

Vocal behaviour of Barred Antshrikes, a Neotropical duetting suboscine bird

Julianne Koloff · Daniel J. Mennill

Received: 21 December 2011 / Revised: 3 April 2012 / Accepted: 25 May 2012 / Published online: 23 June 2012
© Dt. Ornithologen-Gesellschaft e.V. 2012

Abstract Despite the high biodiversity that characterizes the tropics, we know little about the behaviour of most tropical birds. Antbirds (Thamnophilidae) are a biodiverse family of more than 200 species found throughout Central and South America, yet their ecology and behaviour are poorly known. In this study, we provide the first detailed description of the vocalizations and vocal behaviour of Barred Antshrikes (*Thamnophilus doliatus*), a widespread Neotropical suboscine passerine. We studied 38 territorial pairs in a population in Costa Rica from 2008 to 2010, using field recordings and observations to quantify their vocalizations and vocal behaviour. Males and females produced similar songs consisting of rapidly repeated chuckling notes. Several aspects of their songs distinguish the sexes: male songs were longer in duration, contained more syllables, and were lower in pitch. Males had a higher song output than females, but within song bouts males and females sang at similar rates. Barred Antshrike song output varied daily, with the highest song output occurring at dawn. Song output also varied seasonally, with increased song output occurring during the breeding period. Males and females combined songs to create duets, overlapping the terminal portion of their mate's song. Most duets were created by females responding to male songs (84 %), and the rest by males responding to female songs. The timing

of duet responsiveness varied between the sexes; males responded more quickly to their partner's song (1.6 s) than females (2.0 s). This detailed account of the vocalizations and vocal behaviour of a population of Barred Antshrikes creates a foundation for future comparative studies of antbirds. Our study highlights similarities and differences in the behavioural patterns of tropical birds and contributes to our understanding of the function of vocal duets and the vocal behaviour of antbirds.

Keywords Antbird · Duet · Song · Thamnophilidae · Vocal behaviour

Zusammenfassung

Gesangsverhalten von Bindennameisenwürgern *Thamnophilus doliatus*, einer neotropischen suboscinen Sperlingsvogelart mit Duettgesang

Trotz der für die Tropen typischen hohen Artenvielfalt wissen wir über das Verhalten der meisten tropischen Vögel nur wenig. Ameisenvögel (Thamnophilidae) sind eine in ganz Mittel- und Südamerika beheimatete artenreiche (>200) Familie; dennoch ist über ihre Ökologie und ihr Verhalten nur wenig bekannt. In diesem Artikel geben wir die erste detaillierte Beschreibung von Lautäußerungen und Gesangsverhalten des Bindennameisenwürgers (*Thamnophilus doliatus*), einem weit verbreiteten neotropischen suboscinen Sperlingsvogel. Zwischen 2008 und 2010 untersuchten wir 38 Revierpaare einer Population in Costa Rica und erfassten Lautäußerungen und Stimmverhalten anhand von Tonaufnahmen und Beobachtungen aus dem Freiland. Männchen und Weibchen zeigten ähnliche Gesänge, die aus rasch wiederholten glucksenden Tönen bestanden. Die Geschlechter unterschieden sich in mehreren

Communicated by J. Fjeldså.

J. Koloff (✉) · D. J. Mennill (✉)
Department of Biological Sciences, University of Windsor,
Biology Building, 401 Sunset Avenue, Windsor,
ON N9B 3P4, Canada
e-mail: j.koloff@gmail.com

D. J. Mennill
e-mail: dmennill@uwindsor.ca

Gesangsmerkmalen: Die Gesänge der Männchen waren länger, enthielten mehr Silben und hatten eine tiefere Tonlage. Männchen zeigten eine höhere Gesangsleistung als Weibchen, allerdings sangen Männchen und Weibchen innerhalb einer Gesangsphase ähnlich viel. Die Gesangsleistung der Bindenameisenvögel schwankte im Tagesverlauf und war in der Morgendämmerung am höchsten. Die Gesangsleistung variierte auch saisonal und erhöhte sich dabei während der Brutzeit. Männchen und Weibchen vereinten ihre Gesänge zu Duetten und überschritten sich dabei mit der Schlussphase des Gesangs ihres Partners. Die meisten Duette entstanden dadurch, dass Weibchen auf die Gesänge der Männchen antworteten (84 %), der Rest durch Männchen, die auf Gesänge der Weibchen reagierten. Die Reaktionszeit beim Duett war zwischen den Geschlechtern verschieden: Männchen reagierten schneller auf den Gesang des Partners (1,6 s) als Weibchen (2,0 s). Die detaillierte Beschreibung der Lautäußerungen und des Gesangsverhaltens von Bindenameisenvögeln schafft eine Grundlage für zukünftige vergleichende Studien an dieser Vogelfamilie. Diese Studie beleuchtet Ähnlichkeiten und Unterschiede in den Verhaltensmustern tropischer Vögel und trägt zum Verständnis der Funktion von Duettgesängen und des Gesangsverhaltens von Ameisenvögeln bei.

Introduction

The biology of many tropical birds is poorly understood when compared to temperate birds, despite the higher biodiversity that characterizes the tropics (Stutchbury and Morton 2001). Suboscine passerines, whose songs are understood to be innate rather than culturally inherited (Kroodsma 1984; Kroodsma and Konishi 1991), are a diverse and widespread suborder in the Neotropics that have received less attention than oscine passerines in studies of avian communication. Typical Antbirds (Thamnophilidae) are suboscine passerines found throughout the Neotropics that are characterized by cryptic behaviour; all thamnophilids are insectivorous, and the habit of some species of following ant swarms lends the family its English name (Zimmer and Isler 2003). The densely vegetated habitats of antbirds reduce visibility, making acoustic signalling an important aspect of antbird behaviour. Previous studies of suboscine acoustic signals have demonstrated the importance of using vocal characteristics to delineate species limits in thamnophilid antbirds (e.g. Isler et al. 1998; Seddon 2005), classify morphologically similar species (e.g. Lanyon 1978; Sedgwick 2001; Isler et al. 2002), study song divergence and reproductive isolation (e.g. Seddon and Tobias 2007), explore the function of seasonal variation in song (Tobias et al. 2011), and distinguish among conspecific

animals by recognizing individuals (e.g. Lovell and Lein 2004, 2005; Kirschel et al. 2009; Westcott 1997).

