



Aggressive responses to playback of solos and duets in a Neotropical antbird

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ARTICLE INFO

Article history:

Received 17 February 2011
 Initial acceptance 21 April 2011
 Final acceptance 14 June 2011
 Available online 23 July 2011
 MS. number: A11-00146R

Keywords:

antbird
 barred antshrike
 conflict
 cooperation
 duet
 playback
 suboscine songbird
 territory defence
Thamnophilus doliatus

Duetting behaviour is a unique form of animal communication that occurs in many diverse taxa in the animal kingdom. Hypotheses for the function of duets can be grouped into two broad categories to explain why individuals coordinate with their partner's songs to create duets: (1) duets are cooperative displays where pair members have a shared goal, such as joint resource defence, and (2) duets are conflicting displays where pair members have different goals, such as guarding against divorce or extrapair copulations. To distinguish between cooperative versus conflicting functions of vocal duets, we conducted a playback experiment to 40 breeding pairs of barred antshrikes, *Thamnophilus doliatus*. We broadcast five playback treatments to territorial pairs of birds: solos of males and females, duets created by males responding to female songs and by females responding to male songs, and a heterospecific control. We categorized subjects' behaviour in terms of vocal and physical responses. Male vocal and physical responses were significantly higher towards conspecific stimuli than towards heterospecific stimuli. Males tended to show more vocal responsiveness towards duet stimuli, although this tendency was not significant. We observed a similar pattern for female vocal responses. However, for physical responses, females showed significantly more intense responses towards female solo stimuli than towards any other conspecific treatment, suggesting that female antshrikes perceive rival females as an especially intense threat. Our results provide some support for a joint resource defence function for duetting in this species, while the high intrasexual aggression observed between females may indicate a form of mate guarding.

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Duetting behaviour is a taxonomically widespread phenomenon that occurs when mated pairs combine their songs in a coordinated acoustic display (Farabaugh 1982; Tobias et al. 1998; Geissmann 2002; Bailey 2003; Burton & Nietsch 2010). Most duetting animals are found in tropical regions (Thorpe 1972; Geissmann 2002); female song, a critical prerequisite for duet song, is rare in animals living in the north temperate zone but more common in the tropics and south temperate ecosystems (Langmore 1998). Animal behaviourists have explored the form and function of vocal duets through both observational and experimental studies (reviewed in Hall 2009; Douglas & Mennill 2010), and have generated more than a dozen hypotheses to explain why pairs of animals coordinate their songs in vocal duets rather than sing alone (reviewed in Hall 2004).

Hypotheses for duet function fall into two broad categories based on whether duets are understood to arise through cooperation or conflict between the sexes. Cooperation-based hypotheses suggest males and females coordinate their songs to achieve

mutual benefits, such as joint territory or resource defence against rival animals (Hall 2004). Conflict-based hypotheses suggest that males and females have separate agendas for contributing songs to duets, such as paternity guarding or mate guarding (Hall 2004). To date, experimental studies have shown support for both cooperation- and conflict-based hypotheses. A few studies have even shown evidence for both cooperative and conflictive functions to occur within a single species (e.g. Grafe & Bitz 2004; Mennill & Vehrencamp 2008), demonstrating that these categories of hypotheses for duet function are not mutually exclusive. Cooperative hypotheses for duetting, particularly the joint resource hypothesis, are the most widely supported to date (primates: Méndez-Cárdenas & Zimmerman 2009; birds: Hall 2009). Research on several bird species, however, has also revealed evidence for a mate-guarding function for duetting (e.g. warbling antbirds, *Hypocnemis cantator*: Seddon & Tobias 2006; eastern whipbirds, *Psophodes olivaceus*: Rogers et al. 2007).

To investigate duet function, many animal behaviourists have used experimental designs involving acoustic playback (e.g. Mennill 2006; Molles & Waas 2006; Illes & Yunes-Jimenez 2009; Odom & Mennill 2010). Playback experiments are versatile tools that allow behaviourists to broadcast realistic stimuli to test specific predictions of the hypotheses for duet function (reviewed

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in Douglas & Mennill 2010). By assessing birds' responses to different stimuli, we can assess how each individual in a mated pair perceives each duet component. Heightened aggressive responses towards playback of duets may highlight the importance of duets in defending resources, whereas heightened responses to same-sex songs may reveal intrasexual aggression.

