In many bird species, pairmates sing together, forming duet songs. Studies on duetting songbirds consistently report nonrandom associations between the male and female song types that constitute duet songs. Previous research has demonstrated that when female black-bellied wrens, *Thryothorus fasciatoventris*, answer male song to form a duet, they abide by individually specific, temporally stable duet codes linking discrete acoustic stimuli (male song types) to discrete vocal responses (female song types). The present study builds on this finding with the goal of understanding the behavioural mechanisms in both males and females that result in nonrandom song type associations. I recorded duets from free-living pairs, and isolated four transitions from male song type to female song type in the duets of each pair. These transitions served as predicted links in the females’ duet codes. The male and female song types from the transitions were played to the pair from which they had been recorded. Both males and females ‘duetted’ with playbacks of their mates’ songs. Females’ answers adhered very closely to the predictions, supporting previous findings. Males also answered according to the predictions at a level exceeding chance, demonstrating that they abide by the same duet codes as do their mates. Stimulus type was a strong predictor of response type in females, but a relatively weak predictor of response type in males. When presented with chimerical male song stimuli, females typically answered with one of the predicted responses for the songs composing the chimera. The song fragments constituting the beginning and end of chimerical stimuli were equally influential in determining female responses, but longer fragments were more influential than shorter fragments. Overall, the findings are consistent with the hypothesis that answering according to a unique duet code communicates the singer’s identity to the mate, facilitating cooperative defence of the pair’s shared resources.

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**Keywords**: behavioural mechanisms; black-bellied wren; cooperative territory defence; duet code; individual recognition; mapping function; *Pheugopedius fasciatoventris*; signal structure; *Thryothorus fasciatoventris*; vocal communication

In over 220 bird species, pairmates vocalize with temporal coordination to produce a more or less stereotyped acoustic pattern known as duet song (Farabaugh 1982). In its simplest form, a duet song is the result of two behaviours: one bird initiates a vocalization, and a second bird quickly answers. Vocal initiation is common to nearly all birds, but answering is unique to duetting and chorus singing birds, and is the behaviour responsible for turning a solo song into a duet song (Hall 2000, 2004). In many duetting songbirds (suborder Passeres), individual males and females sing repertoires of discrete song types. Typically these species produce duets in which male song types and female song types are associated nonrandomly. The phylogenetic distribution of nonrandom song type associations in duet songs indicates that this pattern has evolved several times (Logue 2006). In some species, pairs sing stereotyped ‘duet types’ general to a population (e.g. Sonnenschein & Reyer 1983; Grafe et al. 2004; Rogers 2005) or specific to each pair (e.g. Mann et al. 2003). In other species, however, duets are not sufficiently stereotyped to justify the term ‘duet type’ (e.g. Souček & Venci 1975). Regardless of the level of stereotypy among duet songs, song type choices in...
duet singing birds are best studied at the level of the individual (i.e. the primary level of selection), rather than the level of the pair. The current study is an attempt to understand the individual-level behavioural mechanisms in males and females that are responsible for the pair-level phenomenon of nonrandom song type associations in duet songs.

Adherence to a duet code is one of several behavioural mechanisms that could produce nonrandom song type associations in duet songs (Logue 2006). A duet code is a set of rules linking discrete types of song input to discrete types of song output during duet singing (Logue & Gammon 2004; Logue 2006). For example, if hearing male song type 7 (MS7) consistently provokes a certain female to answer with female song type 15 (FS15), then the transition from MS7 to FS15 represents one link in that female’s duet code. Experiments on the black-bellied wren, Thryothorus fasciatoventris (nominates Pheugopedius fasciatoventris, Mann et al. 2006), have shown that females of that species adhere strictly to individually distinctive, temporally stable duet codes when answering the recorded songs of their mates (Logue 2006). These experiments, however, relied on small sample sizes and variable numbers of song stimuli presented to each female. In the present study I replicate the test of whether females adhere to a duet code, using a larger sample of females and a consistent number of stimuli across females.

