Duets defend mates in a suboscine passerine, the warbling antbird *Hypocnemis cantator*

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Despite the widespread occurrence of avian duets, their adaptive significance is poorly understood. Most research indicates that they function in territory defense, but no study has yet distinguished this hypothesis, which invokes cooperation between the sexes, from mate defense, which invokes conflict. Further, most duetting studies have focused on oscine passerines, yet duets are performed by a number of suboscines. We therefore tested the mate defense hypothesis in the warbling antbird *Hypocnemis cantator* of Amazonia, a suboscine that produces sex-specific songs and duets. We carried out acoustic analyses of song in conjunction with playback experiments and found support for the hypothesis that females respond to male songs to prevent themselves from being usurped by same-sex rivals. We found that (1) duets were initiated by males, (2) the structure of male but not female song changed during duet formation, (3) swift responses by females resulted in males producing shorter songs comprising fewer notes, (4) solos elicited strong responses from paired birds of either sex, (5) duets elicited weaker responses than same-sex solos from paired birds of either sex, and (6) females responded more strongly to same-sex solos, answering a higher proportion of their partner's songs and doing so more promptly than after playback of male solos or duets. Predictions (1)−(3) showed that—rather than being collaborative signals with each sex contributing equally—duetting and the extent of a male's contribution to a duet depended on female behavior. Although (4) could result from intrasexual territorial defense, this does not explain (5) and (6), which indicated that same-sex intruders were more threatening than opposite-sex or paired intruders, suggesting that the perceived threat was to the partnership rather than the resource. Together these findings make a strong case for the mate defense hypotheses and the importance of conflict in the evolution and maintenance of avian duets. *Key words:* duets, *Hypocnemis cantator*, mate defense, playback experiments, territory defense, warbling antbird. *[Behav Ecol]*

The adaptive significance of coordinated vocal duets between pair members is poorly understood, and, until recently, this fascinating form of animal communication was neglected by behavioral ecologists (Hall, 2004; Langmore, 2002). This is despite the fact that duetting occurs in birds with at least as much frequency as cooperative breeding and interspecific brood parasitism (i.e., 3% of species), subjects that, conversely, have been intensively studied for decades (Clutton-Brock, 2003, Davies, 2000).

The past 5 years, however, have seen a resurgence of interest in the behavior (Hall, 2004) with research indicating that—in support of the traditional stance—duets are primarily used in joint territory defense (Grafe and Bitz, 2004; Grafe et al., 2004; Hall, 2000; Langmore, 1998; Sonnenschein and Reyer, 1983). Several recent studies have also provided at least tentative support for the idea that they may additionally arise through conflict, that is, with males and/or females responding to their partner's solo songs either to prevent them from deserting (Appleby et al., 1999; Hall, 2000; Mulder et al., 2003) or to prevent themselves from being usurped by same-sex rivals (Grafe and Bitz, 2004; Seddon et al., 2002). However, these studies could not distinguish between cooperation and conflict because the territory and mate defense hypotheses generate similar predictions, that is, that duets are loud, locatable, used in interactions with neighbors, and are incited by playback of solos and duets, with solos eliciting sex-specific responses (Hall, 2004).

Nonetheless, there are at least two predictions that distinguish these hypotheses. One is that playback of same-sex solos elicits stronger responses than duets or opposite-sex solos from paired birds because solitary intruders are more threatening than paired intruders, the threat being to the partnership rather than the resource. The second is that paired birds should respond to more of their partner's songs and should do so more promptly after playback of same-sex solos than opposite-sex solos or duets. The logic is that frequent and prompt responses to a partner's solo songs signal the presence of a well-defended bird that is unavailable for pairing with the intruder.

Only three studies have explicitly tested these predictions, and the support they provide is mixed and to a certain extent limited by small sample sizes. No support was found for the first prediction in the tropical boubou *Laniarius aethiopicus* (Grafe and Bitz, 2004) and the Australian magpie-lark *Grallina cyanoleuca* (Mulder et al., 2003), and although males (but not females) respond to more of their partner's songs after same-sex solos in the boubou, neither males nor females have been shown to do so in the magpie-lark. Although there is tentative support for both predictions in the subdesert mesite *Monias benschi*, in this case interpretation is made difficult by the fact that this is a group-living, chorusing species in which the vocal behavior of other group members is probably confounding (Seddon et al., 2002). Thus, there is still uncertainty as to whether duets arise through conflict between the sexes and further experimental tests are required.

Another limitation of previous work is that almost all studies have been carried out on oscine passerines from the Old World tropics (Hall, 2004). Apart from a single study of dusky antbirds, *Cercomacra tyrannina*, carried out more than a decade ago (Morton, 1996; Morton and Derrickson, 1996), scant attention has been paid to the suboscine passerines (suborder

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Tyranni) of the Neotropics. This is despite the fact that they account for at least 20% (1151 species) of all passerine species (Sibley and Monroe, 1990) and include diverse families such as tyrant flycatchers (Tyrannidae), ovenbirds (Funariidae), and antbirds (Thamnophilidae) in which duetting is fairly common (see reviews in del Hoyo et al., 2003). Of these families, duetting appears to be prevalent in the antbirds, where at least 20 species (10% of the family) perform duets (Zimmer and Isler, 2003). Given that the total number of duetting bird species is currently estimated at 222 species (Farabaugh, 1982), studies into the adaptive significance of duetting in antbirds could provide key insights into how the behavior evolves and is maintained.

We therefore investigated the role of conflict in the duetting behavior of the warbling antbird *Hypocnemis cantator*, a suboscine passerine common and widespread in the understory of the Amazon rainforest. As a territorial and socially monogamous species that produces structurally simple solos and duets, it is ideal for testing ideas about the function of duetting. Moreover, unlike most duetting species studied to date (Hall, 2004), warbling antbirds have sexually dimorphic plumage, making it possible to quantify male and female behavior in the field without the need for invasive color ringing and post hoc molecular sexing.