The majority of acoustic playback experiments have been conducted with one group of birds, the oscine passerines (Douglas & Mennill 2010), a group of birds that are understood to learn their songs (Catchpole & Slater 2008). More research across diverse taxa is needed before we can understand whether the same patterns that hold true for oscine songbirds hold true more generally. One highly biodiverse group of tropical, duetting animals are the suboscine songbirds, a group of animals whose songs are understood to be inherited directly from parent to offspring without vocal learning (Kroodsma & Konishi 1991). The suboscines are concentrated in the Neotropics and contain many duetting species, yet the form and function of vocal duets have only recently begun to be explored in this group. Two playback studies testing duet function have been conducted on suboscine songbirds to date, with mixed results. A study on 18 pairs of warbling antbirds provided support for the mate-guarding hypothesis, in that birds responded more aggressively to same-sex solos than towards duets (Seddon & Tobias 2006). Conversely, a study on 15 pairs of white-bellied antbirds, *Myrmeciza longipes*, found no evidence that duets function in mate guarding or joint resource defence; males and females responded with low levels of aggression towards all conspecific stimuli regardless of the type (solos or duets) or sex of the singer (Fedy & Stutchbury 2005). Unlike playback experiments on oscine songbirds, neither of these antbird studies found support for the joint resource defence hypothesis for duet function. Considering the diversity of duetting suboscine species in the tropics, suboscine duet function is an important and largely unexplored avenue for understanding animal communication.

In the current study, we used playback to investigate the function of vocal duets in territorial pairs of barred antshrikes, *Thamnophilus doliatus*, a Neotropical suboscine songbird. Barred antshrikes are nonmigratory, territorial songbirds with a widespread distribution throughout much of Central America and the northern half of South America (Skutch 1969). They consume a variety of fruits, lizards, seeds and a large variety of invertebrates, and opportunistically forage on ant swarms when ant swarms move through their territories (Koloff & Mennill 2011). Male and female barred antshrikes both produce a single song type that may be sung as a solo (approximately 80% of songs are solos), or temporally overlapped with a mate to create a duet (approximately 20% of songs are duets; J. Koloff & D. J. Mennill, unpublished data). Most duets (84%) are created by females when they sing in response to male song; the remainder (16%) are created by males singing in response to female song (J. Koloff & D. J. Mennill, unpublished data). Barred antshrikes tend to duet in close proximity, typically with less than 5 m between the duetting animals. Their territories are small and densely packed (Koloff & Mennill 2011). Consequently, pairs are often within communication range of one or more duetting neighbours. Barred antshrikes are highly territorial and respond aggressively to conspecifics; both males and females increase their vocal output and closely approach rival conspecific animals during territorial interactions in natural settings, producing both solos and duets.

Using acoustic playback to simulate the voices of rival birds, we assessed the vocal and physical responses of pairs of barred antshrikes to simulated territorial intrusions. If duets function as a cooperative behaviour in this species, we predicted that (1) duet stimuli would evoke more intense responses than solo stimuli, and (2) both sexes would display equivalent intensities of response

regardless of the sex of the stimulus. In this case, duet playback is understood to simulate a rival territorial pair prospecting for a territory, and is therefore a threatening stimulus for both of the playback subjects. Conversely, if duets are associated with intersexual conflict, we predicted that (1) solo stimuli would evoke more intense responses than duet stimuli, and (2) birds would display more intense responses towards same-sex solo stimuli than towards opposite-sex solo stimuli or duet stimuli. In this case, solo song playback is understood to simulate an individual prospecting for a new partner or an extrapair mating opportunity, and is therefore a more threatening stimulus to a same-sex playback subject (Douglas & Mennill 2010).

METHODS

General Field Methods

We studied a population of 40 pairs of barred antshrikes in the Neotropical dry forest in Sector Santa Rosa of the Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W) from 1 May to 16 July 2009. These birds live in socially monogamous pairs that hold year-round territories (Koloff & Mennill 2011). Males and females are highly dimorphic and easy to distinguish in the field; males have zebra-striped black and white plumage whereas females have solid cinnamon coloured plumage. We succeeded in capturing birds in mist-nets in 15 of our 40 study territories; in eight territories, we banded both the male and female with unique colour band combinations, and in seven territories, we banded the male only. We carefully monitored the colour-banded animals in these 15 territories throughout the field season and reliably found all animals in the same small areas. Therefore, we feel confident that the 25 unbanded pairs in this study were also site-faithful pairs of animals and represent unique pairs.