Prior to the present study, it was not known whether male black-bellied wrens also adhered to a duet code. I observed many natural vocal sequences in which females switched the song type used to initiate a duet, but males continued to answer with the same song type that they had been singing previously. Such observations indicated that males choose song types independently of the female’s prior song. On occasion, however, female song switches appeared to precipitate male song switches. In some of these cases, the male switched according to the reverse of the mate’s code. For example, a male whose mate’s code included the link from MS7 to FS15 was singing MS10 until his mate sang FS15. He then answered her with MS7, as predicted by the reverse of her code. Observations like this suggested that males may know part or all of their mate’s code and use it in reverse, a hypothesis tested in the present study.

Male black-bellied wrens sing repertoires of approximately 40 discrete song types, and birds of both sexes commonly switch mates (Logue 2006, unpublished data). Thus for females to adhere to duet codes, they must accurately categorize many male song types. I examined song type categorization of male songs.

As Horning et al. (1993) point out, proportional influence could operate in concert with either primacy or recency effects.

The song playback experiments described in this report are attempts to investigate further the mechanisms underlying nonrandom song type associations in the duet songs of the black-bellied wren. Building on techniques developed by Watson (1969), Thorpe (1972), Seibt & Wickler (2000) and Logue (2006), I stimulated birds to answer the recorded songs of their mates. This technique generates duets in which the experimenter chooses the initiating song type and the test subject chooses the answer, allowing the experimenter to test for causal relationships between stimuli and responses. I used this playback technique to address three research goals: (1) to replicate, using improved methodology, an experimental test (Logue 2006) of whether females adhere strictly to duet codes; (2) to determine the male’s role in generating nonrandom song type association in duet songs. Specifically, I tested whether males adhere to reversed versions of their mate’s duet codes, and compared their strength of adherence to that of females; and (3) to test the proportionality, primacy and recency hypotheses with respect to female categorization of male songs.

**METHODS**

**Study Population**

Recordings and experiments were conducted in and around the village of Gamboa, Republic of Panama (9° 07′ N, 79° 41′ W). All of the birds in this study were captured in mist nets and colour-banded except for one male, who evaded several capture attempts. Two of the experimental pairs lived in a small woodlot known as the Gamboa Woods, seven pairs lived on the edge of the 22 000-ha Parque Nacional Soberanía, and the remaining three pairs lived along Old Gamboa Road. The first two sites were connected by fragments of suitable habitat, but were separated from the Old Gamboa Road site by the Chagres River. All study sites comprised secondary growth, semi-deciduous, lowland forest. All territories included forest edges, as is characteristic of this species.

Black-bellied wrens are socially monogamous and remain paired throughout the year. Males are larger than females, but birds appear monochromatic to the human observer. Both sexes sing repertoires of sex-specific song types. Male and female songs show consistent differences in several temporal and frequency characteristics (Logue 2004), making it easy to distinguish male song (MS) from female song (FS) in the field. Genetic sexing and field observations support the ubiquity of these acoustic patterns (Logue & Gammon 2004). Owing in part to the low natural rate of song switching, I have not recorded complete repertoires. The maximum known repertoires are 38 song types from a male and 19 song types from a female, but these are probably slight underestimates of these birds’ full repertoires. Both males and females share approximately half of their song types with local birds of the same sex (D.M.L., unpublished data).
Both sexes initiate song and answer the songs of their mates. Answers may overlap the mate’s song, or may follow very shortly (<1 s) after the end of the song. The simplest vocal duets in this species comprise two songs (an initiation and an answer), but pairmates may continue to answer one another to form extended duets. The songs used in duets are identical to solo songs, so I refer to discrete song variants as ‘song types’ whether they are used as solo songs or as part of a duet.

Recordings, Predictions and Stimuli

The recordings used to generate playback stimuli and female coding predictions were made during 10 June–17 August 2004. Recordings were made with a Sennheiser omnidirectional microphone (ME62) mounted in a 45-cm aluminium parabolic reflector, connected to a Sony Mini-disc recorder (model MZ-N1; Logue et al. 2005). Recorded songs were played through the microphone input of a Compaq Presario 1693 (ESS Solo sound card) and digitized at 44.1 kHz in the program Syrinx (John Burt, http://www.syrinxpc.com/index.html).

