus, it is possible that producing faster calls near *jump display endings*, as we report here, helps stimulate females. It is also possible that this acceleration is indicative of males' quality, if *wahs*' production involves energetic costs. Although data from other manakins suggest that displays may involve high heart rates but low energetic costs (Barske et al. 2011, 2015), pulse production rates of Swallow-tailed Manakins are extremely high (~300 cycles/s). *Jump displays* tend to last from 2 to 4 min, but males usually restart the performance after ending, repeating it several times (Foster 1981; Ribeiro and Manica, unpubl. data). Males display ~7 min/day (Ribeiro and Manica, unpubl. data) and there are records of up to 20 min when display bouts are disrupted by other males (Foster 1981). In comparison with Golden-collared Manakins (*Manacus vitellinus*), for which display costs are negligible because males expend minimal time in such activities (~5 min/day, Barske et al. 2014), *jump displays* in Swallow-tailed Manakins demand much more energy. Thus, pulse modulation during a long-time interval may require sustained energy investment and would likely be susceptible to physiological constraints. Exacerbating these constraints would result in increasing pulse production toward the ends of displays. Faster movements and vocalizations should also be more prone to synchronization errors because they require a greater ability to integrate their behaviour with that of others. A high-quality male should be able to synchronize his motor and acoustic signals effectively, while adjusting pulse emission rate appropriately.

In summary, Swallow-tailed Manakins deviate in several ways from the typical dual display pattern of the genus, e.g. Lance-tailed Manakins (DuVal 2007) and Long-tailed Manakins (Trainer and McDonald 1993), by including stereotypical display sounds such as highly complex choruses and calls, and several mechanical sounds. Among Long-tailed Manakins, the number of calls and frequency matching by duetting males predicts female visitation rates to display courts (McDonald 1989; Trainer and McDonald 1995), suggesting that these acoustic parameters are

correlated with display quality (Trainer and McDonald 1995; Trainer et al. 2002). Alternatively, the apparent variable participation of male Swallow-tailed Manakins in cooperative displays suggests that complex mechanisms mediate coordination, the consistency of songs and displays, and possibly frequency matching in this species. Thus, since female Swallow-tailed Manakins may assess male quality amidst a lot of information, future studies should focus both on how the variable number of individuals attending different courts and how interactions between individuals during calling and displaying behaviour affects female choice. The complexity and intricacy of the display of Swallow-tailed Manakins further supports its possible role as an indicator of male quality that can be used by females to assess prospective males. Our study highlights the components of motor and acoustic display repertoires shared across the clade, as well as the importance of basic descriptions for analysing the causes and consequences of sexual selection on display evolution. Although robust technical comparisons of manakin species are currently limited by the lack of some detailed information, coordinated research efforts on Pipridae should change this scenario in the near future allowing deeper insights on its reproductive behaviour.

## Acknowledgements

This work was funded by a National Council for Scientific and Technological Development (CNPq) scientific initiation scholarship to LMS and a grant to LTM (#455908/2014-1), a Coordination for the Improvement of Higher Education Personnel (CAPES)/ PNPd Fellowship to ACG (#1459754) and an Animal Behavior Society grant to PHLR. A crowdfunding initiative and its over 90 supporters also ensured the development of this study. We thank Idea Wild, R. H. Macedo, M. A. Marini, M. A. Pizo, and A. E. Jahn for equipment donations and sharing, and Instituto Ambiental do Paraná, Chico Mendes Institute for Biodiversity Conservation and National Center for Bird Conservation (ICMBio/CEMAVE, license number 44439) for research permits. We thank R. H. Macedo and members of the Manakin Genomics Research Coordination Network (NSF-DEB grant #1457541) for useful discussions, and J. Podos, M. Foster and anonymous referees for improvements in previous versions of this manuscript. We are also in debt to R. Charif and E. Greig for important discussions about acoustic analyses. All procedures were approved by the Animal Experiment Ethics Committee of the Federal University of Paraná (process number 23075.028690/2014-05).

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was funded by a National Council for Scientific and Technological Development (CNPq) scientific initiation scholarship to LMS and a grant to LTM [#455908/2014-1]; a CAPES/PNPd Fellowship to ACG [#1459754] and an Animal Behavior Society grant to PHLR.

## ORCID

Laura M. Schaedler  <http://orcid.org/0000-0003-4371-9376>

Pedro H. L. Ribeiro  <http://orcid.org/0000-0002-7922-7042>

André C. Guaraldo  <http://orcid.org/0000-0003-1705-2926>

Lilian T. Manica  <http://orcid.org/0000-0001-6005-7103>

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