Previous studies indicate that males and females produce sex-specific songs and that duets are formed when females respond vocally to their partner (Isler et al., in press; Zimmer and Isler, 2003). If these duets do not function in collaborative territory defense and instead arise through conflict, with females responding to prevent themselves from being usurped by rivals, we make the following predictions about duet structure and response to playback (see Table 5). We predict that (1) duets are initiated by males, (2) the structure of male but not female songs change during duet formation, (3) swift responses by females result in males producing shorter songs comprising fewer notes, (4) solos elicit strong responses from paired birds of either sex, (5) duets elicit weaker responses than same-sex solos from paired birds of either sex, and (6) females respond more strongly to same-

sex solos, answering a higher proportion of their partner's songs and doing so more promptly than after male solos or duets. Predictions (1)−(3) are consistent with mate defense because they suggest that—rather than being collaborative signals with each sex contributing equally—duet formation and the extent of a male's contribution to a duet depends entirely on the behavior of the female. Although sex-specific responses to playback (prediction 4) could be accounted for by intrasexual territorial aggression, this would not explain why they respond more strongly to same-sex solos than duets (prediction 5). Indeed, prediction (5) indicates that solitary same-sex intruders are more threatening than opposite-sex or paired intruders and hence that the threat is to the partnership rather than the resource. If duets are collaborative ventures between paired birds, we would expect the frequency and speed of female responses to male songs to be greatest after playback of duets (contra prediction 6), the threat being to the resource and hence deserving of a unified response.

In the first detailed experimental study of duetting in a suboscine bird, we used playback experiments in conjunction with acoustic analyses to test these predictions and found compelling support for the mate defense hypothesis.

METHODS

Study species

The warbling antbird is a medium-sized (11–12 cm, 10–14 g), sexually dimorphic and socially monogamous passerine bird found throughout Amazonia (Zimmer and Isler, 2003). Pairs maintain year-round territories (Terborgh et al., 1990), and their offspring have low levels of dispersal (Bates, 2000). In common with many antbirds, males and females produce loud vocalizations on a daily basis and throughout the year, consisting of multiple notes delivered in a stereotyped pattern as solos or duets. Because this differs from the traditional, rather narrow definition of song—that is, complex male vocalizations used in mate advertisement (Catchpole and Slater,
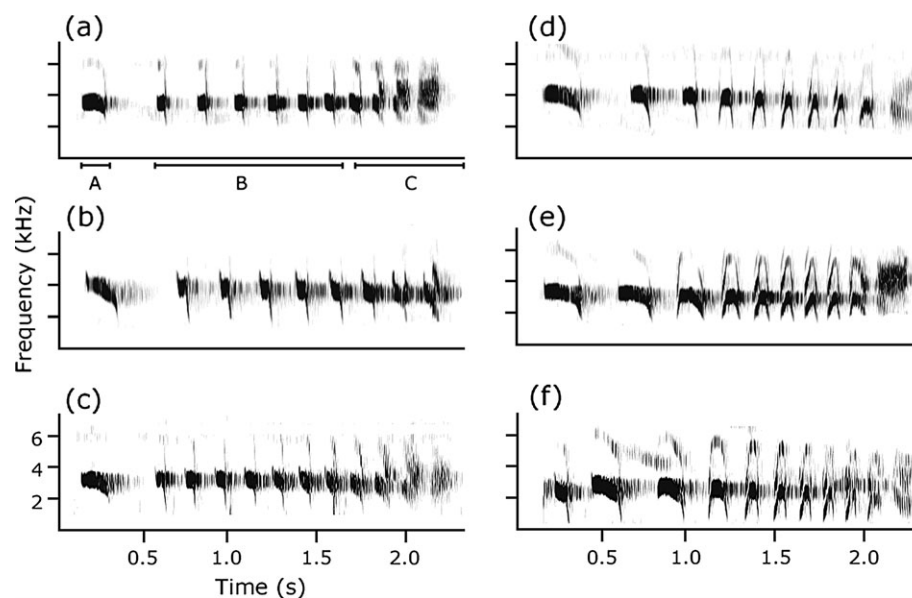

Figure 1
Audiospectrograms of loudsongs of three different males (a–c) and females (d–f), illustrating variation between individuals and between the sexes and showing: A (the introductory note), B (the main phrase), and C (the terminal phrase) of the male loudsong.

1995)—the term "loudsong" has been coined (Willis, 1967; Zimmer and Isler, 2003). Although loudsongs are probably functionally analogous to "songs," we retain the term loudsong to be consistent with previous work. In this study we use the following definitions.

Loudsong: a more or less discrete unit repeated during a bout of singing consisting of a stereotyped series of notes in which the interval between successive notes is smaller and more even than that occurring between successive loudsongs (Figure 1). In the warbling antbird, male and female loudsongs consist of a series of 6–18 notes descending in both pitch and pace. Male loudsongs have a single introductory note, an even-pitched, even-paced main phrase, and usually terminate in 1–4 low-pitched, slow-paced raspy notes (Figure 1a–c). Female loudsongs have 1–4 introductory notes and an even-paced main phrase that descends slightly in pitch and usually terminate in 1–4 raspy notes (Figure 1d–f).

Solo: a series of male or female loudsongs.

Duet: a single pair of loudsongs comprising one male and one female loudsong where the interval between male and female loudsongs within a duet is always much shorter than that between successive duets (see Figure 2). For a detailed description of the acoustic properties of warbling antbird vocalizations, see Isler et al. (in press).

Once considered to be a single species, the *H. cantator* complex probably contains six, each species occupying a more or less distinct geographic region within the Amazon basin and foothills of the southern Andes (Isler et al., in press). The focus of the present study is *H. c. spixii*, a subspecies restricted to lowland rainforest in south-central Brazil.

Study population

In May–July 2004 we studied a total of 22 pairs of warbling antbirds at Rio Cristalino Jungle Lodge, located 40 km northeast of the town of Alta Floresta in Mato Grosso State, south-central Brazil (9° 41′ S, 55° 54′ W). The site consists of approximately 100 ha of pristine lowland tropical moist forest and is accessed by a grid of trails encompassing the territories of at least 30 pairs of warbling antbirds. For a full description of the site see Zimmer et al. (1997). Although we did not color ring individuals, the points at which experiments were carried out and recordings made were marked with coded flagging; no further experiments or recordings were made from the same pair. Warbling antbirds are highly territorial, sedentary, and vocal, and we were able to delimit territories by tracking

the movement of singing birds and marking the location of countersinging individuals. Where territory boundaries were less clear, we ignored any male heard singing within 100 m of our flagged locations. Given the small size of known territories, this rule of thumb provided a safeguard against pseudoreplication.

