



## Duet song and sex roles during territory defence in a tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*

DAVID M. LOGUE & DAVID E. GAMMON

Department of Biology, Colorado State University  
and

Smithsonian Tropical Research Institute, Republic of Panama

(Received 18 February 2003; initial acceptance 11 August 2003;  
final acceptance 21 October 2003; published online 23 August 2004; MS. number: A9557)

A diverse array of bird species show a behaviour known as duet singing, in which mated pairs sing temporally coordinated songs. Several studies have shown that simulating territory intrusion with conspecific song playback evokes duet song from duetting bird species, but the adaptive significance of coordinated song during territorial defence remains unclear. The function of duetting is further obscured by our poor understanding of the roles of the sexes in territory defence among year-round territorial species. We developed a simple optimality model that predicts the conditions under which intersexual territorial defence is most likely to occur. We used male solo song and female solo song playback as well as a novel method called 'stereo duet playback' to test the predictions of the model and to explore the function of song initiation and song answering during territorial encounters. We conducted these experiments in the field on the black-bellied wren, a year-round territorial passerine. Birds of both sexes responded to all treatment types. Males initiated more songs during opposite-sex playback than during same-sex playback and both sexes were more likely to answer their mates' songs when mates were physically closer. We argue that the acoustic mate-guarding hypothesis does not adequately account for these results, and suggest that duetting during territorial encounters allows mates to identify one another, thus preventing intrapair aggression. As predicted by our model, females showed a strong same-sex bias in territory defence, whereas males approached playback of both sexes. Also in support of the model, males with dependent juveniles showed stronger intersexual territoriality than males not involved in a breeding effort.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Avian vocal duetting is especially common in species in which a mated male and female defend a shared territory throughout the year (Farabaugh 1982). Although the adaptive significance of this behaviour varies among species, sexes (Levin 1996b) and contexts (Sonnenschein & Reyer 1983), simulated territory intrusion evokes heightened levels of duet song in many species of year-round territorial birds. Pairs of robin chats, *Cossypha heuglini*, duet when presented with conspecific mounts and playback (Hultsch & Todt 1984). Female bay wrens, *Thryothorus nigricapillus*, initiate song more often and are more likely to form duets by answering their mates during conspecific

versus heterospecific playback (Levin 1996b). Magpie lark, *Grallina cyanoleuca*, pairs coordinate a higher proportion of their songs to form duets during conspecific playback versus prior to playback (Hall 2000). Similar results have been found for stripe-backed wrens, *Campylorhynchus nuchalis* (Wiley & Wiley 1977), usambiro barbets, *Trachyphonus usambiro*, slate-coloured boubous, *Laniarius funebris*, and striped kingfishers, *Halcyon chelicuti* (Wickler 1976). In all of these experiments, an elevated level of duet song during playback was associated with other measures of agonistic response (e.g. flights, approach to speaker).

It is clear that pairs duet more during simulated territorial intrusions, but what is the adaptive significance of coordinated song to individual birds? One obstacle to answering this question is our poor understanding of territory defence in year-round territorial birds (see Table 5 in Hall 2000 for a review of duetting and joint territorial

Correspondence: D. M. Logue, Department of Biology, Colorado State University, Fort Collins, CO 80523-1878, U.S.A. (email: [dlogue@lamar.colostate.edu](mailto:dlogue@lamar.colostate.edu)).

defence). Several studies have reported a strong same-sex bias in territorial defence (Greenberg & Gradwohl 1983; Freed 1987; Levin 1996b; Morton & Derrickson 1996; Hall 2000; Bard et al. 2002; Seddon et al. 2002). The evidence presented in such studies typically shows that birds respond more strongly to intrasexual versus intersexual solo song playback. All of these studies, however, also revealed that mated birds respond physically (e.g. by approaching the speaker) to opposite-sex playbacks. It has been suggested that this apparent intersexual territory defence represents intersexual protection against infanticide (Freed 1987) or a means of mate retention when unattended individuals are likely to advertise for a new mate (Morton & Derrickson 1996).

We developed a simple model that predicts the conditions under which intersexual territory defence should occur. The model assumes strict social monogamy; either an intruder is rebuffed or it replaces the same-sex territory holder. Consider the case in which a solo female intrudes upon a mated pair's territory. The paired male will have a lifetime fitness of  $V_1$  if he keeps his current mate and a fitness of  $V_2$  if the intruder becomes his mate. If the male does not attempt to drive the intruding female from his territory, there is a probability  $p$  that she will achieve residence on the territory and become his mate. We assume that if he does help to defend the territory against the intruder, he will retain his current mate. Finally, defending the territory against the intruding female imposes a cost  $C$  to the male. With these assumptions, we can generate a simple model that predicts that a mated male will optimize his fitness by defending his territory against intruding females when

$$V_1 - C > pV_2 + (1 - p)V_1$$

The left side of the inequality represents the fitness payoff to the male if he defends the territory against the intruding female. The right side of the inequality represents his average fitness payoff if he does not defend; the average payoff if the male does not defend will depend on both  $V_1$  and  $V_2$  because either female could potentially occupy the territory after the conflict. The inequality can be simplified to yield

$$V_1 - V_2 > C/p$$

This model suggests that a male should defend his territory against an intruding female given the conditions that (1) the male assesses that his fitness with the current mate would exceed his fitness with the intruder and (2) the cost of intersexual territory defence is sufficiently low. Of course, one could apply the model to a mated female during a solo male intrusion to make predictions about intersexual territorial defence by females.

For species in which one sex is larger than the other, we expect that the larger sex will pay lower costs for intersexual territoriality than the smaller sex. Therefore, all else being equal, the model predicts that in species where one sex is larger, the larger sex is more likely to practice intersexual territoriality. The model also predicts increased

intersexual territoriality when retention of the current mate stands to provide high fitness benefits. This is likely to be the case during the period of nestling and juvenile care if stepparents do not aid in raising the young (as in female black-bellied wrens; D. M. Logue, unpublished data) or if they commit infanticide (as in male house wrens, *Troglodytes aedon*; Freed 1987).

The model does not address mate following during opposite-sex playback as a means of mate retention, although in some cases it may provide a simpler explanation for the observed pattern of intersexual approach to the playback speaker. In the interest of keeping the model simple, we did not consider the cost represented by an injury to the mate who has defended alone. Including such a cost would increase the conditions under which intersexual defence is less costly than the alternative. The model applies equally well to a pair of intruders, rather than a single intruder, if we bear in mind that the cost  $C$  to the focal individual is likely to be greater if the individual also must defend against a same-sex intruder. Until now, it has been impossible to address the question of intersexual territoriality during simulated pair intrusions because traditional duet playbacks broadcast both male and female duet contributions from a single speaker. We developed a method of broadcasting duet recordings from two sources to more realistically simulate a duetting pair.

We conducted song playback experiments on free-living black-bellied wrens to address the following questions. (1) How and why do these birds initiate song and answer their partners' songs to form duets during territorial intrusions? (2) Does either sex show intersexual territorial defence? Black-bellied wrens maintain all-purpose territories throughout the year. Both males and females sing repertoires of sex-specific song types, some of which they share with other individuals in the population. These songs may be sung independently or coordinated with the song of the mate to form a duet. In contrast to the congeneric bay wren (Levin 1996b), both sexes of black-bellied wrens initiate duets. Individuals typically alternate duet contributions to form duet trains (sensu Brown & Lemon 1979) that vary in length from two to 16 contributions.