Vocal duets are temporally coordinated acoustic displays that are usually performed by members of a mated pair. Duet behaviour has been observed in many avian species, and many studies have tested hypotheses for the function of duets in oscine passerines (Farabaugh 1982; reviewed in Hall 2004, 2009), with several recent studies focussing on antbirds. The function of male–female duets has only been experimentally investigated in three species of thamnophilid to date (Spix’s Warbling Antbirds, *Hypocnemis striata*, White-bellied Antbirds, *Myrmeciza longipes*, and Barred Antshrikes, *Thamnophilus doliatus*; Seddon and Tobias 2006; Fedy and Stutchbury 2005; Koloff and Mennill 2011a). These studies reveal that duets appear to play a role in mate guarding, avoiding misdirected aggression from mates, and joint resource defence. Anecdotal accounts suggest that duetting may be widespread in antbirds (Zimmer and Isler 2003), but quantitative data are lacking.

There are at least 209 species of antbirds that are widely distributed across the Neotropics, yet our knowledge of their vocal behaviour remains rudimentary, with only a small minority of Neotropical antbirds having received detailed behavioural studies (Bard et al. 2002; Zimmer and Isler 2003; Fedy and Stutchbury 2005; Seddon and Tobias 2006; Koloff and Mennill 2011a). By studying acoustic communication in these birds we may gain greater insight into antbird behaviour, ecology, and evolution. Our research focusses on Barred Antshrikes (*T. doliatus*), an interesting species for studying suboscine vocalizations because they are widespread, produce loud and locatable songs, and respond well to conspecific playback. To date, only brief anecdotal descriptions of Barred Antshrike vocalizations have been reported, and their communication has never been explored with any quantitative measurements. We describe the vocalizations of male and female Barred Antshrikes based on analyses of a multi-year recording effort for a population of birds in northwestern Costa Rica. Our specific objectives were: (1) to quantify the characteristics of the vocalizations of a population of Barred Antshrikes, including any sex-specific differences in songs and calls, (2) to describe variations in Barred Antshrike vocal behaviour throughout the day and during the breeding season, and (3) to describe the duetting behaviour of Barred Antshrikes. Our description provides a benchmark for future comparative studies of antshrike vocalizations.

Methods

Barred Antshrikes are territorial, sexually dimorphic suboscine passerines with a range extending from Mexico to Argentina (Skutch 1969; Koloff and Mennill 2011b).

We studied a population of Barred Antshrikes in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W) over a three-year period. From 2008 to 2010, we studied birds from the end of the dry season (late April and early May) to the early months of the rainy season (mid-May through mid-July). We recorded pairs in 38 territories. Males and females exhibit plumage dimorphism, making them easy to distinguish; males have prominent black and white bars across their entire body, whereas females are cinnamon-rufous with ochraceous-buff underparts (Zimmer and Isler 2003). We captured and colour-banded 21 birds with mist nets and song playback; we captured both pair members in six territories and the male in nine additional territories. We measured mass (± 0.1 g), as well as tarsus length, tail length, culmen length, and wing chord length (± 0.5 mm) for all birds captured, except for one female that was about to lay an egg and was released immediately after weighing. The other birds in our study were unbanded, and we distinguished between territorial pairs based on their territory position, noting the specific locations of birds on maps using a hand-held global positioning system (Garmin GPS-60SCx). Observations of the colour-banded individuals indicated that birds were consistently found in the same section of forest during each field season, so we were confident we could reliably distinguish unbanded pairs based on regular encounters in the same location.

Definitions of vocalizations

We defined a solo song as a song produced by one individual and not overlapped by songs of its mate. We defined a duet as songs produced by a mated pair, where one bird's song temporally overlapped at least some portion of the mate's song. We defined male-created duets as those where a male sang to overlap the song of his singing mate, and female-created duets as those where a female sang to overlap the song of her singing mate. Our definition of duets is more conservative than those of other investigators that required only that birds sing within 1.0 s of their partner (e.g., Mennill and Vehrencamp 2005), and provides a relatively strict definition of duets that matches our understanding of this species' singing behaviour. We defined duet responsiveness as the proportion of a partner's songs that an individual joined to create duets (Levin 1996b; Hall 2004, 2009). We defined duet precision as the variability in the time delay between the start of one bird's song and the start of their partner's song (Farabaugh 1982; Levin 1996a; Hall 2009). We defined a call as a short, simple vocalization given in specific contexts outside of territory defense and mate attraction.

Recording techniques and sample sizes

To analyze the structural details of songs, we recorded pairs in 38 territories (76 birds) from May to July 2009. We made recordings using a directional microphone (Audio-technica AT815b) and a digital recorder (Marantz PMD-660; sampling rate 22,050 Hz; accuracy 16 bits; format WAVE). During recording sessions, we stood as close as possible to the birds without disrupting their behaviour (typically 5–10 m from focal birds). After each vocalization, we dictated into the microphone the sex and colour-band combination of the focal bird. For analyses of song structure, we used three solo songs of each male ($N = 38$) and female ($N = 38$), selecting songs recorded between 05:00 and 08:00.

To analyze duet timing and duetting behaviour, we required long recordings to quantify how often Barred Antshrikes perform duets. We collected recordings of banded and unbanded pairs in 34 territories (68 birds) from March to June 2008, May to July 2009, and in February and March 2010 using autonomous recorders. Autonomous recorders consisted of an omnidirectional microphone (Sennheiser ME62/K6) connected to a digital recorder (Marantz PMD-670; sampling rate 22,050 Hz; accuracy 16 bits; format MP3, which we converted to WAVE format in the laboratory) powered by a sealed lead-acid battery. We attached the microphone to a 3 m pole and fastened it to a small tree within a pair's territory using two bungee cords (full details of this apparatus are given in Hill et al. 2006). Autonomous recordings allowed us to monitor vocal behaviour continuously during day-long recording periods without being present in the birds' territories. Given the small territories of Barred Antshrikes (mean = 0.34 ± 0.08 ha; Koloff and Mennill 2011b), these recorders allowed us to sample the vocal behaviour of birds throughout their territories. We moved autonomous recorders to new territories approximately every 48 h, changing memory cards and batteries every 24 h. To distinguish male and female songs in the duets in autonomous recordings, we used differences in song duration and peak frequency (see "Results"). If more than two birds were recorded, we dismissed the more distant songs as being neighbours, so that only one pair was represented at each site. In some recordings, we assessed male and female contributions in duets through direct observation at the time of recording; these recordings confirmed that the recorders could sample birds anywhere in their territories, and that duration and pitch characters permitted accurate identification of the sexes.