I used Syrinx to generate sonograms of the recorded duets (Hanning window, FFT = 512 points) and isolated recordings of four different MS–FS transitions from each of the 12 experimental pairs (Fig. 1a). Each of these transitions represented a predicted link in the female’s duet code. Most transitions were supported by several recorded duets (mean ± SD = 4.2 ± 3.2 duets), but even one high-quality recording was sufficient basis for a prediction. With two exceptions, exactly one female answer type was recorded in response to each of the male song types used to generate predictions. Stimuli from the two inconsistent transitions failed to provoke responses during playback, so effectively, predictions were based on absolutely consistent recorded transitions. Pairmates occasionally (ca. 5% of duets) sing overlapping, but temporally uncoordinated songs. To the human listener this type of duet sounds rushed and disorganized, and the lack of temporal coordination between the pairmates is evident in sonograms. These duets were not used to generate predictions.

I prepared the following four types of playback stimuli: (1) stranger duets, (2) male songs, (3) female songs and (4) chimerical male songs. During the playback trials, birds were not expected to answer stranger duets. The purpose of these stimuli was to draw a pair to the location of the playback in their territory and to increase the rate at which birds answered the subsequent test stimuli. I prepared 12 stranger duets from birds in the Old Gamboa Road area, and 12 from birds in the other study areas. The distance between these two areas (6 km) and the intervening Chagres River made it unlikely that birds from these two areas were familiar with each other. I assigned recordings from each location to the groups 1, 2 and 3, resulting in six sets of stimuli, each comprising four stranger duets. Half of the stranger duets in each set had the form ‘MS → FS → MS’, and the other half were ‘FS → MS → FS’.

I created male song stimuli and female song stimuli from recordings of each song type used to generate female coding predictions (Fig. 1a–c). This resulted in four MS stimuli and four FS stimuli from each pair. Most MS and FS stimuli were isolated from duets using Syrinx’s cursor-delimited filter (from trials that contributed to statistics, 30/36 MS and 37/40 FS were from duet recordings); the remainder were recorded as solo songs. The choice to take a song from a duet or a solo depended solely on which method would produce the best quality stimulus. I used the cursor-delimited filter to remove extraneous animal sounds.

Chimerical male song stimuli were made from the beginning of one MS stimulus and the end of another (Fig. 2). The four MS stimuli from each of the male subjects were randomly grouped into two pairs, the beginnings of which were exchanged using the CUT and PASTE functions in Syrinx. I developed a repeatable method for cleaving songs that produces chimerical songs with approximately equal representation of both song fragments and a syntax that appears similar to natural male song. I cleaved songs immediately prior to the first

Figure 1. I recorded duet songs from free-living black-bellied wren pairs (a), noting the transitions from male song types to female song types within each duet. Four such transitions served as predicted links in each pairmate’s duet code. I then generated playback (pb) stimuli for each male (b) and female (c) song type transition. Playing these stimuli on the territory of the birds from which they were recorded elicited rapid answering (d and e), as if the birds were duetting with the playback stimuli. In this example, a male answers a female song stimulus (d) with a song that does not match the prediction (compare to ź in a), and his mate answers a male song stimulus (e) with the predicted song type (compare to ? in a). See text for statistics. Sonagrams were generated in Syrinx (Hanning window, FFT = 1024 points).
note beginning at a lower fundamental frequency than the highest fundamental frequency in the preceding note, unless that note was the second note in the song and the first note was less than 250 ms. In those cases, I cleaved immediately prior to the second note beginning at a lower fundamental frequency than the highest fundamental frequency in the preceding note.

All stimuli were subjected to a high-pass filter at 400 Hz and amplitude maximization in Syrinx. They were then recorded onto separate tracks on a Minidisc.

Playback Trials

Playback trials were conducted with the help of a field assistant. We conducted trials between 0600 and 1120 hours, from 27 July to 4 September 2004. This period is entirely within the black-bellied wren’s breeding season. We observed dependent juveniles on the territories of four pairs during at least one trial; no pairs were known to have active nests during the trials. There were three types of trials: MS, FS and chimerical male song (CMS). For each pair used in the experiments, MS trials and FS trials were presented in random order, and CMS trials were presented last. Consecutive trials were separated by at least one week. The territorial female was the focal bird during MS and CMS trials, and the territorial male was the focal bird during FS trials.