Acoustic analysis of loudsong structure

A Sennheiser ME66-K3U directional gun microphone and a Sony TC-D5 Pro II tape recorder were used to record solos and duets onto 60 min TDK metal tapes. Using Avisoft SASLabPro Version 4.15 (© 2002 Raimund Spect, Berlin, Germany) with a 16-bit acquisition sound card (0 VIA [Wave] 5.10), taped loudsongs were automatically filtered at half the Nyquist frequency to prevent aliasing and digitized twice, once at a sampling frequency (SF) of 44.1 kHz and once at a SF of 12 kHz. We obtained 300 min of recordings of solos and duets from a total of 22 males and 16 females. Using only high-quality recordings (i.e., those with low background noise made 5–15 m from singing birds), loudsongs were described quantitatively by taking a variety of temporal and frequency measurements from audiospectrograms using Avisoft's on-screen cursors. To achieve maximum temporal resolution (1.5 ms), time features were taken from audiospectrograms from recordings sampled at 44.1 kHz using the broadband (323 Hz) filter settings (FFT = 512, Frame = 50%, Window = FlatTop, Overlap = 88%). To maximize frequency resolution (11 Hz), audiospectrograms were also produced from recordings digitized at 12 kHz using the narrowband (55 kHz) filter settings (FFT = 1024, Frame = 100%, Window = hamming, Overlap = 88%). Loudsong structure was quantified using the following standard time (in seconds) and frequency (in kilohertz) measures (see Figures 1 and 2): (1) total number of notes, (2) number of terminal raspy notes, (3) duration of loudsong (excluding final raspy notes because of uncertainty as to when these notes ended), (4) overall pace (number of notes, excluding terminal raspy notes, divided by loudsong duration), (5) pace of middle phrase (number of notes in middle phrase divided by duration of middle phrase); (6) duration of first note, (7) duration of interval between the first and second notes, (8) bandwidth of first note, (9) bandwidth of middle phrase, (10) maximum frequency of loudsong, (11) minimum frequency of loudsong, and (12) bandwidth of loudsong. Frequency measures could not be measured reliably from amplitude spectra because of interference by background noise, especially the songs of other birds and insects.

Playback experiments

Selecting only those recordings made in natural situations, that is, without playback, we viewed broadband audiospectrograms of stimulus loudsongs with Avisoft to ensure that there was no background noise in the frequency range of warbling antbird loudsongs. We then normalized their amplitude and digitally filtered them to remove low- and high-frequency background noise (FIR bandpass filter set between 1 and 8 kHz). Stimulus sound (uncompressed "wav") files 1-min long were then created using Avisoft. Each consisted of the same loudsong repeated every 15 s, matching the natural rate of four loudsongs per minute. These stimulus wav files were then transferred in uncompressed format to a minidisk using SonicStage Software Version 1.5 (© 2001, 2002, Sony Corporation).

Playbacks were conducted on a total of 18 pairs from 10 June–5 July 2004 at 0600–1000 h to minimize effects on
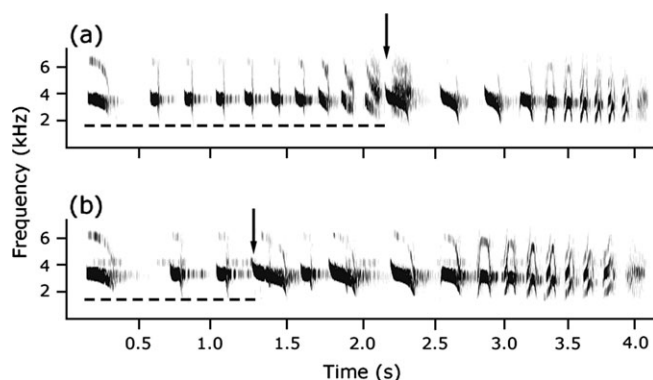

Figure 2
Audiospectrograms of duet songs given by the same pair of warbling antbirds showing (a) slow and (b) rapid responses of the female to her partner's loudsong. Arrows show the point at which the female starts to sing; dashed lines denote female response time.

responses of date and time of day. Experimental subjects and their neighbors were at different stages of their breeding cycle. Because it was not possible to determine stage of breeding cycle of all pairs when carrying out the experiments, we used date of trial instead. Each pair received three playback treatments: male solo (a series of four male loudsongs), female solo (a series of four female loudsongs), and duets (a series of four duets with minimal overlap between male and female loudsongs; e.g., Figure 2a). We used 18 unique sets of solos and duets as stimuli for 18 pairs to avoid pseudoreplication (Kroodsma, 1989). Treatments were separated by an interval of 48 h to minimize habituation, and each pair received the treatment in a random order. All playbacks were given from the same location and at a similar time of day (to within 1 h). To avoid the problems of habituation and non-independence of trials, pairs on adjacent territories were not tested on the same day. Although no evidence of neighbor-stranger recognition was found in the spotted antbird *Hylophylax naevioides* (Bard et al., 2002), it does occur in another species of suboscine, the alder flycatcher *Empidonax alnorum* (Lovell and Lein, 2004). As recognition of neighbors may have confounded our results, we ensured that all pairs received loudsongs from birds recorded from territories at least three territory diameters away (>500 m).

Each trial lasted 10 min (1 min of playback and 9 min of silence). During the first minute, loudsongs were played through a Sony SRS-58 loudspeaker connected to a Sony Net MD Walkman (MZ-N710). The loudspeaker was placed at least 20 m from a territory boundary, approximately 0.2 m up and facing the subjects, which were always located 15–20 m away. The peak sound pressure level was adjusted to approximate that of natural loudsongs, that is, 60 dB SPL at 10 m measured with an Adastra handheld analog sound level meter (set at "C" weighting and fast response). Playback experiments were started once the subjects and their neighbors had been silent for at least 5 min. The timing of trials started at the beginning of the first loudsong of the playback.

Quantifying response to playback

During each 10-min trial, one observer used a tape recorder to record as much of the vocal response as possible, and a second observer used a dictaphone to record the location and behavior of subjects. We noted which sex was the first to vocalize (i.e., give a loudsong or a call) and which was the first to approach (i.e., fly toward) the loudspeaker. Responses of each pair member were further quantified by recording the following continuous measures: (1) time from the start of playback to the first visible flight towards the loudspeaker (approach latency in seconds), (2) closest distance (in meters) to the loudspeaker, (3) maximum song perch height (in meters), (4) time (in seconds) spent <5 m from the loudspeaker, and (5) time from the start of playback to the first loudsong (song latency in seconds). Low values for (1), (2), and (5) and high values for (3) and (4) indicated strong responses. In addition, we recorded whether or not the white interscapular feathering was exposed and whether or not the birds flew around the loudspeaker in short rapid flights; these measures indicated high levels of aggression (Robinson and Terborgh, 1995).