To analyze song rate, we used autonomous recordings of banded and unbanded pairs of Barred Antshrikes in 24 territories (48 birds) collected from March to June 2008, May to July 2009, and in February and March 2010. To analyze diel variation in song output, we used 24 h

autonomous recordings of banded and unbanded pairs of birds in 16 territories (32 birds) collected from March to June 2008, annotating the number of songs recorded in each one-hour time interval during a continuous 24 h recording. In preliminary analyses, we did not detect Barred Antshrike vocalizations before 04:00 or after 18:00 (i.e., before dawn or after dusk), so we restrict our analysis to 04:00–18:00. To analyze seasonal variation in Barred Antshrike song output, we used recordings of pairs in 25 territories sampled 1–3 times from mid-February to late June 2008–2010. We collected recordings using the autonomous recording setup described above. We annotated all songs in a 60 min period starting with the first song of the morning (between 05:00 and 07:00).

To better study the non-song calls of Barred Antshrikes, we conducted playback experiments to six pairs of birds, playing back *caw* and *mew* calls (see “Results”) over a two-day period in mid-June 2010. For four pairs, we broadcast both call types near the centers of their territories where birds had been observed during previous observations. The following day, we broadcast both call types to two different pairs when pairs were visible and close to the speaker prior to the start of playback. For both pairs, the birds were within 3 m of the loudspeaker and 5 m of their nests during playback.

Sound analysis

We visualized all recordings as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, USA). To compare male and female songs in the 38 focal recordings, we selected three songs from each sex (identified based on direct observations of the singer during the recording) with a high signal-to-noise ratio and minimal background noise. We exported songs into Avisoft SASLab Pro (R. Sprech, Berlin, Germany) and used the automated parameter measurement tool to extract quantitative measures, thereby minimizing human bias in song measurements. Within Avisoft, we used a threshold of -16 dB relative to maximum to standardize the amplitudes of the measured songs, and a hold time of 20 ms to determine when each syllable began and ended. From these automated measurements, we recorded 25 variables for every song, including duration of the entire song, total number of syllables, average frequency of maximum amplitude (FMA), FMA of the first, second, and middle syllables, FMA of the penultimate and terminal syllables, average bandwidth of the entire song, bandwidth of the first, second, and middle syllables, bandwidth of the penultimate and terminal syllables, average syllable length, duration of the first, second, and middle syllables, duration of the penultimate and terminal syllables, average duration of the internote interval, duration of the interval between the first and second syllables,

duration of the interval between the second and third syllables, duration of the interval between the middle and following syllables, and duration of the interval between the penultimate and terminal syllables. We adjusted spectrogram parameters in Avisoft to achieve a measurement accuracy of 2.9 ms for temporal measurements and 21 Hz for pitch measurements. Dominant frequencies were usually between 1 and 2 kHz (see Fig. 1). To ensure that we consistently measured the same part of the song, we occasionally used the eraser cursor in Avisoft to exclude harmonics or background sounds.