Playback Stimuli

Single-channel stimuli for playback were created using Audition software (Adobe, San Jose, CA, U.S.A.) using recordings of birds of known sex collected from our population between 1 May and 20 May 2009. We selected songs from recordings that had a high signal-to-noise ratio and minimal overlap from heterospecific birds. Recordings were filtered to remove background noise below 200 Hz. We created stimuli for five treatments: (1) male solos, (2) female solos, (3) male-created duets (a duet where a male song overlaps a female song), (4) female-created duets (a duet where a female song overlaps a male song), and (5) a control stimulus. As a control stimulus, we selected a heterospecific sound from an animal commonly found at our study site; the male–male duet song of long-tailed manakins, *Chiroxiphia linearis*. We considered this an appropriate control stimulus because it allowed us to evaluate the responses of antshrikes to any sound broadcast from a loudspeaker placed within their territory, while it also allowed us to evaluate whether antshrikes were responding to playback of conspecific duets and not any duet per se. We created eight unique stimulus sets from recordings at eight locations to minimize the effect of pseudoreplication. We cycled through the eight stimulus sets, so that we broadcast each stimulus set either four or five times over the course of the 40 trials. We normalized all stimuli to a standard amplitude of –1 dB. We created duet stimuli by overlapping male and female solos; prior analyses confirmed that birds use the same songs when singing solos or duets (J. Koloff & D. J. Mennill, unpublished data). The average delay from the first song to the second song for all duet stimuli was 1.88 s, and we varied the degree of overlap around this mean by up to 0.12 s to simulate natural variation in duetting behaviour (these time delays are

typical of duets in this species; J. Koloff & D. J. Mennill, unpublished data). Each stimulus was 2 min long, with the same solo or duet song repeated once every 10 s. Stimuli were saved as 16-bit WAV files with a sampling rate of 44.1 kHz.

Playback Technique

We conducted playback trials between 21 May and 9 July 2009, corresponding to the early part of the rainy season at this site (Topp & Mennill 2008), a time of year when barred antshrikes engage in their first nesting attempt of the year (Koloff & Mennill 2011). We observed pairs during the dawn chorus prior to playback treatments to estimate their territory boundaries and to inform loudspeaker placement. We mounted loudspeakers 1 m off the ground, placing the speaker in an area where we had observed the focal pair during the dawn chorus. Barred antshrike territories are small (mean \pm SE = 0.36 ± 0.08 ha; Koloff & Mennill 2011) and we chose the specific location for playback to maximize the distance from neighbours' territories, attempting to minimize the influence of neighbours on the focal birds. We conducted all playback trials between 0700 and 1100 hours, a time of day when barred antshrikes have finished their dawn chorus singing performance, but bouts of solo and duet song are relatively common (J. Koloff & D. J. Mennill, unpublished data).

Sounds were broadcast from a loudspeaker (Califone VoiceSaver, model PA285AV) attached to a 24 m cable and a portable digital audio player (Apple iPod). Previous field observations (J. Koloff & D. J. Mennill, unpublished data) confirmed that barred antshrikes duet in very close proximity to each other, and therefore, we considered a single-speaker design appropriate for playback in this species (Douglas & Mennill 2010). The loudspeaker was set to a volume that corresponded to natural levels based on comparison to singing birds in the field, and this volume was held constant across all 40 trials. We used flagging tape to mark horizontal distances of 1 m, 2 m and 5 m and vertical distances of 1 m and 2 m from the loudspeaker for reference during the trials. One observer sat 24 m away and dictated all observed behaviours of each bird into a microphone (Audiotechnica AT815b) mounted to a tripod and attached to a digital recorder (Marantz PMD-660). The microphone set-up allowed us to record the vocalizations of the territorial birds and the observer's description of their behaviours simultaneously.

Each of the five treatments consisted of 5 min of observation, including 2 min during the broadcast of the playback stimulus and 3 min during the silent period after the broadcast was complete. We then allowed each pair 10 min of silent recovery time before each subsequent treatment; this period was consistently enough time for birds to stop singing and leave the playback area. Each pair received all five treatments consecutively, so that each playback session lasted 75 min in total. We varied the order of presentation of the five stimuli according to a sequential block factorial design. During each trial, the observer noted the identity and sex of the singer, the distance between each bird and the loudspeaker, and any flights made over the loudspeaker. When selecting a stimulus set, we chose songs recorded from at least 700 m away from the playback site to avoid effects of familiarity (this minimum distance corresponds to approximately 10 territories; Koloff & Mennill 2011). Trials were not conducted in adjacent territories for at least 48 h.