We also used the aforementioned Sennheiser microphone and Sony tape recorder to record any solos and duets given after playback. Where possible, we analyzed at least the first six successive male and female loudsongs or duets given after playback, ignoring the first two, the quality of which was often compromised by the gain adjustments made by the recordist. Using broadband audiospectrograms generated from the recordings as previously described, we measured (1) the proportion of male loudsongs responded to by females and (2) female response time (i.e., the time elapsing between the start of a male's loudsong and the beginning of his mate's; see Figure 2). When a female was present but did not answer her partner's loudsong, the response time was scored as 1.3 (i.e., the mean duration of a single male loudsong; Table 1).

Statistical analyses

In the acoustic analyses, for each pair we calculated a mean value for each time and frequency variable measured from male and female loudsongs and a mean female response time. We tested whether among-individual and among-sex loudsong differences exceeded within-individual and within-sex differences, using one-way ANOVAs on each of the nine acoustic measures. We used linear regression to test for the effects of female response time on the duration and number of notes in the male loudsong they followed. Wilcoxon signed-rank tests were used to examine the effects of duetting on the structure of male loudsongs, but we were unable to carry out an equivalent

Table 1
Differences between solos and duets in the structure of the loudsongs of male warbling antbirds

Acoustic measure	Male loudsong		Statistics	
	Solo	Duet	z	p
Total number of notes	12.2 ± 1.3	9.3 ± 1.3	−3.52	**<.0001**
Number of terminal raspy notes	4.2 ± 0.9	2.0 ± 0.5	−3.52	**<.0001**
Loudsong duration	1.3 ± 0.14	1.24 ± 0.11	−3.35	**.001**
Pace of notes in loudsong	9.2 ± 7.5	7.5 ± 0.2	−3.52	**<.0001**
Pace of notes in middle phrase	10.0 ± 1.6	9.6 ± 1.6	−1.24	.215
Duration of first note	0.14 ± 0.02	0.14 ± 0.02	−0.909	.363
Duration of first interval	0.24 ± 0.02	0.24 ± 0.03	−0.517	.605
Bandwidth of first note	0.64 ± 0.17	0.60 ± 0.16	−0.724	.469
Bandwidth of middle phrase	0.48 ± 0.19	0.37 ± 0.11	−1.81	.07
Maximum frequency of loudsong	3.10 ± 0.19	3.08 ± 0.14	−1.81	.07
Minimum frequency of loudsong	2.62 ± 0.21	2.71 ± 0.15	−2.019	**.044**
Bandwidth of loudsong	0.48 ± 0.15	0.39 ± 0.12	−2.792	**.026**

Time variables are given in seconds and frequency variables in kilohertz. Statistics are from Wilcoxon signed-rank tests; $n = 16$ males.
Significant values are denoted in boldface.

Table 2

Comparisons within and between the sexes in the response of warbling antbirds to playback of solos and duets, as quantified by three binary variables

Response	Male solo	Female solo	Duet	Q	p	MF	MD	FD
Number of occasions when								
♂ initiated vocal response	18	8	15	14.4	.001	NS	NS	NS
♀ initiated vocal response	0	7	2	9.75	.008	*	NS	NS
χ_1^2	18	0.07	9.94					
p	<.001	NS	<.01					
♂ approached first	17	2	10	21.1	<.0001	**	NS	NS
♀ approached first	0	14	3	23.3	<.0001	**	NS	**
χ_1^2	17	9	3.77					
p	<.001	<.01	NST					
♂ gave rapid flights + exposed white mantle	12	2	6	12.7	.002	**	NS	NS
♀ gave rapid flights + exposed white mantle	0	7	1	10.8	.005	**	NS	NS
χ_1^2	12	2.78	3.57					
p	<.001	NS	NS					

Values for chi square and associated p derive from chi-square tests; values for Q and associated p derive from Cochran Q tests. Asterisks denote significant differences after Bonferroni adjustment between pairs of treatments using McNemar tests: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet). NS, nonsignificant; NST denotes a nonsignificant trend ($p < .1$).

$*p < .02$, $**p < .01$.

analysis for females because they rarely produced solo loudsongs. Many of the acoustic variables were intercorrelated. To investigate the effect of playback on overall loudsong structure, we therefore carried out principal component analysis (PCA) to reduce the separate measures to uncorrelated synthetic variables. This method generated three PCs with eigenvalues greater than 1.0, explaining 79.6% of the variance in the acoustic measures. PC1 and PC3 were strongly correlated with temporal characteristics and PC2 with frequency characteristics (see Appendix). To achieve normality and constant variance required by parametric tests, prior to carrying out the forgoing analyses we square-root transformed two variables (number of notes per loudsong and pace), and log transformed all others.

Table 3

Comparisons within the sexes in the response of warbling antbirds to playback of solos and duets, as quantified by six continuous variables

Response variable	Male solo	Female solo	Duet	$F_{2,34}$	p	MF	MD	FD
Male ($n = 18$)								
Approach latency	17.6 ± 12.5 (2–50)	49.7 ± 35.4 (10–120)	108 ± 183 (10–601)	12.7	<.0001	.0001	.002	1
Closest distance	2.8 ± 3.4 (0–10)	5.1 ± 2.5 (1–10)	6.7 ± 5.5 (0–20)	11.3	<.0001	.005	.007	1
Maximum height	3.9 ± 1.3 (3–7)	2.7 ± 1.4 (1–7)	3.7 ± 1.4 (2–9)	8.09	.001	.007	.593	.043
Time <5 m	112 ± 98 (0–330)	104 ± 94 (0–330)	117 ± 154 (0–601)	1.2	.549	—	—	—
Song latency	148 ± 82 (40–354)	164 ± 204 (30–601)	160 ± 140 (20–540)	0.62	.546	—	—	—
PC1	−0.99 ± 0.84 (−2.15 to 0.14)	0.12 ± 0.61 (−1.01 to 1.02)	−0.03 ± 0.76 (−1.55 to 1.47)	14.7	<.0001	.0001	.003	1
				$F_{2,26}$	p			
Female ($n = 14$)								
Approach latency	270 ± 265 (3–601)	34.1 ± 37.6 (5–120)	138 ± 200 (10–601)	9.53	.001	.009	.256	.023
Closest distance	11.1 ± 7.6 (1–25)	3.9 ± 2.6 (1–10)	7.6 ± 5.6 (3–20)	5.59	.01	.024	NS	.118
Maximum height	1.9 ± 1.0 (1–4)	3.9 ± 1.3 (2–7)	3.1 ± 1.6 (1–7)	11.3	<.0001	.002	.044	.216
Time <5 m	30 ± 80 (0–300)	118 ± 69 (0–180)	76 ± 102 (0–601)	7.9	.022	<.05	NS	<.1
Song latency	340 ± 220 (70–601)	168 ± 190 (35–601)	307 ± 220 (81–601)	4.49	.021	.019	1	.1
PC1	1.17 ± 1.04 (−0.46 to 2.47)	−0.45 ± 0.55 (−1.08 to 0.94)	0.44 ± 0.82 (−0.61 to 1.66)	12	<.0001	.002	.17	.015

Values are mean ± SD (range). Time variables are given in seconds and distance and height variables in meters. Statistics derives from repeated-measure GLMs, except for variable "time <5 m" for which Friedman tests were used. Significant probabilities after Bonferroni corrections are denoted in boldface ($p\alpha < .02$).