We conducted playbacks on the territories of the birds from which the playback stimuli were recorded. On the day that we intended to test a particular pair, we located the focal pair and set up the playback apparatus within 40 m of the birds. If we could not locate the focal pair, we left and tried again later. The playback apparatus consisted of a Minidisc unit (Sony MZ-N1) and two 5-W loudspeakers (Saul Mineroff Electronics, SME-AFS) placed on the ground, face up 8 m apart from each other. A speaker cable ran from each speaker to the place where I operated the Minidisc unit, allowing me to choose the speaker through which each stimulus would play. I attempted to present stimuli every 15 s, but imperfectly responsive equipment and competing sounds (from the test subjects, passing trains, etc.) introduced variance into this interval. Prior to trials, we adjusted the speaker settings so that peak volume levels reached 84 dB at 1 m, as measured by a sound level meter (Radio Shack No. 33-2050). This volume is within the natural range. Stimuli were presented in predetermined, randomly ordered blocks of one to three repetitions because black-bellied wrens typically sing the same song type several times before switching song types. The nonindependence of stimuli within a block was accounted for in the data analysis. My assistant recorded the trials to Minidisc. Recordings included the playback stimuli, vocalizations from the subjects, and verbal notes from the playback operator and recordist.

Each trial consisted of a luring phase and a testing phase. During the luring phase, I played stranger duet stimuli from the speaker furthest from the nonfocal bird. Stranger duet sets 1 and 2 were randomly assigned to MS and FS trials, and stranger set 3 was used for CMS trials. The luring phase comprised four consecutive repeats of each of the four stranger duets assigned to that trial. I ended the luring phase when both birds were within 40 m of the playback apparatus and had produced two duets. If all 16 stranger duets were played before these criteria were met, I returned to the beginning of the stranger duet set and continued the luring phase.

The testing phase began immediately after the luring phase and comprised 24 randomly ordered blocks of stimuli. These included eight blocks of stranger duet stimuli (one block of one repetition and one block of two repetitions for each of the four stimuli) and 16 blocks of test stimuli (two blocks of two repetitions and two blocks of three repetitions for each of the four stimuli, totalling 40 test song stimulus presentations per trial). I played stranger duet stimuli through the speaker furthest from the nonfocal bird and test stimuli (FS, MS, or CMS) through the speaker nearest to the nonfocal bird. The rationale for the two-speaker design was as follows: because stranger duet stimuli simulate an intruding pair

![Figure 2. Two black-bellied wren song types from the same male (a and b) were cleaved approximately in half (arrows; see text for a complete description of song cleaving) and recombined to generate a complementary pair of chimerical stimuli (c and d), each comprising the first half of one song type and the second half of another. Two complementary pairs were generated for each male. Sonagrams were generated in Syrinx (Hanning window, FFT = 1024 points).](image-url)
and test stimuli simulate vocalizations from the nonfocal mate, these two types of stimuli should come from different locations. Trials ended when I had played all of the stimuli.

**Data Extraction and Analysis**

Trial recordings were viewed as sonagrams in Syrinx (Hanning window, FFT = 512 points). All answers were saved as wav files (sampling rate = 44.1 kHz). I searched all of my recordings from ad libitum sampling, capture attempts and playback trials over four field seasons and counted the number of song types I had recorded from each of the test subjects. These counts represent known repertoire sizes and are almost certainly underestimates of true repertoire sizes.

The first goal of the data analysis was to replicate the test of whether females adhered strictly to duet codes. Because stimuli were presented in blocks (and were therefore not independent of other stimuli within their own block), I considered only the first answer within each block. To reduce variance attributable to carry-over effects from the subject's previous choice of song type, I considered only those answers that were also song type switches. Females' responses to MS stimuli were compared to predictions (see **Recordings, Predictions and Stimuli** above). If a given response was identical to the prediction, the response was scored as 'predicted', otherwise it was scored as 'not predicted' (Fig. 1c).