Male black-bellied wrens are substantially larger than females (all  $N_s > 21$ ;  $\bar{X}_{\text{mass}}$ : 28.0 g versus 22.3 g;  $\bar{X}_{\text{tarsus}}$ : 26.7 mm versus 24.0 mm;  $\bar{X}_{\text{wing}}$ : 67.7 mm versus 63.5 mm, respectively). Unmated males regularly obtain and hold solo territories. We have no evidence that females naturally acquire or maintain solo territories, nor do we have evidence that older offspring help in the rearing of younger offspring. Social monogamy is the only known mating system in this species. Both sexes are highly active in nest building and nestling and juvenile care (personal observation).

## METHODS

### Study Population

We performed a series of field playback experiments on 16 pairs of free-living black-bellied wrens near Gamboa,

Republic of Panama. Experiments were conducted from 15 May to 15 August 2002, a period that corresponded with the tropical wet season and the approximate middle of the black-bellied wren's breeding season. Four of the pairs lived in the Gamboa Woods, a small (~25 ha) wood lot surrounded by residential areas on three sides. The remaining 12 pairs lived near railroad tracks that run parallel to the Panama Canal, on its south side. Creation of the railroad generated swaths of second-growth and edge forest on both sides of the tracks. Black-bellied wrens are partial to such regenerating and edge habitats (Ridgely & Gwynne 1989). Both study sites were characterized by mixed-level forests with dense undergrowth and high densities of tangled woody vines, a preferred foraging substrate.

Prior to the study, permits for conducting song playback experiments and for banding birds were obtained from the Colorado State University Animal Care and Use Committee and from Autoridad Nacional del Ambiente in Panama. Of the 32 birds used in this study, 12 males and eight females were uniquely colour-banded prior to the onset of experimental manipulation. We banded the remaining four males and five of the remaining eight females before the end of the study. Over two field seasons of field observations, we never observed pairs to move together to a new territory. We have observed five instances in which females left (or died) and were quickly replaced, but these were followed by greatly heightened levels of spontaneous duet song. Despite frequent observation periods (at least twice weekly), we did not encounter any drastic changes in the level of spontaneous duet song, so it was unlikely that we misidentified individual birds.

We observed dependent juveniles on six of the 16 territories during the 2002 season. The presence of juveniles was unambiguous because males produced loud 'cream-o-wheat' (D. M. Logue, unpublished observation; onomatopoeic device after F. O. Chapelle cited in Ridgely & Gwynne 1989) calls almost continuously while attending to dependent juveniles but used this call rarely in the absence of juveniles. Also, the presence of juveniles is readily apparent from their distinctive 'pizeet' calls and their grey (rather than white) throat feathers (Ridgely & Gwynne 1989; Stiles & Skutch 1989). During the study, we sexed the birds by morphology and song. Subsequent amplification and visualization of the sex-chromosome-linked CHD gene with 1237L and 1272H primers (Kahn et al. 1998) from a subset of 10 of the birds (seven males and three females) confirmed that those individuals were correctly sexed.

## Stimuli

All of the recorded vocalizations used as playbacks were obtained during May–August of 2001 and 2002 from free-living birds near Gamboa, Republic of Panama. Songs used as stimuli were recorded during or shortly after stimulating the birds with song playback. During the 2001 season, recordings were made with a Marantz tape recorder (PMD 222) and a Radio Shack omnidirectional microphone (product number 33-3014) mounted in a 45-cm aluminium

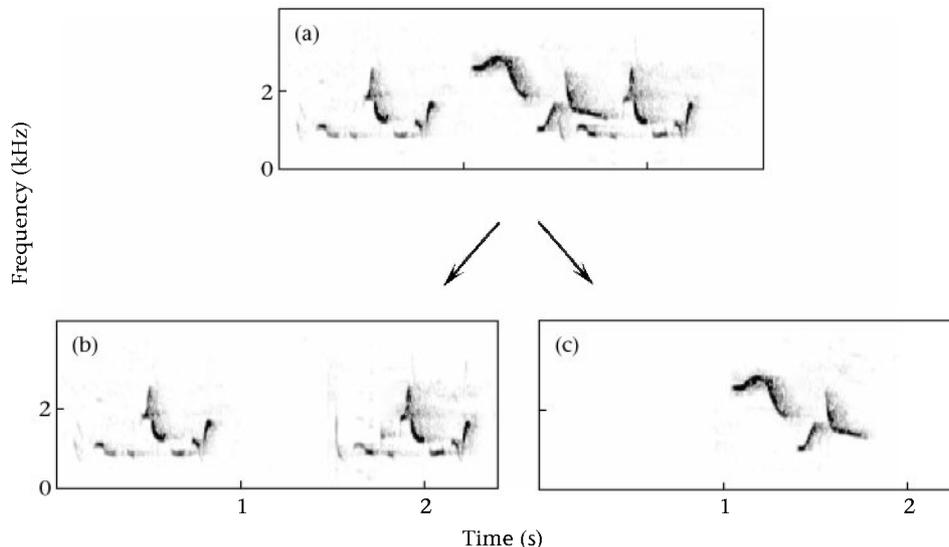
parabolic reflector. During the 2002 season, the recordings used as playback stimuli were made with a Sony Minidisc recorder (MZ-R700) and a Sennheiser omnidirectional microphone (ME62) mounted in a 60-cm Telinga Pro-universal parabola. True pitch for the recordings was verified using a tuning fork.

Using the program Real Time Spectrogram (Kay Elemetrics, version 2.3), we digitized the recorded songs at a sampling rate of 44 100 Hz and visually examined sonagrams for quality. When choosing recordings, we attempted to maximize signal-to-noise ratios and minimize reverberation. We used cursor-defined filters in Syrinx (John Burt: <http://syrinxpc.com/>) and Canary (Charif et al. 1995) to remove low-frequency noise. Filters were never used to remove high-frequency noise because we did not want to delete the high-frequency harmonics, which have been shown to contribute to sound-source localization in this genus (Naguib 1995). After filtration, we adjusted the amplitude of the signals so that the maximum amplitude of each signal was the same.

Because our access to computers changed throughout the course of this study, we used both Canary (which runs on a Macintosh platform) and Syrinx (PC) to create stereo duet stimuli. We believe that stimuli made with the two programs are indistinguishable. In this report, we describe how to create stimuli using Canary, although the process is similar to the one that we employed using Syrinx.