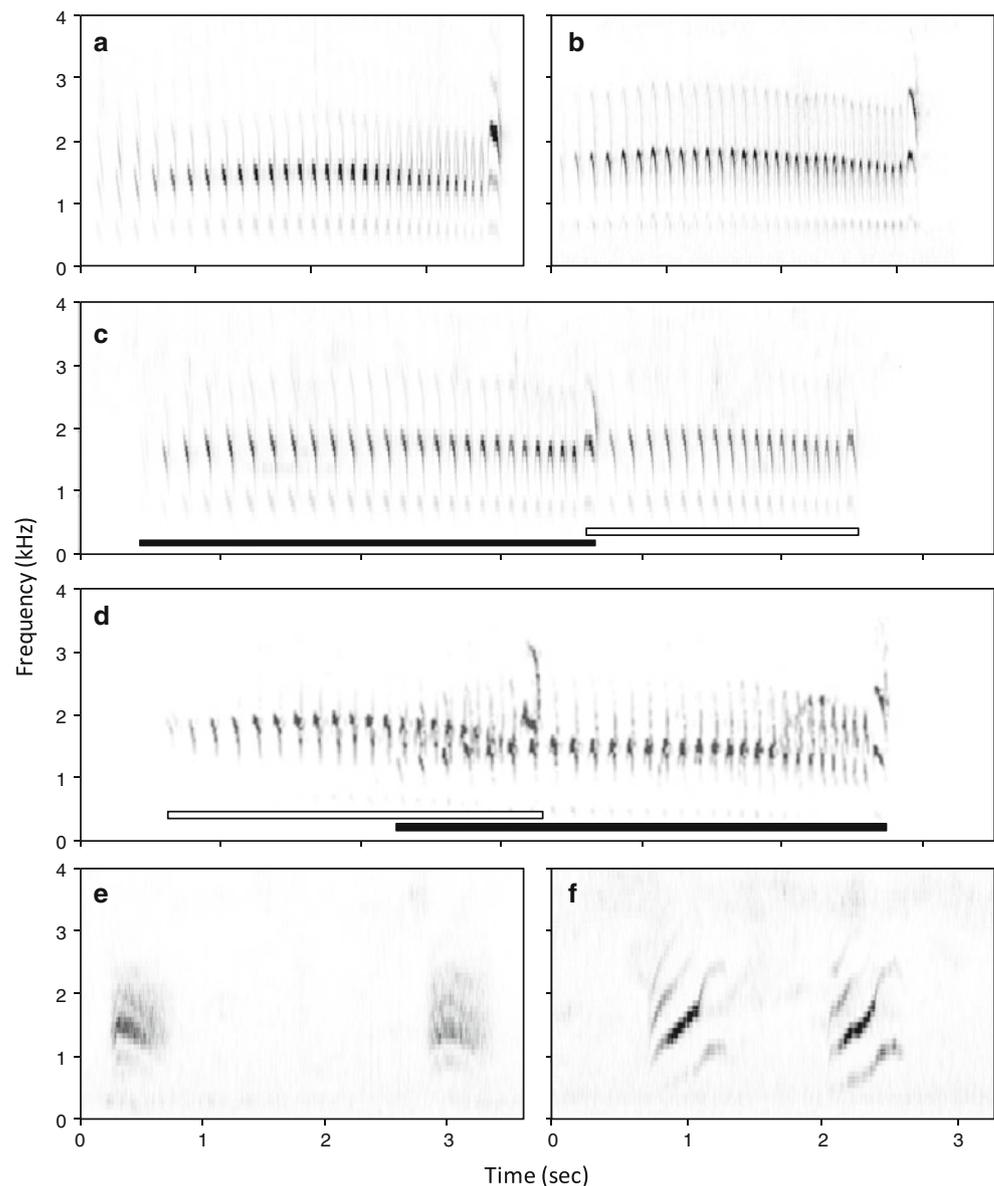
Statistical analyses

To analyze differences between the sexes, we used discriminant function analysis with cross-validation based on the 25 structural characteristics. Using the random selection feature in JMP 8.0 (SAS Institute, Cary, NC, USA), we selected 70 % of the data, constructed the canonical discriminant analysis, and then evaluated our ability to correctly identify sex in the remaining 30 % of the data. We report accuracy as the percentage of the 30 % of the data assigned to the correct sex in the cross-validation. We report the contributions of the original measurements to the discriminant functions for all song measures with factor loadings greater than 0.6 (Kline 1994). We used ANOVA to analyze differences in song structure measurements between males and females. For each individual, we used the mean values of the three measured songs.

We calculated male duet responsiveness as the number of male-created duets divided by the sum of the number of female solos and the number of male-created duets (Hall 2009). We used similar calculations to quantify female duet responsiveness. We assessed duet precision as the coefficient of variation between the delay from the start of the first song to the start of the second song in a duet, where the coefficient of variation is the quotient of the standard deviation and the mean multiplied by 100 (Levin 1996a; Mennill and Vehrencamp 2005). We quantified song rate as the time delay between the onset of consecutive vocalizations. Because Barred Antshrikes often produce a bout of songs and then pause for extended silent intervals, we also reported song rates after removing periods of silence ≥ 60 s (following Mennill and Vehrencamp 2005) to determine how often birds sang without the influence of these long pauses.

To analyze diel variation, we used repeated measures ANOVA ($N = 16$ pairs of birds). We could not use the same statistical approach to analyze the seasonal variation in recordings because different pairs were sampled during different periods, with just a few pairs sampled during multiple periods ($N = 25$ pairs sampled 1–3 times for a total of 57 recordings). We analyzed these data using a linear mixed model with time of year as a fixed factor

Fig. 1 Sound spectrograms of Barred Antshrike vocalizations depicting a **a** male solo song, **b** female solo song, **c** female-created duet, **d** male-created duet, **e** mew call, and **f** *caw* call. For duets, *solid* and *open bars* denote male and female vocalizations, respectively



(recordings were grouped into the first or second half of each month) and pair as a random effect; we used the restricted maximum likelihood method to estimate fixed effects. Song output, expressed in songs per hour, was square-root transformed to achieve normality, although we show untransformed data in the figures. We conducted all analyses in JMP 8.0. We report values as the mean \pm SE.

Results

Solo song structure

The songs of male and female Barred Antshrikes consisted of a series of staccato chuckling notes that subtly rise and

then fall in pitch, concluding with an emphasized, higher-pitched terminal syllable (Fig. 1a, b). Male songs had more syllables than female songs (males: 29.5 ± 0.45 ; females: 22.4 ± 0.42 ; $F_{1,74} = 132.3$, $P < 0.0001$, $N = 76$ individuals) and were longer in duration (males: 3.06 ± 0.04 s; females: 2.31 ± 0.04 s; $F_{1,74} = 168.0$, $P < 0.0001$). All five measures of frequency of maximum amplitude (FMA) differed by sex, with male songs lower in pitch than female songs in all cases (all $F_{1,74} > 13.8$; all $P \leq 0.0004$). None of the other song features we measured differed statistically between the sexes (all $F_{1,74} < 3.7$; all $P \geq 0.06$).

Based on 25 variables, canonical discriminant analysis assigned songs to the correct sex with 91 % accuracy, well above the 50 % accuracy expected by chance ($\chi^2_{21} = 15.6$, $P < 0.0001$). Variables that contributed strongly to this

discrimination included duration and pitch measurements (particularly song duration, number of syllables, and FMA of the second syllable, the middle syllable, and average of all syllables). For most song features measured, there was an approximately 10 % overlap between male and female songs; in our measurements of song length, for example, the 90th percentile for females (the longest female songs) overlapped with the 10th percentile for males (the shortest male songs). Anecdotally, we did not observe distinctiveness between the songs of different individuals within each sex; repeated sampling of colour-marked individuals would be required to empirically quantify this pattern.

Duet description

During duets, male and female Barred Antshrikes used the same songs they sang as solos (Fig. 1c, d). Most duets (84 ± 2 %) were created by females overlapping male songs (e.g., Fig. 1c), and the remainder were created by males overlapping female songs (e.g., Fig. 1d). Proportionately fewer male songs (mean = 23 ± 4 %) than female songs (mean = 38 ± 4 %) were given during duets ($F_{1,65} = 7.6$, $P = 0.008$, $N = 34$ pairs). We only observed duets performed by members of mated pairs.

Duet behaviour

Females were significantly more responsive to their mate's songs in creating duets; females created duets in response to 11.5 ± 1.5 % of their mate's songs, whereas males created duets in response to 8.3 ± 1.3 % of their mate's songs (matched pairs t test: $t = 2.5$, $P = 0.009$, $N = 34$ pairs).

The average delay between the start of a bird's song and the start of their mate's song was 1.8 ± 0.1 s ($N = 34$ pairs). For female-created duets, the delay was 2.0 ± 0.1 s from the start of the male song to the start of the female song, whereas the delay was 1.6 ± 0.1 s from the start of the female song to the start of the male song for male-created duets ($F_{1,53} = 21.7$, $P < 0.0001$, $N = 34$ pairs). The delay between the first bird's song and their mate's song had a coefficient of variation of 30.4 %, with no difference between duets created by females (28.7 ± 2.4 %) and males (30.0 ± 2.7 %; $F_{1,53} = 0.1$, $P = 0.72$, $N = 34$ pairs).