I used a Monte Carlo test to determine whether females adhered to duet codes (Logue 2006). Monte Carlo tests use an assumed model to generate a null distribution of test statistics, to which the observed test statistic is compared for significance testing (Manly 1997). The model in the present Monte Carlo test (described in detail below) is a simulation of the MS playback experiment that assumes females chose answers at random from their repertoires. If a simulated answer matches the prediction, it is scored as 'predicted'. Therefore, some proportion (0.0–1.0) of simulated answers from each female are predicted answers, and the median proportion of predicted answers across the nine simulated females can be determined. The simulation is run 10,000 times to generate a distribution of median proportions of predicted answering. I then used this distribution to construct the ratio (number of simulated medians ≥ observed median)/10,000. This ratio is an exact \( P \) value, which can be interpreted as the realized probability of random answering generating the observed median (or higher) proportion of predicted answers.

The simulation assumes that female answering follows a binomial distribution, where the probability of any one answer meeting the prediction is 1/(known repertoire size \( \times f \)). The factor \( f \) is an estimate of the proportion of song types in the repertoire that females use as answers. This factor accounts for the possibility that birds do not use all of the song types in their repertoires as answers. I estimated \( f \) from catalogued recordings of two females, averaged the results, and applied this \( f \) to all of the females in the experiment. I chose these two females because I had more recorded duets from them than from any of the other females (accurate estimation of \( f \) requires a thorough sampling of duets). It is very likely that repertoire size and \( f \) are underestimated. For both values, underestimation increases the probability that the simulated females will answer correctly (i.e. increases the null distribution), introducing conservative (type II) error.

Each iteration simulated one complete run of the MS experiment. For example, during the experiment female BI sang one independent answer in response to stimulus 111 and two independent answers in response to stimulus 112. I therefore used BI's known repertoire size to simulate one random answer to 111 and two random answers to 112, and so on for all stimuli answered by each female. The model determined the proportion of predicted answers to each stimulus type within female, and averaged these values within female. Therefore, all answered stimulus types contributed equally to a female's simulated proportion of predicted answers. The median proportion of predicted answers was determined in each of 10,000 iterations of the simulation. These 10,000 medians constituted the null distribution used to generate exact \( P \) values (medians were used because distributions were non-normal, but unreported tests using means produced qualitatively identical results). Individuals were treated as independent sampling units (i.e. \( N = \) the number of subjects). I conducted the same type of simulation to test whether males adhered to the reverse of their mates' duet codes at a level exceeding that predicted by random answering (Fig. 1d). I estimated a separate \( f \) for males from two well-recorded individuals.

All predictions used in the preceding Monte Carlo analyses were based on recorded MS \( \rightarrow \) FS transitions. As a result, those analyses tested whether a mated male and female adhered to the female's predicted code. To compare the strength of code adherence in males versus females generally, it is necessary to compare the strength of association between stimuli and responses during playback in males versus females. All answers from the MS and FS trials were included in this analysis. There was no need to omit second and third answers within a block of stimuli because males and females were subjected to stimulus sets with identical blocking schemes. Omitting answers that were not song type switches would bias the results by overestimating the strength of association in birds that were insensitive to stimulus type (e.g. those that continued to answer with song type X regardless of the stimulus type). I quantified the strength of association between stimuli and responses using a modified version of techniques developed by Mann et al. (2003) and Menzil & Vehrencamp (2005).

For each MS and FS trial, I constructed a matrix of stimulus types (columns) versus response types (rows), with the observed frequency of each stimulus–response combination in the interior cells. Each of these ‘observed’ matrices was compared to an ‘expected’ matrix, to quantify the strength of association between stimuli and responses. I used the Poisson distribution to determine the expected number of cells in each column containing frequencies 0, 1, 2, 3, 4 and \( \geq 4 \). Generating expectations separately for each column controls for among-stimulus-type variance.
in the number of answers. Expected response frequencies were summed across columns, generating the expected distribution of answer types from each bird given random association between stimuli and responses. I calculated a G score based on the observed and expected frequencies. This G score indicates the strength of association between stimuli and responses. I compared the strength of stimulus–response associations in males versus females with an ANCOVA in which sex was a fixed factor, number of answers was a covariate and G score was the dependent variable. The covariate accounts for the G score’s dependence on sample size.