Response Measures

To assess levels of aggression towards the playback loudspeaker, we measured both vocal and physical responses. We measured three aspects of the vocal responses for each sex (i.e. six vocal response measures per pair): (1) number of independent songs

(details below), (2) number of created duets (details below) and (3) latency to first song (in seconds). We calculated the number of independent songs as the sum of the number of solos each bird produced and the number of duets where they sang the first contribution (i.e. their partner overlapped their song and thereby created a duet). Calculations of independent songs provided an estimate of how much an individual sang independently of the duetting behaviour of its partner. We calculated the number of created duets as the number of times a bird overlapped its partner's song, resulting in a duet (if they had not done so, the partner's song would have been broadcast as a solo; Hall 2004). Together, the number of independent songs and the number of created duets summed to all of the songs produced by any playback subject.

We also measured three aspects of the physical responses for each sex (i.e. six physical response measures per pair): (1) closest approach to the loudspeaker (in metres), (2) number of passes over the loudspeaker and (3) latency to reaching within 5 m from the loudspeaker (in seconds). If a bird never came within 5 m during the treatment, we recorded a value of 300 s (5 min) for the response.

We used Syrinx-PC (J. Burt, Seattle, WA, U.S.A.) to visualize field recordings of the playback trials. We used the time and frequency cursors to annotate all songs from the birds and all comments from the field observations in order to extract the three measures of vocal response and the three measures of physical response.

Statistical Techniques

We conducted statistical analyses in JMP 8.0 (SAS Institute, Cary, NC, U.S.A.). We summarized birds' responses to playback using principal components analysis with varimax rotation, conducting a separate analysis for each sex. We report the contributions of the original measurements to the principal component scores for all measurements with factor loadings greater than 0.6 (Kline 1994). We used a principal components approach that allowed us to minimize the number of comparisons, and we present a table of the absolute values of male and female responses for reference.

For males, principal components analysis yielded two factors with eigen values greater than 1, which cumulatively explained 77.1% of the variation in male responses (Table 1). Factor 1 was influenced heavily by number of independent songs, number of male-created duets and latency to first song as well as by the latency to approach within 5 m; we refer to this factor as 'singing intensity'. Males with high singing intensity scores displayed a high frequency of independent songs and duets and a short latency to sing after the onset of playback. Male factor 2 was heavily influenced by closest approach to the loudspeaker, number of passes over the loudspeaker and latency to approach within 5 m of the loudspeaker (Table 1); we refer to this factor as 'physical intensity'. Males with high physical intensity scores approached the

Table 1

Factor loadings from principal components analysis of male and female barred antshrikes' ($N = 40$ pairs) responses to playback

Response variable	Male		Female	
	Factor 1	Factor 2	Factor 1	Factor 2
Number of independent songs	0.90	-0.14	0.83	-0.16
Number of created duets	0.62	-0.22	0.76	-0.13
Latency to first song (s)	-0.93	0.06	-0.89	0.28
Closest approach (m)	-0.36	0.86	-0.57	0.73
Number of passes over speaker	-0.09	-0.84	0.01	-0.91
Latency to approach within 5 m (s)	0.87	0.88	-0.58	0.72
Eigen value	3.18	1.44	3.72	1.00
% Variance explained	53.0	24.1	62.2	16.5

Factor loadings >0.6 are shown in bold.

loudspeaker closely, had a short latency to flight within 5 m and passed over the loudspeaker many times.

For females, principal components analysis also yielded two factors with eigen values greater than 1, with nearly identical loadings to male factors, which cumulatively explained 78.7% of the variation in female responses. We interpreted female factors in the same way as males (Table 1).

We evaluated variation in responses to playback using a linear mixed model where playback treatment type and order of playback were two independent variables, pair was included as a random effect (to account for the fact that some pairs may be more responsive than others), and the principal component response scores were the dependent variables. For analyses that revealed a significant effect of treatment, we used Tukey post hoc test of honestly significant differences to explore which treatments were significantly different. All tests were two tailed with a significance threshold of 0.05. All values are presented as means \pm SE.

Ethical Note

This research involved presentation of short acoustic stimuli that elicited aggressive responses from the territorial study animals. The level of aggression we observed was typical of naturally occurring territorial interactions between pairs and did not appear to have any lasting effects; birds returned to their normal activities within a few minutes after the conclusion of each playback treatment. This study was conducted in compliance with regulations of the Animal Care Committee of the University of Windsor and the government of Costa Rica.