We found that similar portions of male and female songs were overlapped by their partner to create duets. When males created duets, 31.1 ± 1.9 % of the female's song was overlapped; when females created the duets, 30.8 ± 2.6 % of the male's song was overlapped ($F_{1,53} = 0.01$, $P = 0.93$, $N = 34$ pairs).

We observed pairs performing duets in at least two different contexts. Duets were sometimes given in response to the duets of neighbouring territorial birds; in this

context, duets appeared to function as territorial signals. At other times, duets were given in a passive context as pairs moved around their territory foraging. Rarely, we observed a female create a duet by responding to her partner's song while she was incubating.

Song rates

The average song rate of male Barred Antshrikes (one song every 88.1 ± 13.4 s) was higher than that of females (one song every 226.8 ± 47.2 s; paired t test: $t = 3.2$, $P = 0.002$, $N = 24$ pairs recorded for a 24 h period during the breeding season). When silent periods >60 s were removed from song rate calculations, however, song rates of males and females were similar (paired t test: $t = 0.4$, $P = 0.72$, $N = 2424$); males sang every 22.4 ± 0.7 s and females sang every 22.7 ± 2.2 s. Therefore, within song bouts, male and female song rates were similar, although males spent more time singing than females.

Diel variation

Song output varied with time of day for both males (Fig. 2a; repeated measures ANOVA: $F_{14,239} = 7.5$, $N = 16$ pairs recorded for a 24 h period, $P < 0.0001$) and females (Fig. 2b; $F_{14,239} = 8.9$, $P < 0.0001$; $N = 16$ pairs recorded for a 24 h period). Vocal output also varied with time of day for both solo songs (Fig. 2c; repeated measures ANOVA: $F_{14,239} = 10.7$, $P < 0.0001$, $N = 16$ pairs) and duets (Fig. 2d; $F_{14,239} = 3.8$, $P < 0.0001$). We detected Barred Antshrike vocalizations during all daylight hours from 05:00 to 18:00 (sunrise occurs at approximately 5:15; sunset occurs at approximately 5:50 at our study site), but vocal output was highest between 05:00 and 07:00 (Fig. 2). Vocal activity was infrequent after 11:00. The first vocalizations of the day occurred between 05:15 and 05:30 (average time of first male song: 05:18 ± 3.3 min; first female song: 05:19 ± 3.7 min; $N = 16$ daylong recordings), with solos occurring earlier than duets (average time of first solo: 05:16 ± 3.0 min; first duet: 05:28 ± 4.9 min).

Seasonal variation

Barred Antshrike vocal output was lowest before the start of the breeding season in late February, but increased and remained at a high level during the breeding season (Fig. 3). This pattern was significant in our analysis of all male songs ($F_{8,39} = 2.3$, $P = 0.04$), but not all female songs ($F_{8,42} = 0.8$, $P = 0.64$); this pattern was also significant in our analysis of all solo songs ($F_{8,43} = 2.3$, $P = 0.03$), but not all duets ($F_{8,38} = 0.8$, $P = 0.65$).

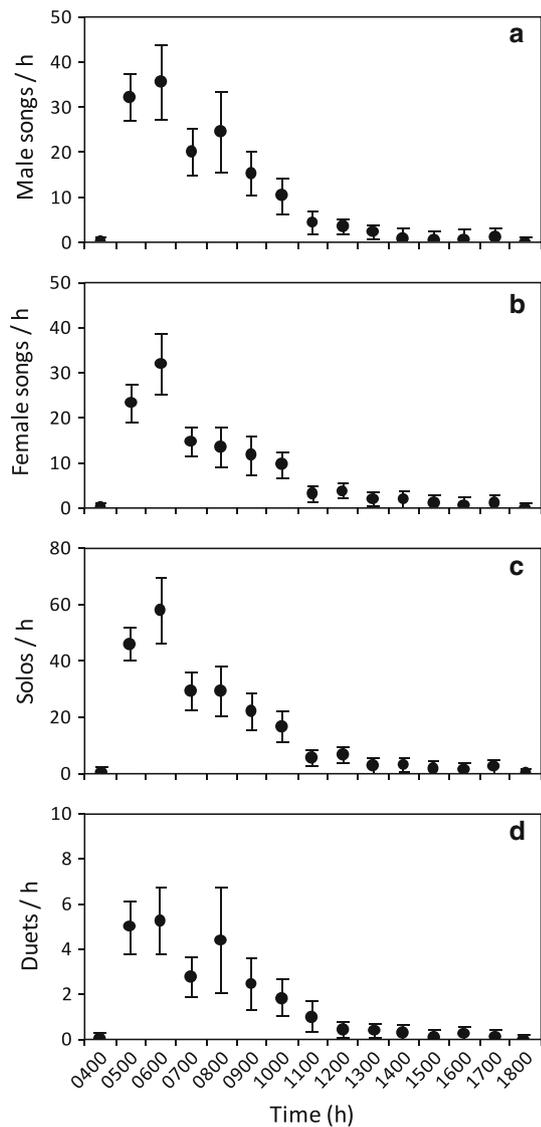


Fig. 2 Diel variations in Barred Antshrike vocal output for **a** male songs/hour, **b** female songs/hour, **c** total solos/hour, and **d** total duets/hour. Vocal output peaked at dawn (~05:00) and tapered off throughout the day

Description of calls

We recorded two calls uttered by Barred Antshrikes. A soft whining *mew* (Fig. 1e) was recorded during three male–male encounters, and a crow-like *caw* (Fig. 1f) was recorded from both sexes. We observed males producing the *caw* call intermittently while pairs foraged, and we observed females producing this call when approaching nests. During playback of *mew* and *caw* calls, birds did not respond vocally or approach the speaker. For the two playback trials where birds were in the immediate vicinity of the playback speaker at the start of the trial, birds showed no response to the speaker whatsoever.