[a] Post hoc multiple comparison tests examining pairwise differences: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet).
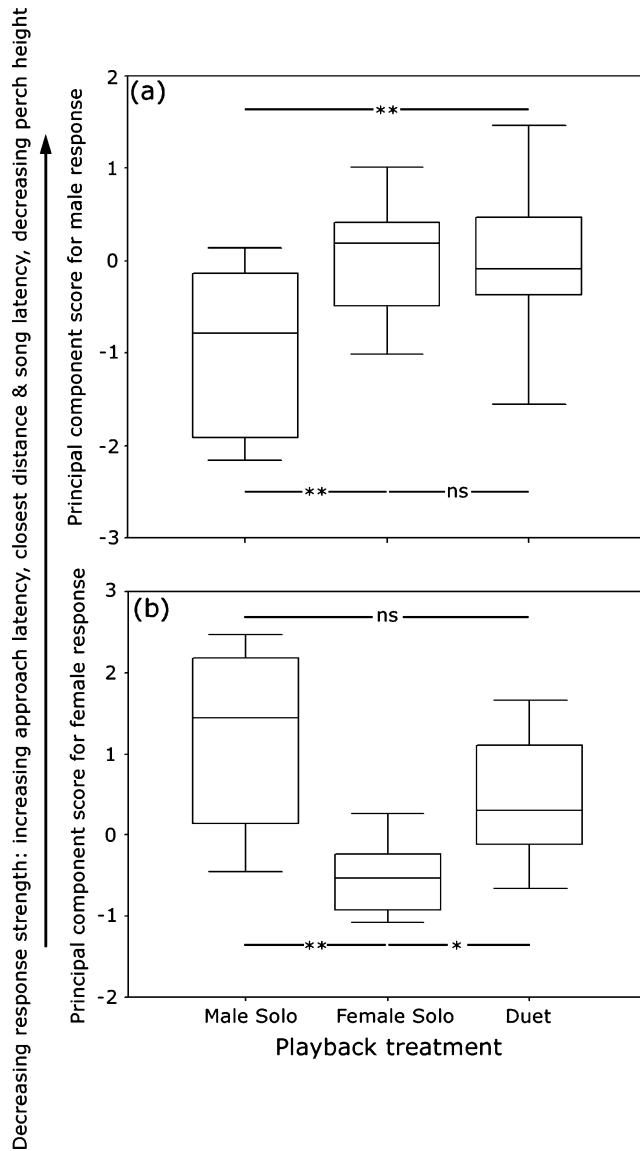
Figure 3
Box plots showing the overall strength of (a) male and (b) female responses to different playback treatments as described by the first principal component (PC1). Boxes indicate the 25th and 75th percentiles, the line in the box marks the median, and the whiskers denote 10th and 90th percentiles. Extreme values are also indicated. Asterisks denote the significance of post hoc multiple comparison tests between pairs of treatments (**$p < .01$, ***$p < .0001$).

For the experiments, we first describe the response of pair members to different playback treatments by calculating mean values for the continuous variables (1)–(5). When there was no approach and/or no vocal response, latency to approach and latency to first loudsong was scored as 601 s. Because the response variables were correlated, we performed a PCA to produce a composite measure of response strength. This generated one PC (PC1) explaining 53.9% of the variance in the response variables (eigenvalue = 2.16). PC1 was strongly correlated with approach latency (factor loading = 0.855), closest distance (0.826), maximum height (−0.738), and song latency (0.446). Thus, high values for PC1 indicated a weak response to playback. Linear regression was used to determine if date or time of day had significant effects on

PC1. We compared response variables and PC scores for each individual and for each sex using repeated-measures general linear models (GLMs) with playback treatment as the between-subject variable. To examine whether there was a difference between the sexes in the overall strength of response to playback, the male and female scores for PC1 were pooled and sex was defined as the between-subject factor. All response variables apart from one (time <5 min) met normality and equality of variance assumptions after transformation and could be used in the PCA and GLM. Each series of loudsongs and/or duets recorded after playback generated a mean value for female response time but one absolute value for proportion of male loudsongs responded to by females. Because females often did not sing after male solo playback and because some pairs did not sing after certain treatments, matched data were not available on the effects of playback on the latter two variables. They were therefore compared using Kruskal-Wallis tests. Friedman, Cochran Q tests, and repeated-measures GLMs were followed by post hoc multiple comparison tests to examine differences between pairs of treatment on behavior. The determination of significance for these tests was based on an alpha level of .02 (Bonferroni corrected p value for three comparisons). Experiment-wide error rates were adjusted with sequential Bonferroni tests (Rice, 1989). Exact p values are given where $n < 15$; otherwise asymptotic p values are given. All p values are two tailed and corrected for ties where appropriate. All statistical tests were carried out using SPSS version 11.01 (SPSS, 1999).

RESULTS

Loudsong and duet structure

Analyzing a total of 278 loudsongs from 22 different males (12.6 ± 5.4 loudsongs per male) and 124 loudsongs from 16 different females (7.8 ± 3.5 loudsongs per female), we found that male and female loudsongs were individually distinct and sex specific. That is, for all loudsong characteristics measured, variation between individuals exceeded that within individuals in both males (one-way ANOVA: $F_{21,256} > 3.98$, $p < .0001$) and females ($F_{15,102} > 4.81$, $p < .0001$). Similarly, for all loudsong characteristics, except duration, between-sex variation exceeded within-sex variation (duration: $F_{1,401} = 1.35$, $p = .247$; all other characters: $F_{1,401} > 12.5$, $p < .0001$).