RESULTS

Male and female barred antshrikes showed strong responses towards all treatments of conspecific playback (Table 2). For most treatments except for the heterospecific control, both sexes produced many vocalizations in response to playback and readily approached the loudspeaker, often passing back and forth over the loudspeaker.

Vocal Responses to Playback

Male barred antshrikes showed significant variation in singing intensity (linear mixed model: whole model: $F_{4,152} = 2.3$, $P < 0.0001$), with a significant effect of playback treatment ($F_{4,152} = 3.9$, $P = 0.005$; Fig. 1), no effect of playback order

($F_{4,152} = 0.5$, $P = 0.71$), and significant variation between individuals ($F_{39,152} = 2.3$, $P = 0.0001$). Male singing responses were strongest towards the two duet treatments, although the responses were not significantly higher than the responses towards the two solo treatments; a post hoc Tukey's test revealed significant differences between the heterospecific control and the two conspecific duet treatments, with intermediate levels for the two conspecific solo treatments (Fig. 1).

Female barred antshrikes also showed significant variation in singing intensity (whole model: $F_{4,152} = 3.2$, $P < 0.0001$), with a significant effect of playback treatment ($F_{4,152} = 13.0$, $P < 0.0001$; Fig. 1), no effect of playback order ($F_{4,152} = 1.0$, $P = 0.44$), and significant variation between individuals ($F_{39,152} = 2.4$, $P < 0.0001$). Female singing responses were strongest towards the two duet treatments and the male solo treatment, although the differences were not statistically higher than for response to the female solo treatment; a post hoc Tukey's test revealed significant differences between the heterospecific control treatment and male solos, male-created duets and female-created duets, with intermediate levels for female solos (Fig. 1).

Male vocal responses were more intense than female vocal responses for both the number of independent songs and the latency to first song; males sang more solos than females and showed shorter latencies than females for all treatments (Table 2). For all four conspecific treatments, females created more duets than males (Table 2).

Physical Responses to Playback

Male barred antshrikes showed significant variation in physical intensity (whole model: $F_{4,152} = 9.0$, $P < 0.0001$), with a significant effect of playback treatment ($F_{4,152} = 62.1$, $P < 0.0001$; Fig. 2), no effect of playback order ($F_{4,152} = 1.7$, $P = 0.16$), and significant variation between individuals ($F_{39,152} = 4.3$, $P < 0.0001$). Male physical responses were equally strong across the four conspecific treatments; a post hoc Tukey test revealed significant differences only between the heterospecific control and the four treatments (Fig. 2).

Female barred antshrikes also showed significant variation in physical intensity (whole model: $F_{4,152} = 3.2$, $P < 0.0001$), with a significant effect of playback treatment ($F_{4,152} = 28.2$, $P < 0.0001$; Fig. 2), no effect of playback order ($F_{4,152} = 1.1$, $P = 0.37$), and no significant variation between individuals ($F_{39,152} = 1.3$, $P = 0.11$). Interestingly, female physical responses to playback of female solos were much higher than their responses to all other treatments;

Table 2
Mean \pm SE responses of male and female barred antshrikes ($N = 40$ pairs) to five playback treatments

Response variable	Sex of subject	Playback treatment				
		Control*	Male solos	Female solos	Male-created duets	Female-created duets
Number of independent songs	Male	4.3 \pm 0.9	8.1 \pm 1.2	8.5 \pm 1.1	10.0 \pm 1.1	11.6 \pm 1.1
	Female	0.6 \pm 0.3	2.9 \pm 0.5	2.0 \pm 0.4	3.1 \pm 0.5	4.1 \pm 0.6
Number of created duets	Male	0.1 \pm 0	0.7 \pm 0.2	0.9 \pm 0.2	1.2 \pm 0.2	1.0 \pm 0.2
	Female	0.1 \pm 0	1.3 \pm 0.3	1.7 \pm 0.4	1.6 \pm 0.4	2.5 \pm 0.4
Latency to first song (s)	Male	174.9 \pm 21.5	138.7 \pm 19.8	131.5 \pm 18.9	115.4 \pm 17.6	108.4 \pm 17
	Female	261.2 \pm 13.4	156.5 \pm 20.2	161.7 \pm 20	125.5 \pm 19.3	129.7 \pm 18.5
Closest approach (m)	Male	17.0 \pm 1	0.8 \pm 0.5	2.6 \pm 0.9	3.5 \pm 1.1	1.7 \pm 0.7
	Female	17.8 \pm 0.9	8.7 \pm 1.3	2.6 \pm 1.2	7.7 \pm 1.3	6.2 \pm 1.3
Number of passes over speaker	Male	0.1 \pm 0.1	2.0 \pm 0.3	1.9 \pm 0.3	2.4 \pm 0.4	2.7 \pm 0.4
	Female	0.0 \pm 0	0.2 \pm 0.1	1.9 \pm 0.1	0.6 \pm 0.2	0.7 \pm 0.2
Latency to approach \leq 5 m (s)	Male	267.4 \pm 13.6	48.4 \pm 8.2	80.8 \pm 13.7	69.2 \pm 16	60.5 \pm 13.6
	Female	278.1 \pm 11.5	159.6 \pm 19.7	80.8 \pm 17.3	142.9 \pm 19.6	132.6 \pm 18.5