To overcome the limitations inherent in the use of a single sound source to simulate a paired intrusion (see Introduction), we converted all duet recordings into stereo stimuli (Fig. 1). This allowed us to broadcast the male and female contributions through separate speakers. Both male-initiated duets (MIDs) and female-initiated duets (FIDs) were converted into stereo stimuli. All duet stimuli consisted of three contributions with mates alternating contributions (MFM or FMF). We used Canary to display two identical sonagrams of the high-pass-filtered recordings. Using the cursor-delimited filter, we erased all of the male contributions from one of the copies and all of the female contributions from the other copy. Subsequently, we set the sonagrams' clipping levels to the lowest settings that maintained a legible signal. By examining the adjusted sonagram and listening to the signal, we determined that our filtering had eliminated the unwanted signals. We then copied the two files and pasted them into the two channels of a blank stereo recording, maintaining the original temporal relationships among the three contributions. For each duet stimulus, a coin flip determined which channel would carry the female and male contribution(s).

We are confident that we correctly distinguished male contributions from female contributions when creating stereo stimuli. Male and female contributions differ in timbre and pattern of frequency modulation, so the experienced listener can accurately assign syllables to one or the other sex. Furthermore, duet contributions are identical to solo songs and males typically repeat a song type alone several times before incorporating that song into a duet. Because a given male song type is highly stereotyped, we could compare the solo songs to the duet songs to identify ambiguous syllables.



**Figure 1.** An example of duet splitting using cursor-delimited filters. (a) A high-pass filtered three-contribution duet is copied twice. This example shows a male-initiated duet. (b) Cursor-delimited filters are used to remove the female contribution from one copy, leaving only the male duet contributions. (c) The male contributions are then removed from the other copy, leaving only the female contribution. The split songs can now be pasted into the two channels of a stereo track and played through separate speakers without altering their temporal relationship (see text).

All solo songs used in playbacks were high-pass filtered in the same manner as the duets. After filtration, duet and solo stimuli were standardized for amplitude and recorded on Minidisc. Each Minidisc track contained a single stimulus followed by enough blank space to bring the track to 30 s. We played stereo stimuli through a pair of identical 5-W speakers (Saul Mineroff Electronics, SME-AFS). The speakers were placed face-up on the ground, 8 m apart. They were connected to a single Minidisc player via a cord composed of a single male stereo plug leading into two male mono plugs. Solo song playbacks were set up similarly, but required only one speaker and a standard connecting cord.

### Playback Trials

We ran stereo duet playback trials from 29 May to 19 July 2002, and solo playback trials from 29 June to 7 August 2002. We lack complete data on the black-bellied wren's breeding season, but we observed nests and young juveniles on territories throughout the course of this investigation. All trials began between 0600 and 0830 hours. We avoided playing birds their own vocalizations or the vocalizations of a neighbour, and no stimuli were used in more than one trial. Before each experiment (duet playback or solo playback), we randomly determined which stimulus type a pair would receive first.

A pilot study had shown that black-bellied wrens do not consistently respond to playback when the broadcast speaker is placed haphazardly within the territory with respect to the focal birds, so we used the following system for placing the speakers. We approached a territory on which we wanted to run a trial and listened for black-bellied wren vocalizations. When a bird (usually the male) was located, we set up the playback speakers at least 15 m

inside the territory and 20–30 m away from the bird. We chose areas with sufficient visibility to allow for distance estimates and with sufficient vegetation to provide numerous perch sites at varied distances from the speaker(s). In the event that we did not detect one of the birds (usually the female) during the playback, we repeated the trial on another day. If we observed only one bird on the second trial, only the first trial was counted ( $N = 2$ ).

Each trial was preceded by 5 min of observation without stimulus (hereafter the 'pretrial period'). During this period, we attempted to record the same response variables that we recorded during the playback (see below). Each observer recorded the focal birds' vocalizations as well as his observations throughout the pretrial and trial periods. One of us (D.E.G.) made recordings with a Sennheiser omnidirectional microphone (ME62) mounted in a Telinga Pro-universal parabola and connected to a Sony Minidisc recorder (MZ-R700). The other observer (D.M.L.) made recordings using a Sennheiser short shotgun microphone (ME-66) and a Marantz cassette recorder (PMD 222). If, during the pretrial observation period, we determined that one or both of the birds were involved in territorial countersinging or nest building, we postponed the trial until the behaviour ceased. At the end of the 5-min pretrial period, one of us began the playback stimulus. We matched playback intensity to the intensity of the vocalizations given by focal birds. The Minidisc was set on 'one-track repeat' mode so that the stimulus was repeated every 30 s for 5 min. We recorded the following responses for each of the two focal birds: vocalizations, distance(s) from the male and/or female speaker, and distance to the mate. Distance measures were estimated using the 8-m speaker cable as a reference. We updated distances after each change in location greater than 1 m.

We each made observations on the bird that was closest to each of us at the time. Care was taken to communicate

the location and sex of the animal under observation (when known) to the other observer. Occasionally, one of us was able to see both of the birds, and the other could not see either bird. When this happened, the observer with the better vantage point recorded observations for both birds.

## Data Compilation

Each trial generated two recordings, which were used to fill in a timeline with the events that transpired. We first analysed the Minidisc recording because this format includes a run-time display that can be used to assign a time to each event. The data from the tape recording were then added to the timeline. When our distance estimates differed, the data from the observer with the better vantage point were used. In the event that it was not clear which observer had a better vantage point, the distances were averaged.

We used the timeline to score the following response variables for each bird: song initiations, answers to the mate's songs, closest approach to each speaker, and the distance between the mated birds (hereafter referred to as the interbird distance or IBD). We were only rarely able to measure the IBD during the pretrial period; therefore, we do not use these data in comparisons of pretrial versus trial behaviour. Vocal initiations included all tonal vocalizations that did not immediately follow a vocalization by the focal bird's mate. An answer was any vocalization that immediately followed a mate's vocalization, thus forming a duet. Only one answer was scored for each duet.

We were interested in the frequencies with which the sexes answered their mates to form duets. We derived answer rates by dividing the number of times an individual answered its mate by the number of initiations by the mate (after Levin 1996b). Derivation of answer rate required that the focal bird's mate initiated a song to which it could respond. Failing this requirement, we logged a missing value.

## Statistical Analysis

Most response variables required transformation prior to analysis with parametric statistics. Arcsine transformations were used for percentage data and  $\ln(X + 1)$  transformations were used for variables with large extreme values. All statistical analyses were conducted with *Mini-tab* (2000) software. We adhered to the standard alpha level of 0.05, but because sample sizes were small, we report  $P$  values where  $0.05 < P < 0.10$  as 'marginally significant'.

We compared male and female behaviour prior to playbacks using ANOVA models blocking for the identity of the pair. Two-tailed paired  $t$  tests were used to compare closest approach (as measured from the nearer speaker for stereo duet playbacks), initiation and answer rate during pretrial and trial periods.

We used one-tailed paired  $t$  tests to test the hypothesis that birds would approach the same-sex speaker more closely than the opposite-sex speaker during stereo duet

playback trials. One-tailed statistical tests were appropriate in this instance because all previous song playback studies have documented a stronger approach to same-sex playback than to opposite-sex playback (see Introduction). Approach distances to the two speakers during stereo duet playbacks were not independent of one another. The paired  $t$  test overcame this problem by subtracting the distance to the opposite-sex speaker from the distance to the same-sex speaker, generating a single variable that described the magnitude and direction of approach bias.