If females require complete male songs to determine song type, they would either not answer chimerical male song stimuli, or answer using a random song from their repertoire. The first prediction assumes unfamiliar songs are not answered, while the second assumes they require the female to create a new link in her duet code. I created a Monte Carlo simulation to test the second prediction. Again I used only responses that came as song type switches, and only the first response to each stimulus block. Each answer was scored as either predicted by the first half of the chimerical stimulus, predicted by the second half of the chimerical stimulus, or not predicted by either half. The null probability of answering according to either prediction was assumed to be 2/(known repertoire size × f), to account for the two predicted answers to each stimulus. In all other respects, the simulation was the same as those described above.

It was determined that females do apply their codes to chimerical stimuli (see Results), allowing me to use the CMS data to investigate song type categorization. The primacy hypothesis predicts that the first half of the chimerical stimuli will have a disproportionately strong influence on female song choice, while the recency hypothesis predicts that the second half will have a stronger influence. I tested these predictions with a Wilcoxon signed-ranks test comparing the number of answers predicted by the first half of the stimulus versus the second half among first answers within a stimulus block that were song type switches. The proportionality hypothesis predicts that the proportion of the chimerical stimulus that constitutes song type S will predict the likelihood of the female responding with the appropriate answer to S. I tested this by generating sonagrams of the chimerical stimuli in Syrinx (Hanning window, FFT = 512 points, temporal resolution = 0.002 s) and measuring the duration of the first and second song fragments. The gap between the fragments did not contribute to either measurement. I ran a probit regression comparing the proportional representation of the first half of the stimulus versus the proportion of answers predicted by the first half, controlling for individual. Answers that were not predicted by either half of the chimerical stimulus did not contribute to this analysis.

Monte Carlo simulations were conducted with the program Crystal Ball (Decisioneering, Denver, Colorado, U.S.A.). I used SPSS for Windows 11.0.1 (SPSS, Chicago, Illinois, U.S.A.) to conduct the ANCOVA, Wilcoxon test and probit regression. Results are summarized as means ± SD, except the results of Monte Carlo analyses and rank-based tests, which are summarized as medians with interquartile range in parentheses.

RESULTS

Female Response to Male Songs

I attempted MS playbacks with 12 females. Two trials resulted in no answers and one trial was marred by answers from a second (unbanded) female, leaving nine usable trials, all of which contained one or more independent responses. Female known repertoires averaged 12.2 ± 4.1 song types. The two females used to estimate f sung 12/13 and 18/19 song types as answers, so f was estimated at 94%. Overall, females answered 14.1 ± 11.3 male song stimuli (35.3 ± 28.4% of stimuli). Among independent answers, 94.4 ± 16.7% of female answers met the predictions (Table 1). The median proportion of predicted answers far exceeded that expected from random answering (Monte Carlo simulation: 10,000 iterations, maximum simulated = 0.33, observed = 1.00(0.0), N = 9, P < 0.0001).

Male Response to Female Songs

I attempted FS playback with 12 males. All of the males answered stimuli, but two never switched song types, and so provided no answers that met the independence criteria. The known repertoire size of the 10 males that contributed to the data set averaged 22.8 ± 10.0 song types. The two males from which I estimated f were observed to use 27/38 and 13/21 song types as answers, respectively, resulting in an estimated f of 67%. Overall, males answered 15.7 ± 8.4 female song stimuli (39.2 ± 21.0% of stimuli). Most of the time (139/176 answers) males did not switch song types to answer stimuli. Among independent answers, 31.3 ± 37.6% of male answers adhered to predictions (Table 2). Five of the males issued no predicted answers, but the other five chose a high proportion of predicted answers (Table 2). The median proportion of predicted answering significantly exceeded

<table>
<thead>
<tr>
<th>Expected Female p(predicted) Answers*</th>
<th>Stimulus types answered*</th>
<th>Observed p(predicted)†</th>
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</thead>
<tbody>
<tr>
<td>BG 0.11 6 4 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BI 0.06 3 3 1</td>
<td></td>
<td></td>
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<tr>
<td>BM 0.10 2 2 1</td>
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<tr>
<td>BU 0.10 2 2 0.5</td>
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<tr>
<td>CB 0.15 10 4 1</td>
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<td>CG 0.13 2 2 1</td>
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<tr>
<td>CM 0.08 12 4 1</td>
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<td>CT 0.08 11 4 1</td>
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<tr>
<td>CW 0.06 6 3 1</td>
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</tbody>
</table>

*Includes only first answers from each stimulus block that were song type switches (‘independent answers’). The average number of total answers is reported in the text.
†Averaged over stimulus types.
the expected median proportion given random answering (Monte Carlo simulation: 10,000 iterations, maximum simulated = 0.42, observed = 0.25(0.56), N = 10, P = 0.0017).