* Male–male duet song of long-tailed manakins, *Chiroxiphia linearis*.

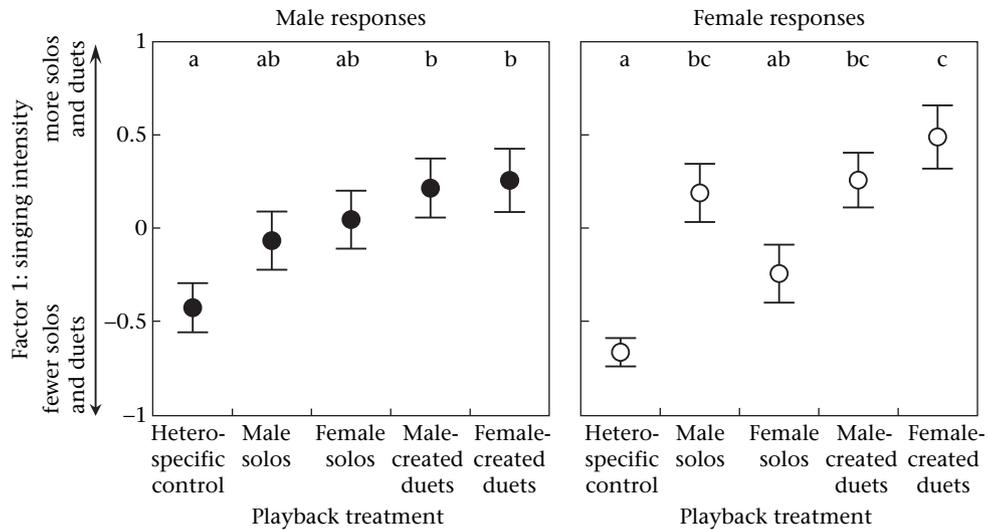


Figure 1. Variation in singing intensity responses of male (left) and female (right) barred antshrikes to five playback treatments. Singing intensity is a principal component score that reflects high output of solos and duets and short latencies to sing. Letters indicate post hoc tests of honestly significant differences, where levels not connected by the same letter were significantly different.

a post hoc Tukey test revealed significant differences between female solos and all the other treatments (Fig. 2).

Male physical responses were more intense than female physical responses for most treatments; males approached the loudspeaker more closely for all treatments except playback of female solos, they made more passes over the loudspeaker for all treatments except playback of female solos, and they showed shorter latencies of response to all treatments except female solos (Table 2). In response to playback of female solos, females showed their most intense responses, matching the intensity of male responses (Table 2).

DISCUSSION

Barred antshrikes displayed high levels of aggression towards conspecific intruders simulated through playback. Both males and females responded with elevated vocal activity, including high output of solos and duets, and close physical approaches towards

a loudspeaker broadcasting conspecific song. Male vocal and physical responses towards conspecific stimuli were greater than their responses towards heterospecific stimuli, but males showed similar intensities of response to playback of male and female solos and male- and female-created duets. Females showed more variation in their intensity of response towards conspecific playback treatments. Females displayed significantly greater aggressive physical responses towards female solos than towards other stimuli. The current study is one of very few experimental studies to evaluate the function of solo and duet song in suboscine songbirds or antbirds, and therefore, helps to expand our understanding of the function of the vocal behaviour of a biodiverse but poorly studied group of tropical animals. We show that playback of solos and duets incite territorial responses involving solos, duets and physical aggression from both members of territorial pairs.