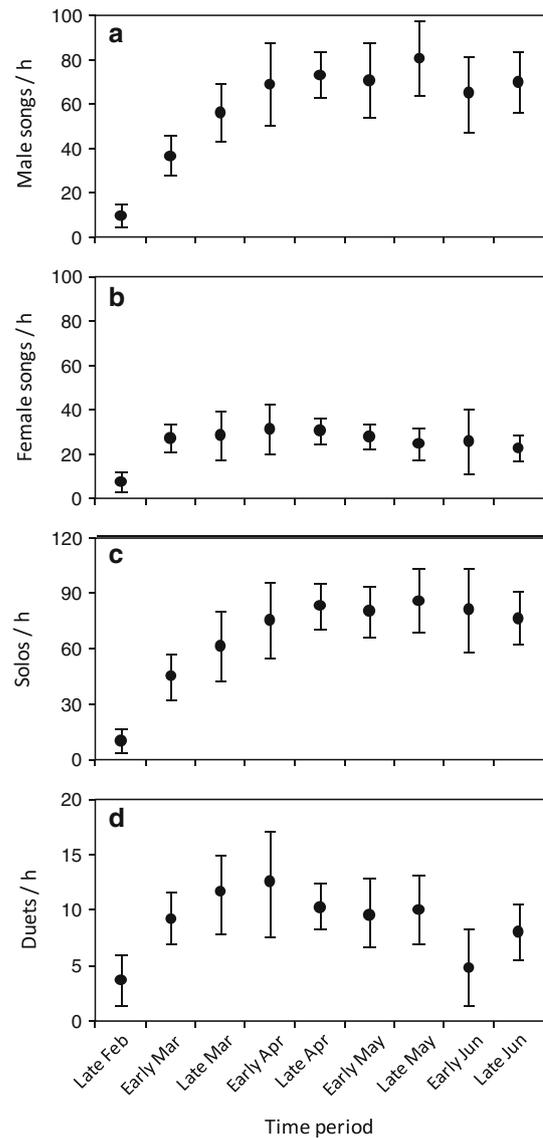


Fig. 3 Seasonal variations in Barred Antshrike song output for the first hour of the morning for **a** male songs/hour, **b** female songs/hour, **c** total solos/hour, and **d** total duets/hour. Vocal output began to increase prior to the nesting period and remained high during the rainy season

Morphometric measurements

Female Barred Antshrikes weighed significantly more than males (Table 1). Two females that showed signs of egg laying when captured were the heaviest females (both weighed 31.8 g); when these two females were removed from the analysis, the sexes did not differ in mass, although females showed a nonsignificant tendency to be heavier (6 females: 28.4 ± 0.8 g; 15 males: 26.5 ± 0.5 g; $F_{1,18} = 11.9$, $P = 0.06$). Male wing chords were longer than those of females, but tail length, tarsus length, and culmen length did not differ between the sexes (Table 1).

Table 1 Measurements for 15 male and 6 female Barred Antshrikes captured in northwestern Costa Rica

Measurement	Male (min)	Male ($x \pm SE$)	Male (max)	Female (min)	Female ($x \pm SE$)	Female (max)	ANOVA
Mass (g)	24.0	26.5 \pm 0.4	29.1	25.8	29.5 \pm 1.1	31.8	$F_{1,21} = 11.9$, $P = 0.003$
Tarsus length (mm)	25.9	27.0 \pm 0.2	28.3	26.0	26.6 \pm 0.3	27.5	$F_{1,19} = 1.3$, $P = 0.21$
Tail length (mm)	56.0	59.9 \pm 0.6	64.0	59.0	59.7 \pm 0.2	60.0	$F_{1,19} = 0.05$, $P = 0.83$
Culmen length (mm)	11.5	12.4 \pm 0.1	13.1	12.6	12.7 \pm 0.1	12.9	$F_{1,19} = 2.6$, $P = 0.12$
Wing chord length (mm)	69.0	71.2 \pm 0.4	74.0	57.1	64.7 \pm 2.9	71.0	$F_{1,19} = 14.1$, $P = 0.002$

Discussion

We described the vocalizations and vocal behaviour of Barred Antshrikes, a Neotropical duetting suboscine songbird, based on three years of recordings collected in northwestern Costa Rica. Both male and female Barred Antshrike songs consisted of staccato chuckling notes, which ascend and then descend in pitch, ending with an emphatic terminal note, as has been reported previously (Zimmer and Isler 2003). Ridgely and Tudor (1994) provided a useful mnemonic for the song: “*hah-ha-hahaha-hahahahaha-hánh*”. Skutch (1969) described their songs as “unmelodious but not unpleasant”. We identified both similarities and differences in the song structure and singing behaviour of males versus females, and we showed that breeding partners coordinate their songs in vocal duets, usually created by females responding to male songs. We quantified patterns of diel variation and seasonal variation in vocal output, where birds showed higher vocal output in the early morning compared to later in the day, and during the rainy season compared to the dry season. This is the first detailed description of the vocal behaviour of this widespread Neotropical songbird. The comparison between the singing behaviour of the sexes as well as the diel and seasonal patterns of variation in vocal output provide insight into the possible function of these vocalizations as well as the importance of song in Neotropical antbirds, a poorly studied taxon.

Our results show that male songs included more syllables and were longer in duration and lower in pitch than female songs. The sexes were similar in body size, so that morphometric dimorphism does not explain these sex differences in song characteristics. Male Barred Antshrikes sang at higher rates than females overall, but when long silences ≥ 60 s were removed from the analyses, singing rates of males and females were similar. Other studies of tropical duetting species have shown that males sing at higher rates overall than females (e.g. Mennill and Vehrencamp 2005), including other studies of duetting antbirds (Fedy and Stutchbury 2005; Stutchbury et al. 2005; Tobias et al. 2011). Taken together, this pattern provides evidence

of sexual convergence in singing behaviour in antbirds, although research on many more antbird species will be required to corroborate this suggestion. Sexual convergence in singing behaviour is a phenomenon that appears to be more common in tropical birds than their temperate counterparts (Slater and Mann 2004); yet many tropical birds show consistent sex differences in their songs and singing behaviour, as we have shown here.