After careful consideration, we chose to conduct univariate, rather than multivariate, comparisons of behaviour among treatment types. Some of our measures were correlated with one another, but this does not detract from the suitability of univariate analysis as long as the different measures are understood to represent 'different aspects of the response elicited by playback' (McGregor 1992).

Closest approach, number of songs initiated and answer rate were used as dependent variables for ANOVA models. We constructed ANOVA models using stimulus type, presence of dependent offspring and an interaction term as our treatment factors. If the interaction term was not found to have at least a marginally significant effect ( $P < 0.10$ ), it was dropped from the model. For the sake of clarity, we report these statistics only in those cases where the presence of offspring was found to have a significant effect. If the presence of juveniles was not found to have a significant effect on the results, data were pooled with respect to presence of offspring. In these cases, we used two-way ANOVAs to test for treatment effects while blocking for individual identity.

We used multiple regression to explore answer rates in relation to IBD and average distances to the speakers. We did not use a model-selection algorithm (e.g. stepwise model selection) because the various spatial variables were nonindependent and it was our aim to determine the usefulness of each spatial variable in predicting answer rates while holding all other spatial variables constant.

Because we conducted all of the duet playback experiments before beginning solo playback experiments, it was not possible to control for the effects of order of presentation when comparing the birds' responses to duet versus solo playbacks. Accordingly, we did not analyse the data in this manner. During the female-initiated duet trial on the mated pair F-BG, the male (F) remained more than 40 m away from the speaker, and his pattern of song suggested that he did not hear the playback. Data from this trial were omitted from all analyses.

## RESULTS

Pooling all pretrial observations, we found that males initiated song at a much higher rate than females ( $\bar{X} \pm \text{SE}$ : males:  $2.46 \pm 0.32$  song initiations/min; females:  $0.06 \pm 0.04$  song initiations/min; ANOVA blocking for pair:  $F_{1,93} = 150$ ,  $P < 0.001$ ). Males were marginally more likely to answer their mates to form duets, answering 47.8% of their mates' songs, compared with an answer

**Table 1.** Summary of results of male-initiated duet (MID) and female-initiated duet (FID) playbacks

Comparison	Male subjects	Female subjects
<b>Trial vs pretrial</b>		
Distance to speaker	Decreased	Decreased
Initiation rate	Unchanged (always high)	Increased
Answer rate	Not testable	Increased*
<b>MID vs FID</b>		
Distance to speaker	No effect	No effect
Initiation rate	No effect	No effect
Answer rate	No effect	No effect
<b>Pooled over treatments</b>		
Speaker bias	No bias	Female speaker bias
Answer rate vs IBD	Negative correlation	Negative correlation

'IBD' represents the distance separating a mated pair.

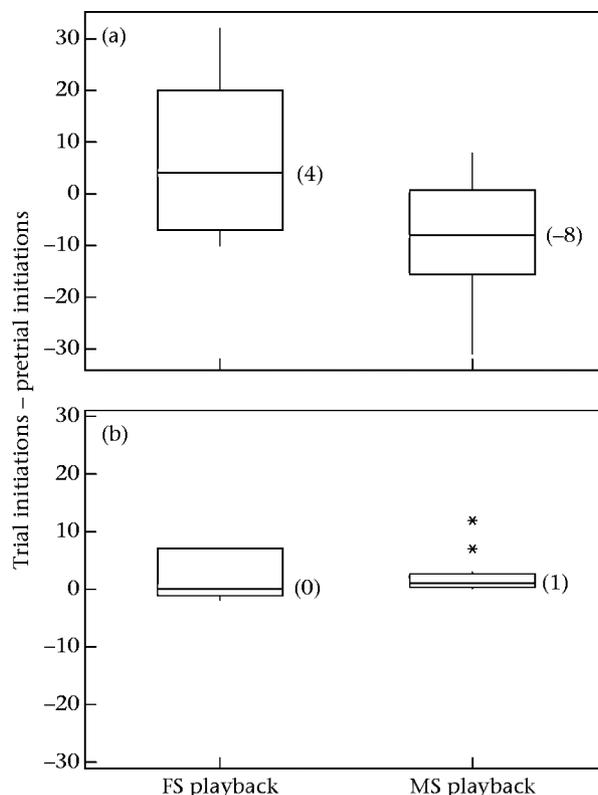
\*Data for male- and female-initiated duet playback treatments were pooled.

rate of 16.3% for females (ANOVA blocking for pair:  $F_{1,37} = 3.81$ ,  $P = 0.059$ ).

### Comparisons to Pretrial Behaviour

Birds of both sexes responded strongly to both duet and solo playbacks (summarized in Tables 1, 2). Males approached the speaker more closely during all trial types than during control periods (paired  $t$  tests: all  $P \leq 0.01$ ). Compared with pretrial (Pre) levels, male song initiation rates were marginally lower during male song (MS) playback ( $\bar{X} \pm \text{SE}$ : Pre:  $14.4 \pm 3.0$  songs; MS:  $5.3 \pm 1.3$  songs; paired  $t$  test:  $t_{12} = 2.07$ ,  $P = 0.063$ ; Fig. 2a) and marginally higher during female song (FS) playback ( $\bar{X} \pm \text{SE}$ : Pre:  $13.6 \pm 4.0$  songs; FS:  $22.1 \pm 4.4$  songs; paired  $t$  test:  $t_{12} = 1.882$ ,  $P = 0.087$ ; Fig. 2a) but were not affected by either duet playback. We were not able to compare male answer rate during the pretrial periods with those during the trials because females rarely initiated song prior to playback.

We detected significant reductions in female distance to the speaker during both FS and FID trials (paired  $t$  tests: FS:  $t_9 = -4.47$ ,  $P = 0.002$ ; FID:  $t_8 = -3.68$ ,  $P = 0.006$ ), but not in MS or MID trials (MS:  $t_8 = -1.71$ ,  $P = 0.13$ ;



**Figure 2.** Boxplots showing variation in the amount of vocal initiations during both types of solo playback for (a) male and (b) female subjects (FS = female song, MS = male song). We subtracted the number of initiations during the pretrial period from the number of initiations during the trial period to obtain input values for the boxplot. Medians (horizontal line within the box and number in parentheses), quartiles (top and bottom of box), the 0.05 and 0.95 quantiles (tips of vertical whiskers), and extreme data points (asterisks) are shown for each boxplot.