If duets serve a cooperative function within a pair, we predicted that duet stimuli would evoke more intense responses than solo stimuli, and that birds would display equivalent intensities of

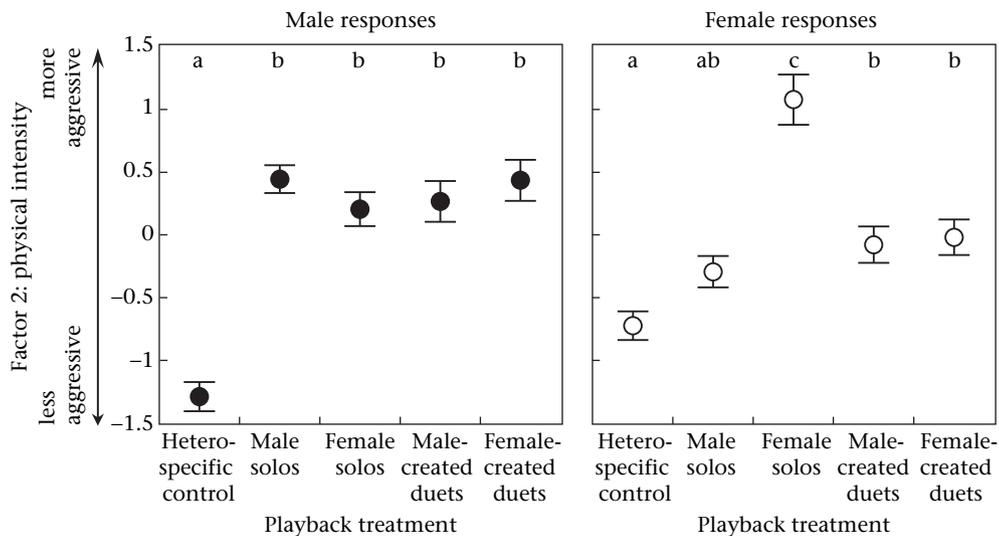


Figure 2. Variation in the physical intensity responses of male (left) and female (right) barred antshrikes to five playback treatments. Physical intensity is a principal component score that reflects rapid and close approaches to the loudspeaker with many passes over the loudspeaker. Letters indicate post hoc tests of honestly significant differences, where levels not connected by the same letter were significantly different.

response regardless of the sex of the stimuli. Although both males and females tended to display more intense vocal responses towards duet stimuli than towards solo stimuli, this tendency was not statistically significant for either sex. Male antshrikes showed similar vocal responses to male and female solo stimuli and to male-created and female-created duet stimuli, and therefore, responded with equivalent levels of intensity regardless of the sex of the stimulus presented. Female antshrikes showed more variation in their vocal responses, with low levels of singing intensity towards female solos, intermediate levels towards male solos and male-created duets, and the highest levels of singing intensity towards female-created duets. This difference was not statistically significant except in comparison to female solos, a result that we suggest may have been driven by female physical responses (see below).

The physical responses of barred antshrikes showed different patterns for male and female subjects. Males responded with equal levels of physical aggression towards all conspecific stimuli, regardless of the sex of the stimulus or the type of stimulus. These aggressive responses indicate that male subjects perceived the simulated conspecific intruders as equivalent territorial threats. Similar to our results for male physical responses, and for male and female vocal responses, other playback studies have reported similar patterns of response to playback of solos and duets. In three studies, tropical duetting birds showed equivalent intensities of response to playback of solos and duets, including two studies of wrens (rufous-and-white wren, *Thryothorus rufalbus*: Mennill & Vehrencamp 2008; rufous-naped wren, *Campylorhynchus rufinucha*: Bradley & Mennill 2009) and a study of another antbird (white-bellied antbird: Fedy & Stutchbury 2005). In all three studies, birds responded by approaching the loudspeakers and producing many solos and duets, and by producing duets at high rates in response to conspecific playback, but not at different levels following solo versus duet playback. Other studies have found contrary findings, including studies that found more intense responses to playback of duets than to playback of solos (reviewed in Hall 2009). Whether this reflects taxonomic differences between independent evolutions of vocal duetting in different taxa is an important area for further study. Although duets appear to be important during aggressive interactions with rival birds for most species that have been studied (Hall 2009; Douglas & Mennill 2010), our results show that duets of rival pairs do not consistently incite stronger responses than do solos of rivals.

If duets represent conflict between members of a pair, we predicted that solo stimuli would evoke more intense responses than duet stimuli, and that birds would display more intense responses to same-sex solo stimuli. We found support for this prediction only in the physical responses of female barred antshrikes. Females responded with significantly higher levels of physical aggression towards female solo stimuli compared to all other stimuli types presented. Although differences between remaining treatments were not significant, females tended to respond with similar levels of aggression to both male- and female-created duet stimuli, and at the lowest levels of aggression towards male solo stimuli and the heterospecific control. It has been suggested that physical approach towards a loudspeaker, and flights over a loudspeaker, are more aggressive responses than increased vocal output (Searcy & Beecher 2009); the intense female physical responses we observed here suggest that solo songs of female barred antshrikes are perceived as a more aggressive signal than lone males or intruding pairs.