Breeding pairs of Barred Antshrikes combined their songs to produce duets with overlapping male and female components. Female Barred Antshrikes created most duets (84 %) by combining their song with their mate’s song. Similar sex roles have been reported for White-bellied Antbirds (Fedy and Stutchbury 2005) and two species of *Hypocnemis* antbirds (Seddon and Tobias 2006; Tobias et al. 2011), and this has been suggested to be a widespread antbird phenomenon (Zimmer and Isler 2003). Indeed, this pattern holds true for the majority of duetting species that have been studied to date (reviewed in Hall 2009). This female bias in creating duets suggests that females may employ an acoustic mate-guarding strategy as a defence against intruding females. In support of this idea, a recent playback study with Barred Antshrikes demonstrated that both sexes respond aggressively to duet playback, but that females are most aggressive in response to female solo playback (Koloff and Mennill 2011a).

Barred Antshrike vocal behaviour varied with time of day. Singing rates of male and female Barred Antshrikes were highest between 05:00 and 07:00. This early-morning peak in song output indicates that Barred Antshrikes participate in dawn chorus singing behaviour (twilight begins at approximately 05:00 at this site), as is common in many bird species (reviewed in Staicer et al. 1996). The presence of dawn chorus singing varies between species of tropical duetting birds. The pattern of dawn chorus singing behaviour we report for Barred Antshrikes parallels the pattern reported for two other antbirds, the Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and the Yellow-breasted Warbling-Antbird (*H. subflava*; Tobias et al. 2011). Song output during the dawn chorus is understood to have a special importance in territory defence (Staicer

et al. 1996; Amrhein and Erne 2006; Tobias et al. 2011). Therefore, patterns of diel variation in three species of antbirds support the idea that both sexes use song to contribute to territorial defense.

Song output by Barred Antshrikes in our study increased just prior to the onset of nesting (early May), and remained high throughout the breeding season. This pattern was significant for male songs, but not female songs. A similar pattern was evident for both sexes (Fig. 3) but the lower number of female songs may have contributed to their lack of statistical significance. The Barred Antshrike territories we monitored during this study were stable across the pre-breeding and breeding seasons. Increased song output immediately prior to breeding may reflect the increased motivation of birds to exclude rivals from their territory at this important time of the year. Alternatively, as the breeding season approaches, increased song output may be related to increased competition for mates. Koloff and Mennill (2011a) found that both sexes respond aggressively to simulated territorial intruders during the breeding season. In particular, females showed intense levels of female–female aggression. These results suggest that song plays a role in mate guarding for female Barred Antshrikes, which could explain heightened song output at the start of the breeding season, when birds are pairing up to commence breeding.

We found no significant seasonal variation in the rate of Barred Antshrike duets, although there was a trend where duetting activity increased in the late dry season, and also decreased later in the breeding season. We expect that this nonsignificant trend arose because of a small sample size in our number of recorded duets, and that with further sampling the seasonal pattern of variation in duets would mirror the significant patterns seen for male songs and solos. Research on other tropical passerines has revealed a significant pattern of higher vocal output at the beginning of the breeding season followed by a decrease in duetting later in the breeding season; in Rufous-and-white Wrens (*Thryophilus rufalbus*), the peak vocal output was highly correlated with the onset of the rainy season and the female's fertile period, and declined after females began laying eggs (Topp and Mennill 2008). A playback study on White-bellied Antbirds demonstrated that birds displayed greater aggression toward intruders during the dry season, prior to breeding, than in the rainy season (Fedy and Stutchbury 2005). Heightened competition for resources early in the breeding season may place increased pressure on tropical birds to defend their territories against intruders. Alternatively, if duets play a role in acoustic mate guarding or paternity guarding (Hall 2004), duets may be especially important just prior to breeding, but less so after breeding has commenced.

In addition to songs, the Barred Antshrikes in our study produced at least two types of calls: *caw* calls and *mew* calls. Other investigators have suggested that the *caw* call is used as a warning (Young 1929). We observed Barred Antshrikes producing this call while foraging or while approaching the nest. During a pilot study involving *caw* call playback, birds did not react to the playback of this call, as one would expect for an effective warning call. This suggests that the function of the *caw* call is not a warning signal; it is possibly associated with maintaining contact between members of a breeding pair. We only observed males producing *mew* calls, and on all three occasions it was produced during aggressive male–male encounters. Nevertheless, six pairs of Barred Antshrikes remained unresponsive to the playback of *mew* calls during a pilot study. The lack of response may be an indication that *mew* calls are only important in the context of an encounter between males where other acoustic and visual signals are also produced. Additional studies of these Barred Antshrike calls are needed to better understand their function.

Other investigators have provided written descriptions of additional types of calls given by Barred Antshrikes that we did not detect during our study, including a low, guttural “*gnaar*” (Slud 1964), a “*croak*” (Skutch 1969), “*graaaaa*” (Hilty 2003), and “*growl, gurrr*” (Hilty and Brown 1986). These descriptions may be alternative descriptions of the *caw* vocalization described above, or they may refer to vocalizations that are rarely used or absent in our study population. In addition, Zimmer and Isler (2003) described long or short clear whistle notes, and Slud (1964) described male and female calls reminiscent of “four or five trogon-like ‘*pyoo*’s”. The function and context of these calls are unknown and they may be a product of vocal variation across populations of Barred Antshrikes. A better understanding of population-specific calls may be useful for defining species limits in Barred Antshrike populations; calls, not songs, have been used to distinguish between other sympatric thamnophilid species (Isler et al. 2007; Tobias and Seddon 2009).

The vocal behaviour of many tropical bird species has yet to be described empirically. Thorough accounts of the vocal behaviour of suboscines may help to clarify the taxonomic status of polytypic species (Kroodsma et al. 1996). Our study of Barred Antshrikes revealed both similarities and differences in vocal behaviour compared to other tropical birds. These findings will be useful in future comparative studies on the behavioural patterns of tropical birds, as well as other duetting species. There is much variation within and across species in how birds form duets; describing duet structure is important for understanding duet function and patterns of duetting among species (Hall 2009). Evaluating the vocal behaviour of tropical species is important for our understanding of

patterns of behavioural ecology, and provides useful comparisons to vocal patterns observed in temperate regions. This study provides a foundation for continued research on this species and other antbirds. Rigorous analysis of vocal characters and behaviour may assist in delineating species limits in closely related sympatric species. Such studies will increase our understanding of a fascinating family of passerines that is widespread in Neotropical ecosystems.

Acknowledgments We thank the staff at Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica for logistical support. This research was funded by grants from the American Museum of Natural History's Frank M. Chapman Memorial Fund Grant to JK and grants from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation (CFI), the Government of Ontario, and the University of Windsor to DJM.