MID:  $t_5 = -1.93$ ,  $P = 0.1$ ). Our failure to detect female approach during MID trials may represent type II error, because missing values reduced our usable sample size to six, and those samples showed a nonsignificant tendency towards reduced distance. Female song initiation rates increased during MS, MID and FID trials (paired  $t$  tests: MS:  $t_{11} = -3.88$ ,  $P = 0.003$ ; MID:  $t_{15} = -7.60$ ,  $P = 0.001$ ; FID:  $t_{14} = -5.21$ ,  $P = 0.001$ ; Fig. 2b), but did not change

**Table 2.** Summary of results of male song (MS) and female song (FS) playback

Comparison	Male subjects		Female subjects	
	MS	FS	MS	FS
<b>Trial vs pretrial</b>				
Distance to speaker	Decreased	Decreased	Unchanged	Decreased
Initiation rate	Decreased*	Increased*	Increased	Unchanged
Answer rate	Not testable	Not testable	Unchanged	Increased
<b>MS vs FS</b>				
Distance to speaker	With juveniles: closer approach during FS Without juveniles: no effect		Closer during FS	
Initiation rate	Higher during FS		No effect	
Answer rate	No effect		Higher during FS	

\*Marginally significant result.

in response to FS playback (paired *t* test:  $t_{11} = -1.67$ ,  $P = 0.12$ ; Fig. 2b). Females answered the songs of their mates at a significantly higher rate during FS and FID trials (paired *t* tests: FS:  $t_9 = -2.34$ ,  $P = 0.04$ ; FID:  $t_{10} = -4.87$ ,  $P = 0.001$ ), but not during MS or MID trials (paired *t* tests: MS:  $t_9 = -0.69$ ,  $P = 0.50$ ; MID:  $t_9 = -0.35$ ,  $P = 0.74$ ). In summary, both males and females responded to all treatment types with a significant change in one or more of the three measured variables.

**Response to Stereo Duet Playback**

*Male response*

During both MID and FID trials, males did not approach the male speaker more closely than the female speaker (closest approach by males over all duet playbacks:  $\bar{X} \pm SE$ : male speaker:  $7.0 \pm 0.63$  m; female speaker:  $6.5 \pm 0.61$  m; one-tailed paired *t* tests: MID:  $t_{16} = -0.02$ ,  $P = 0.49$ ; FID:  $t_{15} = 0.78$ ,  $P = 0.78$ ; Fig. 3a). We detected no difference in the males' closest overall approach to a speaker during MID versus FID playbacks (two-way ANOVA blocking for pair:  $F_{1,14} = 1.78$ ,  $P = 0.20$ ). Male initiation rates (two-way ANOVA blocking for pair:  $F_{1,14} = 2.37$ ,  $P = 0.15$ ) and answer rates (two-way ANOVA blocking for pair:  $F_{1,11} = 1.31$ ,  $P = 0.28$ ) were also unaffected by duet

playback treatment type. Taken together, these measures suggest that male response to duet playback is independent of the sex that initiates the stimulus duet.

*Female response*

During playback of MIDs, females did not approach the female speaker significantly more closely than the male speaker ( $\bar{X} \pm SE$ : male speaker:  $7.2 \pm 1.1$  m; female speaker:  $6.7 \pm 1.1$  m, one-tailed paired *t* test:  $t_{17} = 0.57$ ,  $P = 0.29$ ). During FID playback, they approached the female speaker more closely than the male speaker ( $\bar{X} \pm SE$ : male speaker:  $8.5 \pm 0.77$  m; female speaker:  $7.0 \pm 1.2$  m, one-tailed paired *t* test:  $t_{15} = 2.50$ ,  $P = 0.013$ ). The level of bias did not differ significantly between treatment types (two-way ANOVA blocking for pair:  $F_{1,14} = 0.60$ ,  $P = 0.45$ ), so we pooled over both playback types and found that females approached the female speaker more closely than the male speaker (one-tailed paired *t* test:  $t_{31} = 1.85$ ,  $P = 0.037$ ), especially during trials when the female approached both speakers closely (Fig. 3b). Duet type did not affect the females' approach to the speaker (two-way ANOVA blocking for pair:  $F_{1,14} = 0.85$ ,  $P = 0.37$ ), song initiation rate (two-way ANOVA blocking for pair:  $F_{1,14} = 0.46$ ,  $P = 0.51$ ), or answer rate (two-way ANOVA blocking for pair:  $F_{1,10} = 0.39$ ,  $P = 0.54$ ). Like males, females responded to stereo duet playbacks without regard to the sex that initiated the stimulus.

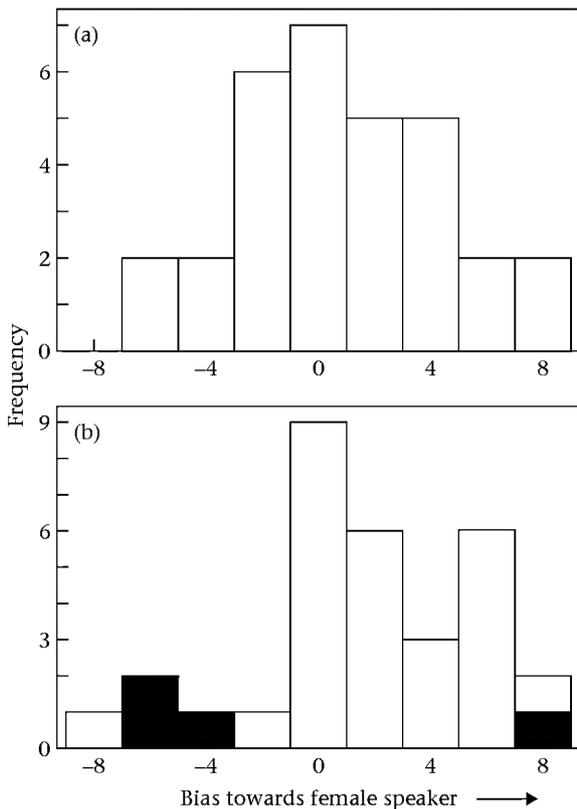
*Answer rate and IBD*

We discovered strong negative relationships between the distance separating pair members and the rate at which mates' songs were answered for both sexes, even when simultaneously accounting for both average and closest distance to both of the playback speakers (multiple regression: male:  $b_{y_j} = -0.54$ ,  $t_{IBD} = -3.78$ ,  $P = 0.001$ ; female:  $b_{y_j} = -0.48$ ,  $t_{IBD} = -3.50$ ,  $P = 0.002$ ; Fig. 4). Table 1 summarizes the results of the stereo duet playbacks.