A total of 114 duets were recorded from 16 pairs; all were initiated by males. Females rarely produced loudsongs in isolation from their partners: only eight (6% of the total recorded) did not immediately follow male loudsongs. The time taken for a female to respond to her partner's loudsong varied from 0.45 to 1.77 s (mean ± SD = 0.95 ± 0.30 s, $n = 114$), and female response time predicted variation in male loudsong duration (linear regression: $F_{1,112} = 41.2$, $r^2 = .27$, $p < .0001$) and note number ($F_{1,112} = 234$, $r^2 = .68$, $p < .0001$). In other words, the more rapidly a female responded to her partner's loudsong, the fewer notes he sang. This suggests that males stop singing when their partners start, an idea corroborated by visual inspection of audiospectrograms. These showed that when females did not respond to their partner's loudsong (e.g., Figures 1a–c) or when they were slow to do so (e.g., Figure 2a), males usually produced a series of terminal raspy notes that are given at a slower pace, lower pitch, and encompass a broader range of frequencies than the notes in the rest of the loudsong. However, when they responded rapidly, fewer terminal raspy notes, if any, were given (e.g., Figure 2b). Perhaps not surprisingly, therefore, we found that the overall structure of male loudsongs differed

Table 4

Effects of playback treatment on the structure of the loudsongs of male warbling antbirds

Acoustic measure	Playback treatment			Friedman tests		Post hoc tests		
	Male solo	Female solo	Duet	χ^2_2	p	MF	MD	FD
Total number of notes	11.6 ± 1.8	10.7 ± 1.9	12.3 ± 2.1	8.4	**.008**	NS	NS	**
Number of terminal notes	3.5 ± 1.0	2.6 ± 1.3	3.9 ± 1.2	8.4	**.008**	*	NS	**
Loudsong duration	1.34 ± 0.14	1.30 ± 0.12	1.4 ± 0.2	0.4	.954	—	—	—
Overall pace of loudsong	8.7 ± 1.2	8.1 ± 1.0	8.9 ± 1.3	7.7	**.019**	NS	NS	**
Pace of middle phrase	10.2 ± 2.2	10.6 ± 2.1	11.8 ± 3.5	1.6	.522	—	—	—
Duration of first note	0.14 ± 0.01	0.14 ± 0.02	0.14 ± 0.02	6.4	**.039**	NS	NS	NS
Duration of first interval	0.23 ± 0.02	0.24 ± 0.01	0.24 ± 0.02	1.6	.522	—	—	—
Bandwidth of first note	0.56 ± 0.03	0.56 ± 0.08	0.63 ± 0.13	1.3	.549	—	—	—
Bandwidth of middle phrase	0.35 ± 0.09	0.27 ± 0.04	0.40 ± 0.15	5.2	.074	—	—	—
Maximum frequency	3.24 ± 0.14	3.15 ± 0.15	3.11 ± 0.19	0.4	.819	—	—	—
Minimum frequency	2.80 ± 0.26	2.86 ± 0.18	2.66 ± 0.22	4.8	.124	—	—	—
Bandwidth	0.38 ± 0.12	0.33 ±0.10	0.45 ± 0.13	4.8	.124	—	—	—
PC1	−0.08 ± 0.38	−0.87 ± 0.49	0.31 ± 0.47	8.4	**.008**	NS	NS	*
PC2	−0.17 ± 0.96	−0.39 ± 0.95	−0.22 ± 1.17	2.8	.367	—	—	—
PC3	−0.07 ± 0.29	−0.05 ± 0.85	0.45 ± 1.51	1.6	.522	—	—	—

Time variables are given in seconds and frequency variables in kilohertz ($n = 6$ males). Significant probabilities are denoted in boldface. Post hoc pairwise tests with Bonferroni adjustments ($p\alpha < .02$) showing effects of treatments on male loudsong structure: MF (male versus female solo), MD (male solo versus duet), and FD (female solo versus duet). NS, nonsignificant.

$*p < .02, **p < .01$.

significantly between solos and duets: compared to loudsongs given as solos, those given as duets were shorter, comprised fewer notes uttered at a slower pace, had a higher minimum frequency, and encompassed a narrower bandwidth (Table 1). Interestingly, however, the acoustic properties of the introductory note and main phrase of male loudsongs did not differ between solos and duets.

Effects of playback on the behavior of males and females

Males responded by singing and/or approaching the loudspeaker in 96% (52/54) of playbacks and females in 72% (39/54; Table 2). Both sexes were more likely to approach and perform rapid flights around the loudspeaker after playback of same-sex solos than opposite-sex solos (all p values < .01; Table 2). Females (but not males) were also more likely to initiate a vocal response after same-sex than opposite-sex solos ($p < .02$) and were more likely to approach same-sex solos than duets ($p < .01$). In addition, males were more likely than females to be the first to vocalize, approach and fly around the loudspeaker aggressively in response to male solos (all p values <.001), and be the first to vocalize in response to duets ($p < .01$). Finally, although males and females were equally likely to be the first to vocalize after female solos, females were more likely than males to approach ($p < .01$; Table 2).

There was also strong significant variation across playback treatments in three out of the five response variables for males and all five for females and in the principal component scores (PC1) for both sexes (Table 3). Males responded more strongly, approaching more quickly and closely, to male solos than to either female solos ($p < .0001$) or duets ($p = .003$; Figure 3a) and also sang from a more elevated perch after male solos than after female solos ($p = .007$; Table 3). Females, on the other hand, responded much more strongly to female solos than to either male solos ($p = .002$) or duets ($p = .015$; Figure 3b), approaching more rapidly and using a higher song perch after female solos than after male solos ($p < .01$), and approaching more rapidly after female solos

than after duets ($p = .023$; Table 3). Neither sex varied their response between opposite-sex solos and duets. Interestingly, there was a strong effect of sex on PC1 (repeated-measures GLM: $F_{1,30} = 17.3$, $p < .0001$), indicating that, overall, males responded to playback more strongly than females. Note that there were no significant effects of time of day or date on response to playback as measured by PC1 for males (linear regression: time of day: $r^2 = .041$, $p = .140$; date: $r^2 = .001$, $p = .799$) or females (time of day: $r^2 = .001$, $p = .868$; date: $r^2 = .021$, $p = .362$).

In summary, we found strong sex-specific effects of playback, with males and females responding much more strongly to same-sex solos than to opposite-sex solos or duets.

Effects of playback on the structure of loudsongs and duets

There was significant variation across playback treatment in the acoustic structure of male loudsongs as described by separate measure and principal component scores (Table 4). Compared to loudsongs given after playback of duets, those given after female solos consisted of fewer notes (both total number of notes and number of terminal raspy notes) and were uttered at a slower pace (all p values <.01; Table 4). In addition, loudsongs given after female solos contained fewer notes than those given after male solos ($p < .02$). Conversely, there were no effects of treatment on the structure of female loudsongs (p values ranged from .575 to .938).