### Comparing Male and Female Answering

In this analysis, G scores indicate the strength of association between stimulus types and answer types. G scores for males were significantly lower than those for females when accounting for the number of answers (males: 10.0 ± 9.7; females: 19.0 ± 17.0; ANCOVA: answers: F_{1,17} = 114.9, P < 0.001; sex: F_{2,17} = 17.1, P < 0.001). Thus, the association between stimuli and responses was stronger in females.

### Female Response to Chimerical Male Songs

Eleven CMS trials were attempted, but in one pair the female that contributed to the predictive recordings had been replaced by a new female, leaving 10 usable trials. The 10 subjects had an average repertoire size of 10.8 ± 3.3 song types. Overall, females answered 9.2 ± 10.1 chimerical stimuli (23.0 ± 25.3% of stimuli). Compared to MS trials, CMS trials tended to elicit a lower overall number of answers, but this difference was not statistically significant (MS: 16.0(21.0) answers; CMS: 4.5(8.5) answers; Mann–Whitney test: U = 35.5, N1 = 9, N2 = 10, P = 0.44), and some females answered many CMS stimuli (e.g. 21 and 32 answers). During the chimerical song trials, 91.1 ± 16.8% of independent answers met the predictions for one of the male songs composing the chimera (Table 3). A Monte Carlo simulation confirmed that the observed median proportion of predicted answering far exceeded that expected from random answering (10,000 iterations, maximum simulated = 0.58, observed = 1.0(0.08), N = 10, P < 0.0001).

I assigned each female answer elicited during the chimerical male song trials to one of three categories: predicted by the beginning of the stimulus, predicted by the end of the stimulus, or unpredicted. Among independent answers, 45.2 ± 28.4% of answers were predicted by the first half, 45.9 ± 34.7% were predicted by the second half and 8.9 ± 16.8% were unpredicted. There was no evidence that females preferentially answered according to either the first or second half of the stimulus (answers to first half: 1.0(1.0); answers to second half: 1.5(1.8); Wilcoxon signed-ranks test: N = 10, P = 0.77). A similar test using all data (not just those that met the independence criteria) produced qualitatively identical results. The proportional representation of a song type in the chimerical stimulus was a strong predictor of the female’s choice of answer (probit regression: χ^2_{1} = 58.1, P < 0.001).

### DISCUSSION

Black-bellied wren duets are structured by a bidirectional duet code to which females adhere strongly and males adhere weakly. Females in the present study could have answered each MS stimulus with many different song types, but they consistently chose the predicted response. The strength of this pattern is remarkable. The FS trials demonstrated that males respond to their mates’ songs according to predictions based on recorded MS → FS transitions. Unlike females, males do not adhere very strictly to duet codes. Taken together, these findings suggest that males learn their mate’s duet codes (see also Marshall-Ball et al. 2006). Answering rules similar to those discovered in the black-bellied wren may be responsible for the nonrandom song type associations reported in the duets and choruses of other wrens (Farabaugh 1983; Levin 1988, 1996; Mann et al. 2003, 2005; Mennill & Vehrencamp 2005) and may explain the limited use of duet matching during simulated counterduetting in the plain wren, *T. modestus* (Marshall-Ball & Slater 2004).

The playback technique used in the present study focused on the individual’s decisions to link response types to stimulus types. This focus on the individual comes at the cost of holism, because the technology...
does not yet exist to apply this type of interactive playback to duets with many components. It is important to acknowledge this limitation, because observational studies on other species have indicated that answering rules change throughout the course of a duet song. Vencl & Souček (1976) recorded 141 duets from one captive pair of white-crested laughing thrush, Garrulax leucolophus, and they concluded that both pairmates follow well-defined ‘control programs’ made up of ordered phases (note: phases, not phrases). Within a phase, pairmates alternate a particular male song with a particular female song, suggesting adherence to a duet code. Males signal the transitions from one phase to the next with a special song type that breaks the loop. Because phases are ordered, song answering rules change throughout the course of a duet song. Position dependent answering rules are also indicated in the African drongo, Dicrurus adsimilis (Wickler 1976), and Australian magpie, Gynohina tibicen (Table 2 in Brown & Farabaugh 1991).