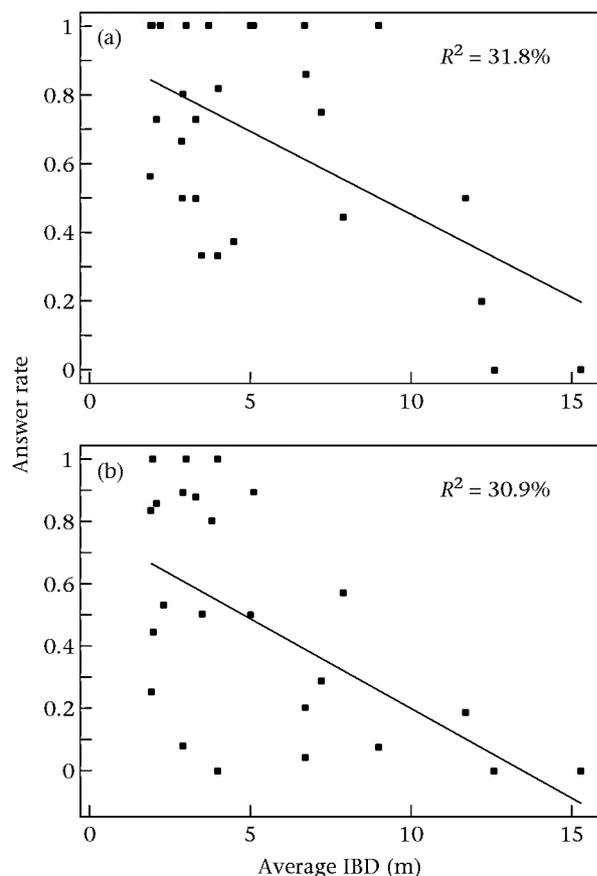
**Response to Solo Song Playback**

*Male response*

The effect of treatment type (MS versus FS) on males' approach to the speaker depended on the presence of dependent juveniles on their territories ( $\bar{X} \pm SE$ : MS with juveniles:  $12.7 \pm 3.8$  m; MS no juveniles:  $8.2 \pm 0.94$  m; FS with juveniles:  $4.3 \pm 0.78$  m; FS no juveniles:  $9.9 \pm 2.4$  m; two-way factorial ANOVA: playback type:  $F_{1,20} = 5.07$ ,  $P = 0.036$ ; juveniles:  $F_{1,20} = 0.58$ ,  $P = 0.45$ ; playback type\*juveniles:  $F_{1,20} = 1.18$ ,  $P = 0.016$ ). Specifically, males without juveniles approached equally close during both treatments, whereas those with juveniles approached closer during FS versus MS (Fig. 5a). Males initiated song at higher levels during FS versus MS playback ( $\bar{X} \pm SE$ : MS:  $5.3 \pm 1.3$  songs; FS:  $22.1 \pm 4.4$  songs; two-way ANOVA blocking for pair:  $F_{1,11} = 7.96$ ,  $P = 0.017$ ; see also Fig. 2a). Male answer rate was not affected by treatment ( $\bar{X} \pm SE$ : MS:  $0.80 \pm 0.12$ ; FS:  $0.61 \pm 0.18$ ; two-way ANOVA blocking for pair:  $F_{1,5} = 0.80$ ,  $P = 0.41$ ; Fig. 6a), but because of several missing values we do not have strong confidence in this result.



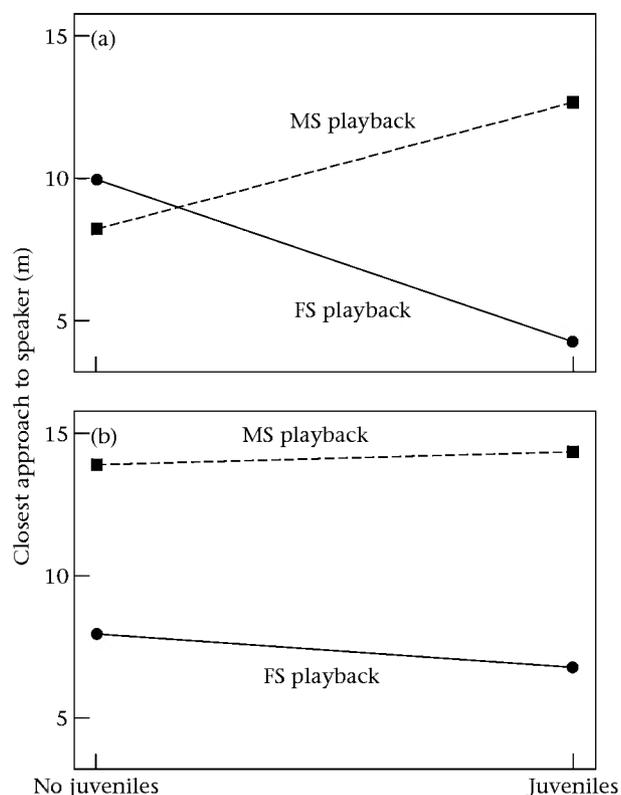
**Figure 3.** Histograms showing same-sex approach bias in (a) focal males and (b) focal females during both types of stereo duet playbacks. The X axis represents the closest approach of an individual to the male speaker (in metres) minus the closest approach of the same individual to the female speaker. The four trials in which the focal female did not approach within 10 m of either speaker are indicated in black.



**Figure 4.** Relationship of (a) male and (b) female answer rates with distance between mates (IBD = interbird distance). Although the figure shows a simple regression, the relationship was still significant when distances between the birds and the speaker were included in the regression equations (see text). Data are from both male-initiated duet and female-initiated duet trials, so each bird is represented by two points.

### Female response

Unlike that of males, the closest approach of females was not affected by the presence of juveniles ( $\bar{X} \pm \text{SE}$ : MS with juveniles:  $14.3 \pm 3.2$  m; MS no juveniles:  $13.9 \pm 1.9$  m; FS with juveniles:  $6.8 \pm 2.3$  m; FS no juveniles:  $7.9 \pm 2.1$  m; two-way factorial ANOVA: playback type:  $F_{1,20} = 9.63$ ,  $P = 0.006$ ; juveniles:  $F_{1,20} = 0.02$ ,  $P = 0.88$ ; playback type\*juveniles:  $F_{1,20} = 0.17$ ,  $P = 0.68$ ; Fig. 5b). Regardless of the presence of juveniles, females approached the speaker more closely during FS playbacks than during MS playbacks ( $\bar{X} \pm \text{SE}$ : MS:  $14.0 \pm 1.5$  m; FS:  $7.5 \pm 1.5$  m; two-way ANOVA blocking for pair:  $F_{1,11} = 17.29$ ,  $P = 0.002$ ; Fig. 5b). Female song initiation rates were unaffected by treatment ( $\bar{X} \pm \text{SE}$ : MS:  $2.4 \pm 1.0$  songs; FS:  $2.2 \pm 0.86$  songs; two-way ANOVA blocking for pair:  $F_{1,11} = 0.001$ ,  $P = 0.978$ ; see also Fig. 2b). Females answered their mates at a marginally higher rate during FS trials ( $\bar{X} \pm \text{SE}$ : MS:  $0.27 \pm 0.09$ ; FS:  $0.49 \pm 0.08$ ; two-way ANOVA blocking for pair:  $F_{1,10} = 4.54$ ,  $P = 0.059$ ; Fig. 6b). Because of the high male initiation rate during FS trials, the doubling of the female answer rate resulted in a dramatic increase in the number of answered male songs



**Figure 5.** Interaction plot showing the closest approach to the speaker for (a) male and (b) female subjects with and without juveniles during playbacks of male song (MS) and female song (FS).