When analyzing the effects of playback on duetting behavior, we found strong significant variation between treatments in the proportion of male loudsongs answered by females (Kruskal-Wallis test: $\chi^2_2 = 18.4$, $p < .0001$, $n_{1,3} = 11$, $n_2 = 13$) as well as in the speed with which they responded ($\chi^2_2 = 10.9$, $p = .004$). Females answered a higher proportion of their partner's loudsongs after female solos than either male solos ($p < .0001$) or duets ($p < .02$; Figure 4a) and responded more promptly after female solos than male solos ($p < .001$; Figure 4b). Finally, although females answered a higher proportion of their partner's loudsong after duets
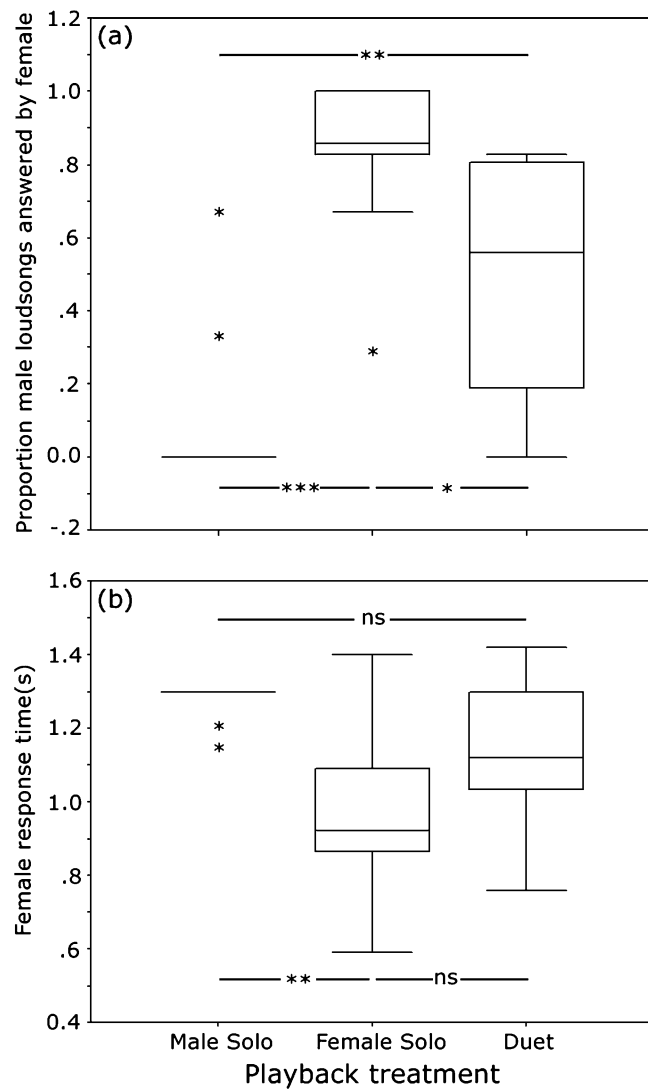
Figure 4
Box plots showing variation between the three playback treatments in (a) the proportion of male loudsongs answered by females and (b) the speed of female responses to partner loudsongs. See Figure 3 for box plot details. Asterisks denote the significance of post hoc multiple comparison tests between pairs of treatments (*$p < .02$, **$p < .001$, ***$p < .0001$).

than male solos ($p < .02$), the speed with which they responded did not differ between these two treatments.

DISCUSSION

Several of the key predictions of the mate defense hypothesis were met in this study, including two that distinguish mate defense from joint territory defense (Table 5). Our results thereby provide compelling support for the idea that duets in warbling antbirds arise through conflict between the sexes, with females responding to male loudsongs to prevent themselves from being usurped from the partnership.

First we showed that, in common with many other duetting species (Hall, 2000; Hall, 2004), male and female warbling antbirds produce sex-specific loudsongs that they combined with variable degrees of temporal precision to produce duets. The sex-specificity of loudsongs is unlikely to be a correlate

of sexual dimorphism because males and females are only dimorphic in terms of plumage and not body mass, bill size, or bill shape (Zimmer and Isler, 2003; N. Seddon, unpublished data). The implication is that loudsong differences are driven by sexual selection acting directly on the communication system itself.

We found that males initiate almost all duets, that females rarely sing in isolation from males, and that duets therefore occur as a result of females responding to male loudsongs. In this respect, the warbling antbird is similar to the Eastern whipbird *Psophodes olivaceous* (Watson, 1969) and the white-browed robin-chat *Cossypha heuglini* (Todt et al., 1981) but different from most other duetting species studied so far in which duets are initiated by females and rely on male behavior (Langmore, 1998, 2002).

Changes in the acoustic structure of the initiator's song during duet formation have been shown in subdesert mesites, Australian magpie-larks, and Canada geese *Branta canadensis* (Hall, 2001; Seddon, 2002; Whitford, 1996) and have been cited as evidence that duets depend on the behavior of both sexes (Seddon, 2002). However, in the warbling antbird several lines of evidence indicate that rather than modifying their loudsongs in a predictable fashion, in general males simply stop singing when females start. First, there was a strong positive relationship between the time taken for a female to respond to her partner's loudsong and the number of notes it contained, such that by responding promptly to her partner's loudsong a female effectively lowered its information content. Second, males produced a series of slow-paced, low-pitched terminal raspy notes when singing alone, which they omitted or reduced in number when singing in concert with a female. Third, although the overall structure of male loudsongs differed between solos and duets, the differences could be largely explained by a reduction in the number of terminal raspy notes. And fourth, there were no significant differences between solos and duets in the acoustic properties of the introductory note and main phrase of the loudsong, which refutes the idea that females respond to acoustic differences in male loudsong structure. Together these findings suggest that, overall, (1) duet formation mainly relies on female behavior, and (2) females may be able to control the extent of their partner's vocal signal.

The highly sex-specific response to playback indicates that solos in both sexes function in intrasexual territorial aggression. However, solos may also attract unpaired birds of the opposite sex. Indeed, recent work in a different subspecies of warbling antbird (*H. c. peruviana*) showed that male solos do attract unpaired females (Seddon N, unpublished data), and the same is likely to be true of *H. c. spixii*. Consistent with this was our finding, albeit anecdotal, that playback of unfamiliar male solos to two different *H. c. spixii* females 1–2 h after their mates had been temporarily removed, resulted in them approaching slowly, duetting with the playback treatment and giving a call usually used between pair members.