Chimerical male song playback demonstrated that females can accurately classify a male song type from recombined fragments of male song. This ability may allow females to generalize between different renditions of a particular song type (e.g. those sung by two different males), or to apply their codes to novel song types composed of familiar elements. Regarding the second possibility, certain male song elements are found in more than one song type, suggesting that recombination of elements plays a role in male song type evolution (D.M.L., unpublished data). I found no evidence to support the primacy hypothesis or the recency hypothesis; female answers were equally influenced by the beginnings and endings of chimerical songs. Attending to both the beginning and the end of songs may allow females to classify more male song types than if they attended to only one half of the song (Horning et al. 1993). The proportional representation of a male song type in a chimera was a good predictor of the female’s answer, supporting the proportionality hypothesis. Eliciting answers to song playback is a promising technique for investigating song type categorization in duet-coding birds. For example, it would be interesting to test how female song classification is affected by natural variation in male song structure or by environmental degradation of stimuli.

It is important to distinguish the functional significance of song answering generally (reviewed in Hall 2004) from the functional significance of answering according to a code. The remainder of this discussion concerns the latter. Ample evidence suggests that duet song mediates the cooperative defence of resources (reviewed in Logue 2005). According to the following two hypotheses, adherence to duet codes complements this function of duet participation by encoding identity into the signal. In the first hypothesis, identity is communicated between pairs; in the second, identity is communicated within pairs. The first hypothesis states that answering according to a duet code is simply a means of generating pair-specific duets that facilitate recognition by neighbours. In at least some species, birds can distinguish the duets of neighbours from those of strangers (Wiley & Wiley 1977; Hall 2000). Adherence to a duet code generates duets composed of pair-specific song type combinations, which could facilitate this type of recognition.

The second hypothesis is that mated birds recognize pairmates by their adherence to a known duet code (Thorpe 1973; Farabaugh 1983; Logue 2006). Duet-singing species are characterized by a high ratio of intersexual to intrasexual aggression during natural and simulated agonistic encounters (Logue 2005). Intersexual aggression complicates the act of defending the territory. For example, when two pairs are involved in a conflict at a territory border, each individual must defend against two enemies and cooperate with one ally while negotiating a three-dimensional battle in dense foliage. In this context, it is critical that birds do not confuse their pairmate with their enemies. Similarly, when both sexes sing to advertise territory ownership, territory owners would benefit from the ability to consistently distinguish the vocalizations of the pairmate from those of neighbours or nonterritorial floaters. In both cases, pairmates share a common interest in knowing each other’s identities and in being recognized by the mate. Furthermore, each pairmate has perfect information of his/her own identity. There is high potential for the evolution of information transfer under these conditions (Bradbury & Vehrencamp 1998).

If identification based on individual variation in song structure is unreliable owing to environmental degradation, selection may favour senders that provide reliable identity information by responding according to a duet code. Similarly, selection may favour receivers that recognize their mates on the basis of this reliable signal. Like many species that duet with nonrandom song type association, black-bellied wrens live in tropical forests where acoustic signals are degraded by high levels of reverberation and attenuation (both global and frequency dependent), and embedded in substantial noise (Morton 1975; Slabbekoorn 2004). These conditions are expected to impair a receiver’s ability to extract information from subtle signal features, including those that contribute to individual variation within song type. Song type itself, however, is not a subtle feature, but a very bold feature that can be recognized (at least by human listeners) in spite of substantial degradation and noise. Solo song type is a poor indicator of identity because types are widely shared within sex. For example, an intruding female who shared one song type with a resident female, could sing the shared song to avoid attack from the resident male. A duet code, however, would be virtually impossible to imitate over multiple answers. A male black-bellied wren could unambiguously determine whether an answering bird is his mate by singing one or more song types and comparing the answers to his mate’s duet code.

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