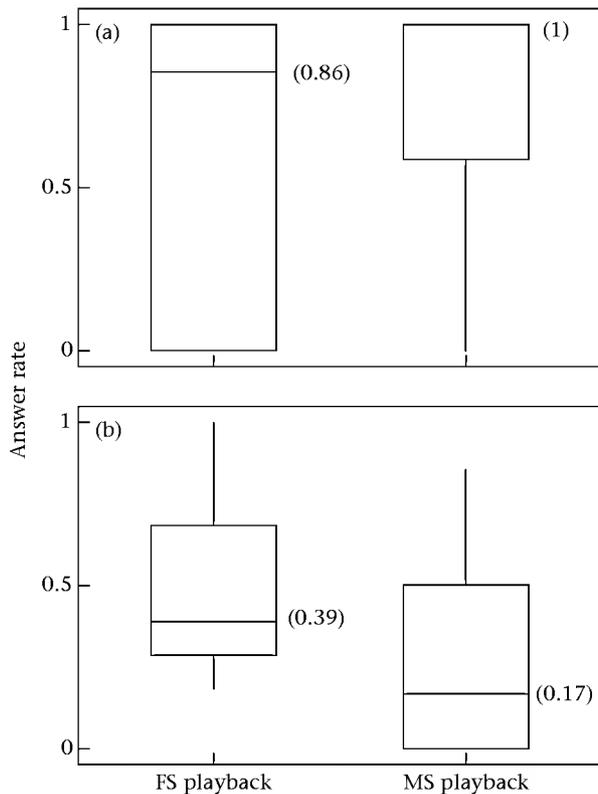
(i.e. MID) during FS versus MS playbacks ( $\bar{X} \pm \text{SE}$ : MS:  $1.5 \pm 0.54$  MID; FS:  $8.5 \pm 1.83$  MID). See Table 2 for a summary of results from the solo song playbacks.

## DISCUSSION

Our study addressed the following two questions. (1) How and why do male and female black-bellied wrens initiate song and answer their partners' songs during territorial intrusions? (2) Does either sex show intersexual territory defence?

Males generally initiated songs at a high rate regardless of whether or not a stimulus was playing. Specifically, male song initiation rate was indistinguishable from pre-trial levels during duet and female solo playback and marginally lower than pre-trial levels during male solo playback (Fig. 2a). Males also initiated song at a higher level during opposite-sex versus same-sex playback. Female song initiation rate was indistinguishable from pre-trial levels during female solo playbacks, but increased during duet and male solo playbacks (Fig. 2b).

We did not detect a difference in male answer rate across playback types or between the playback and pre-trial periods, but recall that the usable sample was quite small, and male answer rates were consistently high ( $\bar{X} > 60\%$  for all playback types). Females generally answered at a lower rate than males, but their answer rates increased during duet trials and increased marginally during female



**Figure 6.** Boxplots showing variation in the rate of answering a mate to form a duet during both types of solo playback for (a) male and (b) female subjects (FS = female song, MS = male song). See Fig. 2 legend for boxplot symbols.

song trials. Relative to male song playback, female song playback provoked females to answer at a marginally higher level (Fig. 6b). Birds of both sexes were more likely to answer their mates' songs as the distance between them decreased (Fig. 4).

Having described how black-bellied wrens duet during simulated territorial intrusions, we now consider why they do so. The acoustic mate-guarding hypothesis (Sonnenschein & Reyer 1983; see Smith 1994 for a variation of this hypothesis) has received considerable attention in recent years. The acoustic mate-guarding hypothesis states that song answering serves to counter the mate-attracting properties of the mate's song. Levin (1996b) suggested that a higher answer rate during same-sex versus opposite-sex playbacks would be evidence of acoustic mate guarding by the answering sex. Although we found that females answer at a higher rate during same-sex playbacks versus opposite-sex playbacks, we believe that an alternative explanation can explain this behaviour as well as other behaviours not explained by the acoustic mate-guarding hypothesis.

We propose that birds engage in duets during agonistic encounters to prevent intrapair aggression (Farabaugh 1982), an idea we term the 'identity hypothesis'. This hypothesis is similar to the 'contact maintenance hypothesis', an old idea (Skutch 1960, page 118; Thorpe 1973) that has received little attention in the last 20 years. The contact maintenance hypothesis states that pairs use duet

songs to coordinate their foraging and other nonagonistic activities. The identity hypothesis extends this hypothesis by stating that individuals use duet songs to identify and localize their mates during both agonistic and nonagonistic activities. The identity hypothesis builds on well-established work showing that birds can recognize individuals on the basis of song alone (reviewed in Stoddard 1996) and can localize singing conspecifics (e.g. Morton 1982; Naguib 1995).

Suppose that a territorial male sees a conspecific but does not know whether that individual is an intruder or his own mate. If the male sings, and the territorial female answers in a way that communicates her identity and location, she can prevent the male from directing his aggression at her by mistake. Reversing the sexes yields an equally plausible scenario. Several predictions of this hypothesis were supported by the data gathered in the present study and by previous duetting studies.

Mate identification may explain why many species duet at high levels during song playback (see Introduction). According to this interpretation, birds initiate song to stimulate their mates to answer and they answer to prevent aggression from the mate. This framework generates several predictions. Initiation rates should be high (but not necessarily exceeding pretrial levels) for both sexes during duet playbacks regardless of whether playback is an MID or FID. During solo playback, initiation rates should be high during opposite-sex playback so that mates can locate each other, and answer rates should be high during same-sex playback. All of these predictions were upheld in the present study. Furthermore, an individual's answer rate should be positively correlated with the risk of misdirected attack. This may explain why the IBD was negatively correlated with answer rate in both sexes. Another prediction of the identity hypothesis is that a bird that fails to duet may come into physical conflict with its own mate during a territorial intrusion. Owings & Morton (1998) reported that a captive male Carolina wren, *T. ludovicianus*, will attack and kill its mate unless the mate answers the male's song. One of us (D.M.L.) observed a similar incident during a single-speaker duet playback to a pair of free-living black-bellied wrens. Both birds were perched near the playback speaker when the male peered at his mate, flew up, seized her by the bill, and wrestled her to the ground. The female freed herself and immediately initiated a duet. After that point, neither bird directed aggression towards its mate.

While promoting the identity hypothesis, we have often faced the question 'why would certain species use coordinated song for identification when others achieve the same result using simple calls'? We believe that certain ecological conditions and evolutionary trajectories might favour identification via coordinated song over individually distinctive calls. Large IBDs and densely vegetated territories tend to distort quiet, broadband calls more than loud, whistled songs. As a simple alternative, birds might use individually distinctive songs, but among song-learning species (e.g. oscine passerines), this type of identifier could be easily copied by another bird, making it evolutionarily unstable. A simple 'duet code', unique to each mated pair, in which initiating song types are linked to

answering song types, would be highly effective in allowing the members of a pair to identify each other reliably. Although an intruder might be able to bluff a few answers, the song initiator could use several different song types in sequence to update the probability that any individual is his mate.

The most compelling evidence that certain species duet for mate identification is that a great number of duetting species use duet codes rather than combining duet contributions at random. Buff-breasted wrens, *T. leucotis* (Farabaugh 1983), bay wrens (Levin 1996a), eastern whipbirds, *Psophodes olivaceus* (Watson 1969), bell shrikes, *Laniarius aethiopicus* (Thorpe 1973), white-crested laughing thrushes, *Garrulax leucolophus* (Souček & Vencel 1975), African drongos, *Dicrurus adsimilis* (Wickler 1976), and slate-coloured boubou shrikes, *Laniarius funebris* (Wickler 1976), all show nonrandom song-type associations and/or pair-specificity in duets. D. M. Logue (unpublished data) confirmed that female black-bellied wrens adhere strictly to individually unique duet codes.