Sex-specific responses to playback have been found in several other duetting species (reviewed in Hall, 2004) and have been cited as evidence for duets being the by-product of independent territory defense (Morton, 1996; Morton and Derrickson, 1996). However, while this is may be true of male solos in this species, it does not explain why paired females respond to their partner's loudsongs. The alternative explanation, therefore, is that females respond to deter their partner from pairing with a rival and to signal the presence of a defended male on territory (Hall, 2000).

The loud and locatable nature of warbling antbird duets and the observations that they are used in interactions with neighbors and are readily incited by playback, all suggest that

Table 5

Predictions of female mate defense hypothesis of duet function and whether they are met in the warbling antbird

Variable	Prediction	Prediction met in present study?
Duet structure	Comprise sex-specific songs	Yes
	Initiated by males (i.e., duets depends on behavior of female)	Yes
	Structure of male but not female song changes in duets	Yes
	Fast responses by females reduces extent of male song	Yes
Response to solos	Attract unpaired birds of the same sex	?
	Elicit strong response from paired birds of same sex	Yes
Response to duets	Repel unpaired birds of either sex[a]	?
	Elicit weak response of paired birds of either sex[a]	Yes
	Females respond to more of their partner's songs and do	
Effect of playback on duet structure	so more promptly after female solos than males solos or duets[a]	Yes

[a] Predictions that distinguish mate defense from territory defense.

they function in cooperative territory defense. However, an important prediction of the mate defense hypothesis, and one that clearly distinguishes it from territory defense, is that duets repel unpaired birds. Although the scarcity of unpaired birds in our population meant that it was not possible to test this directly, we nonetheless found support for a related prediction, namely that duets elicit much weaker responses from paired birds than same-sex solos. Indeed, we found that, although not uniformly the case, males and females appeared to respond to duets with less vigor than they did to same-sex solos. As highlighted previously, there are two possible alternative interpretations of such a finding (Seddon et al., 2002). One is that by signaling the presence of a pair of intruders, a duet is more intimidating than a solo and therefore elicits a more cautious response. However, this is refuted by our finding that, overall, paired birds responded to opposite-sex solos and duets with equal strength. The second interpretation, therefore, is that predicted by the mate defense hypothesis, that is, duets represent less threatening signals than solos. The logic is that if a duet advertises the intrusion of a mated pair then the threat is to the pair's resources and is thus a territorial issue deserving a unified response, rather than a more direct and insidious threat to the partnership. Our results are consistent with this latter scenario.

Also in support of the idea that duets are a form of mate defense was the finding that, overall, females responded to more of their partner's loudsongs and usually did so more promptly after playback of female solo than male solos or duets. Moreover, in responding rapidly, a female appeared to reduce the extent of the male's signal: male loudsongs comprised fewer terminal notes after playback of female solos than after male solos or duets. In other words, in response to the simulated presence of a same-sex rival on territory, females may be able to reduce the amount of signal produced by their mate by responding rapidly to his loudsongs. It could be argued that rapid female responses are simply the product of strong intrasexual territorial aggression. However, this does not explain why a female always waits until her partner sings before she starts to do so herself. The most parsimonious explanation is acoustic mate defense.

Apart from mate defense and territory defense, there are two other important hypotheses regarding the primary function of avian duets: one is that they prevent a partner from being usurped, and the second is that they signal commitment (Hall, 2004). We did not explicitly test these predictions because anecdotal observations suggested that they were not relevant to the warbling antbird. Duets are unlikely to prevent

a partner from being usurped as this predicts that solos of the opposite sex should increase the likelihood of duetting with a partner (Appleby et al., 1999; Hall, 2000; Mulder et al., 2003), yet in response to male solos, female antbirds rarely sang at all. Similarly, although duetting in some species might discourage desertion because it represents time-consuming, pair-specific investment and thereby signals commitment (Wickler, 1980), this is unlikely to be true in the warbling antbird whose duets are structurally very simple and presumably unlearned, given that song-learning is not thought to occur in suboscines (Kroodsma, 1996). Moreover, playback experiments in conjunction with temporary removals have shown that, in common with other avian duetters (e.g., tropical boubou; Grafe and Bitz, 2004), females readily perform duets with new and artificial partners (Seddon N, unpublished data); time-consuming investment is clearly not required.

Thus although duets in the warbling antbird, as in other duetting species, may serve a variety of proximate or secondary functions (e.g., maintenance of contact and synchronization of reproductive physiology; see Hall, 2004), this study indicates that their ultimate function is the acoustic defense of males by females against same-sex rivals. In other words, it seems that duet evolution in the warbling antbird has been driven by conflict between the sexes over same-sex rivals, rather than cooperation over territory defense, and the same is probably true of the numerous other antbird species whose duets result from female behavior. Such a conclusion might seem surprising given the existence of long-term pair bonds and permanent territoriality in these birds (Zimmer and Isler, 2003). However, although it is widely assumed that conflict between the sexes is low in most tropical passerines (Morton, 1996; Stutchbury and Morton, 2001), the fact that the warbling antbird has sexually dimorphic plumage and song invokes the existence of strong sexual selection at least in the species' recent evolutionary history, if not in the current mating system. Further work is therefore needed to quantify the extent of conflict between the sexes (e.g., levels of extrapair paternity) in this and other duetting suboscines and relate it to patterns of duetting behavior.

In conclusion, our study provides the first strong support for the idea that avian duets are used in acoustic mate defense, with females responding to their partner's songs to advertise the mated status of the pair and prevent her from being usurped. Further, it indicates that by responding promptly to their partner's solos, females may be able to control the extent of their partner's vocal signal, an intriguing possibility that warrants further study.

APPENDIX

Factor loadings on the first three principal components for the nine acoustic measurements taken from the loudsongs of male warbling antbirds

	Factor loadings		
	PC1	PC2	PC3
% of variance	38.7	25.1	15.8
Eigenvalue	3.10	2.01	1.26
Factor loadings			
Total number of notes	**0.915**	−0.344	0.141
Number of terminal raspy notes	**0.885**	−0.331	−0.202
Loudsong duration	**0.451**	−0.192	**0.692**
Overall pace	**0.841**	−0.286	−0.343
Pace of middle phrase	—	—	—
Duration of first note	0.060	0.031	**0.766**
Duration of first interval	—	—	—
Bandwidth of first note	0.206	**0.669**	0.073
Bandwidth of middle phrase	**0.499**	**0.774**	−0.101
Maximum frequency of loudsong	—	—	—
Minimum frequency of loudsong	—	—	—
Bandwidth of loudsong	**0.521**	**0.785**	0.029

Loadings $r > |.04|$ are shown in boldface. Emdashes (—) are given for variables that could not be included in the PCA because they violated parametric assumptions.

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