For female vocal responses to the four conspecific treatments, female barred antshrikes showed their lowest singing intensity scores in response to female solos, which was not significantly lower than their responses to male solos or male-created duets, but

was significantly lower than their responses to female-created duets. We interpret these low singing intensity scores (Fig. 1) as a trade-off against the strong effect observed in female physical intensity scores (Fig. 2). The ability of an animal to respond both vocally and physically may trade off against each other; a responding animal may not be able to produce an elevated singing response while simultaneously approaching and making passes over a loudspeaker. If physical attack is the most aggressive response from a territorial animal (Searcy & Beecher 2009), then lower song output may be associated with the most aggressive responses of territorial animals.

For most of the variables we measured, we found significant variation in the intensity of response between different individuals (males: vocal and physical responses; females: vocal responses). This result is not surprising; there is often variation between the behaviour of individuals (Bell et al. 2009), and we interpret the difference between individuals as evidence that barred antshrikes vary in how intensely they respond to territorial intrusion. Interestingly, we found no significant individual variation in female physical responses; all females responded to female solo stimuli with similarly high levels of physical aggression.

Increased aggressive behaviour towards same-sex solo stimuli may be consistent with a female mate-guarding strategy. A solo female present on an antshrike's established territory probably simulates a female prospecting for a new partner, which may explain females' highly aggressive physical responses to simulated rival females. Barred antshrikes have biparental care, where both males and females play an active role in incubation and nestling provisioning (Koloff & Mennill 2011). Given that we conducted playback during the start of the birds' breeding season, this might explain the high levels of female–female aggression. Previous work on duetting birds found high levels of same-sex aggression for males and, occasionally, for females. A stereo playback study on duet function in rufous-and-white wrens (Mennill 2006) demonstrated evidence for joint resource defence as well as an additional mate-guarding function for males. Wrens displayed high levels of aggression towards both loudspeakers, but males were more aggressive towards male stimuli, while females showed no such differentiation (Mennill 2006). Similar results have been demonstrated in the duets of plain wrens, *Thryothorus modestus*, where duets evoked aggressive responses from both males and females, but both sexes responded to same-sex stimuli with elevated levels of aggression (Marshall-Ball et al. 2006). Lastly, Grafe & Bitz (2004) demonstrated experimental evidence for joint resource defence and mate guarding in a playback study on tropical boubous, *Laniarius aethiopicus*. They broadcast solo and duet stimuli and found that pairs approached all intruders together and sang in close proximity to each other, but individuals overlapped their partner's songs and created more duets when same-sex solos were broadcast, suggesting that duets may also function as an acoustic mate guard (Grafe & Bitz 2004). Taken together with the present study, these results suggest that duets may be context dependent, and reiterate that cooperative and conflict-based hypotheses for duet function are not mutually exclusive.

Sex specificity in response to intruders might be associated with territory defence if there is a skewed sex ratio, or sexual size dimorphism within the population (Hall 2009). The sex ratio in our population appears to be 50:50; we have only observed birds as pairs, not as solo individuals. Yet, antshrikes show fairly cryptic behaviour, living in dense thickets of foliage where they are hard to observe, and it is possible that there is a female bias in this population contributing to heightened levels of female–female aggression. Concerning size dimorphism, male and female barred antshrikes are similar in size (Koloff & Mennill 2011); we have no reason to believe the birds are more aggressive to same-sex

individuals as a result of attempts to size-match intruders. To further explore why female barred antshrikes display elevated physical aggressive responses towards same-sex intruders, future studies should focus on identifying the different selection pressures that are acting on males and females. Like many tropical animals (Stutchbury & Morton 2001; Macedo et al. 2008), the mating behaviour of barred antshrikes is poorly understood. It is unknown whether birds engage in extrapair matings, egg dumping, or divorce. Further research on the mating behaviour and natural history of this species will help to provide context to our interpretation of the high level of intrasexual aggression we observed in female barred antshrikes.

Acknowledgments

We thank the staff at Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica for logistical support. Our research was funded by grants from the American Museum of Natural History's Frank M. Chapman Memorial Fund Grant to J.K., and by 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 D.J.M. We thank two anonymous referees for valuable comments that improved the manuscript.

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