The model that we developed in the Introduction suggests that intersexual territorial defence could arise under realistic conditions. The model made the novel predictions that males are more likely than females to show intersexual territory defence and that birds engaged in a parenting effort are more likely to defend intersexually than those that are not. Both predictions of the model were upheld in our study. In accordance with the first prediction, stereo duet playbacks revealed that females, but not males, approached the same-sex stimulus more closely than the opposite-sex stimulus (Fig. 3). Solo song playbacks revealed a similar tendency, with females approaching solo female song more closely than male song, whereas males approached both types of solo song. Additionally, during female song playback, males with dependent juveniles approached the speaker more closely than males without juveniles (Fig. 5a). Given that black-bellied wren fledglings require a great deal of parental care and that replacement females do not aid in caring for the juveniles (D. M. Logue, unpublished data; see Freed 1987 for a detailed description of mate replacement in house wrens), it is unlikely that this strong male response was an attempt to encourage the intruding female to join him on the territory. It is much more plausible that fathers attempt to oust intruding females because it is in their best interest to retain their current mates. We did not find any evidence that the presence of juveniles encourages opposite-sex territoriality in females. Furthermore, females did not approach the speaker during male song playback (Fig. 5b), perhaps because size dimorphism in this species renders females incapable of defending territories against males without incurring unacceptably high costs.

In conclusion, we wish to emphasize that intrasexual territoriality is generally stronger than intersexual territoriality. The results of our playback experiments, however, suggest that intersexual territorial defence occurs at non-trivial levels in this species. Its occurrence in males with juveniles is consistent with a model that predicts that intersexual territory defence can be an optimal strategy in territorial, socially monogamous species. Understanding the roles of the sexes in territory defence promises to

improve our understanding of the behavioural ecology of tropical birds in general.

### Acknowledgments

We thank Gene Morton for his ample assistance throughout this study and Mike Baker for all of his valuable advice. Thanks to Michelle Hall, Leah Katz and Jessica Meehan for lively discussion and assistance in the field. Mike Antolin, Bill Black and Shelly Ballard de Volo assisted in the genetic sexing procedure. D.M.L. received generous support from Smithsonian Tropical Research Institute, the Cooper Ornithological Society and an Abbott grant to E. S. Morton administered via the Smithsonian Office of Fellowships and Grants. D.E.G. received support from a National Science Foundation Graduate Research Fellowship. Permission to work with birds was granted to D.M.L. by the Animal Care and Use Committee of Colorado State University (Protocol number 01-105A-01) and by Autoridad Nacional del Ambiente in the Republic of Panama (Permit number SE/A 034-02). Permission to work at the study site was granted by the Panama Canal Railway Company.

### References

- Bard, S. C., Hau, M., Wikelski, M. & Wingfield, J. C. 2002. Vocal distinctiveness and response to conspecific playback in the spotted antbird, a Neotropical suboscine. *Condor*, **104**, 387–394.
- Brown, R. N. & Lemon, R. E. 1979. Structure and evolution of song form in the wrens *Thryothorus sinaloa* and *T. felix*. *Behavioral Ecology and Sociobiology*, **5**, 111–131.
- Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary 1.2 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.
- Farabaugh, S. M. 1982. The ecological and social significance of duetting. In: *Acoustic Communication in Birds* Vol. 2. (Ed. by D. E. Kroodsma & E. H. Miller), pp. 85–124. New York: Academic Press.
- Farabaugh, S. M. 1983. A comparative study of duet song in tropical *Thryothorus* wrens. Ph.D. thesis, University of Maryland.
- Freed, L. A. 1987. The long-term pair bond of tropical house wrens: advantage or constraint? *American Naturalist*, **130**, 507–525.
- Greenberg, R. & Gradwohl, J. 1983. Sexual roles in the dot-winged antwren (*Microrhopias quixensis*), a tropical forest passerine. *Auk*, **100**, 920–925.
- Hall, M. L. 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour*, **60**, 667–677. doi:10.1006/anbe.2000.1517.
- Hultsch, H. & Todt, D. 1984. Spatial proximity between allies: a territorial signal tested in the monogamous duet singer *Cossypha heuglini*. *Behaviour*, **91**, 286–293.
- Kahn, N. W., St John, J. & Quinn, T. W. 1998. Chromosome-specific intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. *Auk*, **115**, 1074–1078.
- Levin, R. N. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour*, **52**, 1093–1106.
- Levin, R. N. 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. *Animal Behaviour*, **52**, 1107–1117.

- McGregor, P. K.** 1992. Quantifying responses to playback: one, many, or composite multivariate measures? In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 79–96. New York: Plenum.
- Minitab.** 2000. *Statistics, Release 13.20 for Windows*. State College, Pennsylvania: Minitab.
- Morton, E. S.** 1982. Grading, discreteness, redundancy and motivational-structural rules. In: *Evolution and Ecology of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 183–212. New York: Academic Press.
- Morton, E. S. & Derrickson, K. C.** 1996. Song ranging by the dusky antbird, *Cercomacra tyrannina*: ranging without song learning. *Behavioral Ecology and Sociobiology*, **39**, 195–201.
- Naguib, M.** 1995. Auditory distance assessment of singing conspecifics in Carolina wrens: the role of reverberation and frequency-dependent attenuation. *Animal Behaviour*, **50**, 1297–1307.
- Owings, D. H. & Morton, E. S.** 1998. *Animal Vocal Communication: a New Approach*. Cambridge: Cambridge University Press.
- Ridgely, R. S. & Gwynne J. A., Jr.** 1989. *A Guide to the Birds of Panama*. 2nd edn. Princeton, New Jersey: Princeton University Press.
- Seddon, N., Butchart, S. H. M. & Odling-Smee, L.** 2002. Duetting in the subdesert mesite *Monias benschi*: evidence for acoustic mate defense? *Behavioral Ecology and Sociobiology*, **52**, 7–16. doi:10.1007/s00265-002-0488-9.
- Skutch, A. F.** 1960. *Life Histories of Central American Birds*. Vol. 2. Berkeley, California: Cooper Ornithological Society.
- Smith, W. J.** 1994. Animal duets: forcing a mate to be attentive. *Journal of Theoretical Biology*, **166**, 221–223.
- Sonnenschein, E. & Reyer, H. U.** 1983. Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarus funebris*). *Zeitschrift für Tierpsychologie*, **63**, 112–140.
- Souček, B. & Vendl, F.** 1975. Bird communication study using digital computer. *Journal of Theoretical Biology*, **49**, 147–172.
- Stiles, F. G. & Skutch, A. F.** 1989. *A Guide to the Birds of Costa Rica*. Ithaca, New York: Cornell University Press.
- Stoddard, P. K.** 1996. Vocal recognition of neighbors by territorial passerines. In: *Evolution and Ecology of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356–376. Ithaca, New York: Comstock.
- Thorpe, W. H.** 1973. Duet-singing birds. *Scientific American*, **229**, 70–79.
- Watson, M.** 1969. Significance of antiphonal song in the eastern whipbird, *Psophodes olivaceus*. *Behaviour*, **35**, 157–178.
- Wickler, W.** 1976. Duetting songs in birds: biological significance of stationary and non-stationary processes. *Journal of Theoretical Biology*, **61**, 493–497.
- Wiley, R. H. & Wiley, M. S.** 1977. Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis*. *Behaviour*, **62**, 10–34.