References

- Amrhein V, Erne N (2006) Dawn singing reflects past territorial challenges in the Winter Wren. *Anim Behav* 71:1075–1080
- 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
- Farabaugh SM (1982) The ecological and social significance of duetting. In: Kroodsma DE, Miller EH (eds) *Acoustic communication in birds*, vol 2. Academic, New York, pp 85–124
- Fedy BC, Stutchbury BJM (2005) Territory defence in tropical birds: are females as aggressive as males? *Behav Ecol Sociobiol* 58:414–422
- Hall ML (2004) A review of hypotheses for the functions of avian duetting. *Behav Ecol Sociobiol* 55:415–430
- Hall ML (2009) A review of vocal duetting in birds. In: Naguib M, Janik VM (eds) *Advances in the study of behavior*, vol 40. Academic, Burlington, pp 67–121
- Hill GE, Mennill DJ, Rolek BW, Hicks TL, Swiston KA (2006) Evidence suggesting that Ivory-billed Woodpeckers (*Campephilus principalis*) exist in Florida. *Avian Conserv Ecol* 1:2
- Hilty SL (2003) *Birds of Venezuela*. Princeton University Press, Princeton
- Hilty SL, Brown WL (1986) *A guide to the birds of Columbia*. Princeton University Press, Princeton
- Isler ML, Isler PR, Whitney BM (1998) Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *Auk* 115:577–590
- Isler ML, Alvarez A, Isler PR, Valqui T, Begazo A, Whitney M (2002) Rediscovery of a cryptic species and description of a new subspecies in the *Myrmeciza hemimelaena* complex (Thamnophilidae) of the Neotropics. *Auk* 119:362–378
- Isler ML, Isler PR, Whitney BM (2007) Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk* 124:11–28
- Kirschel ANG, Earl DA, Yao Y, Escobar I, Vilches E, Vallejo EE, Taylor CE (2009) Using songs to identify individual Mexican Antthrush (*Formicarius moniliger*): a comparison of four classification methods. *Bioacoustics* 19:1–20
- Kline P (1994) *An easy guide to factor analysis*. Routledge, New York
- Koloff J, Mennill DJ (2011a) Aggressive responses to playback of solos and duets in a Neotropical antbird. *Anim Behav* 82:587–593
- Koloff J, Mennill DJ (2011b) Neotropical Birds: Barred Antshrike (*Thamnophilus doliatus*) (website). TS Schulenberg, Cornell Lab of Ornithology, Ithaca. http://neotropical.birds.cornell.edu/portal/species/overview?P_p_spp=367746. Accessed 10 Oct 2011
- Kroodsma DE (1984) Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *Auk* 101:13–24
- Kroodsma DE, Konishi M (1991) A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Anim Behav* 42:477–487
- Kroodsma DE, Vieliard JME, Stiles FG (1996) Study of bird sounds in the Neotropics: urgency and opportunity. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 426–453
- Lanyon WE (1978) Revision of the Myiarchus flycatchers of South America. *Bull Am Mus Nat Hist* 161:429–627
- Levin RN (1996a) Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. I. Removal experiments. *Anim Behav* 52:1093–1106
- Levin RN (1996b) Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. *Anim Behav* 52:1007–1117
- Lovell SF, Lein MR (2004) Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behav Ecol* 15:799–804
- Lovell SF, Lein MR (2005) Individual recognition of neighbors by song in a suboscine bird, the alder flycatcher *Empidonax alnorum*. *Behav Ecol Sociobiol* 57:623–630
- Mennill DJ, Vehrencamp SL (2005) Sex differences in the singing and duetting behavior of Neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). *Auk* 122:175–186
- Ridgely RS, Tudor G (1994) *The birds of South America. The Suboscine Passerines*, vol 2. University of Texas Press & Oxford University Press, Texas
- Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. *Evolution* 59:200–215
- Seddon N, Tobias JA (2006) Duets defend mates in a suboscine passerine, the Warbling Antbird (*Hypocnemis cantator*). *Behav Ecol* 17:73–83
- Seddon N, Tobias JA (2007) Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biol J Linn Soc* 90:173–188
- Sedgwick JA (2001) Geographic variation in the song of willow flycatchers: differentiation between *Empidonax traillii* adastus and *E. t. extimus*. *Auk* 118:366–379
- Skutch AF (1969) Life histories of Central American birds III. *Pac Coast Avifauna* 35:1–580
- Slater PJB, Mann NI (2004) Why do the females of many bird species sing in the tropics? *J Avian Biol* 35:289–294
- Slud P (1964) The birds of Costa Rica—distribution and ecology. *Bull Am Mus Nat Hist* 128:1–430
- Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 426–453
- Stutchbury BJM, Morton ES (2001) *The behavioral ecology of tropical birds*. Academic, New York
- Stutchbury BJM, Woolfenden BE, Fedy BC, Morton ES (2005) Nonbreeding territorial behavior of two congeneric antbirds, *Myrmeciza exsul* and *M. longipes*. *Ornitol Neotrop* 16:397–404
- Tobias JA, Seddon N (2009) Signal design and perception in *Hypocnemis* antbirds: evidence for convergent evolution via social selection. *Evolution* 63:3168–3189
- Tobias JA, Gamarra-Toledo V, Garcia-Olaecha D, Pulgarin PC, Seddon N (2011) Year-round resource defence and the evolution

- of male and female song in suboscine birds: social armaments are mutual ornaments. *J Evol Biol* 24:2118–2138
- Topp SM, Mennill DJ (2008) Seasonal variation in the duetting behaviour of Rufous-and-white Wrens (*Thryothorus rufalbus*). *Behav Ecol Sociobiol* 62:1107–1117
- Westcott DA (1997) Neighbours, strangers and male-male aggression as a determinant of lek size. *Behav Ecol Sociobiol* 40:235–242
- Young CG (1929) A contribution to the ornithology of the coastland of British Guiana, part 2. *Ibis* 5:34
- Zimmer KJ, Isler ML (2003) Family Thamnophilidae (typical antbirds). In: Del Hoyo J, Elliott A, Christie DA (eds) *Handbook of the birds of the world. Volume 8: broadbills to tapaculos*. Lynx Edicions, Barcelona, pp 448–681