



Aggressive responses of male and female rufous-and-white wrens to stereo duet playback

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Hypotheses for the function of animal vocal duets fall into three broad categories. Male and female breeding partners may use duets to communicate with each other, to communicate with same-sex outsiders, or to communicate with opposite-sex outsiders. To evaluate these categories of duet function, I gave stereo duet playback to territorial pairs of duetting rufous-and-white wrens, *Thryothorus rufalbus*, in northwestern Costa Rica. I simulated duets of a rival pair of wrens by simultaneously broadcasting male and female duet components through separate loudspeakers. Territorial males and females responded aggressively to duet playback by rapidly approaching the speakers and singing both solo songs and duets. Males sang more songs in response to playback than females, but both sexes responded to approximately half of their partner's songs to create duets. The aggressive responses of territorial pairs were consistent with a territorial defence hypothesis for duet function. Males spent more time near the male speaker and approached the male speaker more closely, suggesting that male duet contributions play a role in intrasexually aggressive extrapair communication. Females approached the male and female speakers with similar intensity, although they tended to respond more strongly to the male speaker. In the few cases where females responded independently of their partner, they responded more strongly on the side of the female speaker. Taken together, responses of rufous-and-white wrens to stereo duet playback suggest that duets play a role in territory defence against conspecific rivals, and, for males, duets may play an additional role in mate guarding and paternity guarding.

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Breeding partners coordinate their songs to produce vocal duets in a variety of taxa, including birds (reviewed in Hall 2004), insects (reviewed in Bailey 2003), frogs (reviewed in Emerson & Boyd 1999) and primates (e.g. Geissmann 2002). The numerous hypotheses proposed to explain the function of vocal duets fall into three categories based on the intended signal receiver: those that propose that duets allow male and female breeding partners to communicate (1) with each other, (2) with same-sex outsiders and (3) with opposite-sex outsiders (Hall 2004). Stereo duet playback, an experimental technique that uses a pair of speakers to simulate the songs of a duetting pair of animals (Langmore 2002), offers unique possibilities for distinguishing between these hypotheses. With male and female duet contributions' broadcast through different

speakers, the responses of territorial birds to same-sex versus opposite-sex outsiders can be examined separately.

Two recent studies have used stereo duet playback to explore the adaptive significance of avian duetting behaviour. Rogers et al. (2004) found that stereo duet playback to magpie-larks, *Grallina cyanoleuca*, elicited more aggressive approach responses than when the same stimuli were broadcast through a single speaker. This result suggests that the distance between duet partners is a salient feature of avian duets. Unfortunately, the sexes of the stimuli used by Rogers et al. (2004) were unknown, and consequently any differential responses to the male versus female stimulus could not be evaluated. Logue & Gammon (2004) used stimuli of known sex to give stereo duet playback to black-bellied wrens, *Thryothorus fasciatoventris*. Black-bellied wren pairs approached the speakers broadcasting the male and female duet contributions with roughly equal intensity, although females were more likely to approach the speaker broadcasting the female duet contribution following playback of female-initiated duets.

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Two-speaker playback experiments with nonduetting European nightingales, *Luscinia megarhynchos*, and black-capped chickadees, *Poecile atricapillus*, have shown that territorial male songbirds are more likely to approach the speaker broadcasting songs that overlap the other speaker (i.e. the last song heard in a countersinging exchange; Naguib & Todt 1997; Mennill & Ratcliffe 2004). In a nonoverlapping context, nightingales preferentially approach the speaker broadcasting a leader role (i.e. the first song heard in a countersinging exchange; Naguib et al. 1999). In many duetting birds, male and female duet components alternate (e.g. magpie-larks: Rogers et al. 2004; black-bellied wrens: Logue & Gammon 2004; plain wrens, *Thryothorus modestus*: Mann et al. 2003; eastern whipbirds, *Psophodes olivaceus*: Mennill & Rogers, in press). In other species, male and female duet components overlap, where one bird begins singing before their partner's song is complete (e.g. rufous-and-white wrens, *Thryothorus rufalbus*: Mennill & Verehncamp 2005; tropical boubous, *Laniarius aethiopicus*: Grafe & Bitz 2004). For both alternating and overlapping duets, the responses of birds to stereo duet playback may be influenced by the order in which the male and female stimuli are presented. That is, birds may be motivated to respond differently to the speaker broadcasting the duet initiator or the duet responder stimulus regardless of the sex of that stimulus.

I used stereo duet playback to evaluate whether male and female rufous-and-white wrens respond differently to speakers broadcasting male versus female duet contributions. Rufous-and-white wrens present a special opportunity to overcome the problem of order effects in birds' responses to stereo duet playback. Male and female rufous-and-white wrens sing duets with clear initiator and responder roles (the average delay between the start of the duet initiator's song and the start of the duet responder's song is approximately 2 s; Mennill & Verehncamp 2005). However, pairs sometimes sing duets composed of male and female songs that are sung simultaneously (personal observation). By broadcasting male and female duet contributions simultaneously, the influence of the order of stimulus presentation can be ruled out.

I simulated the duets of rufous-and-white wrens by simultaneously playing male and female songs through stereo speakers positioned 16 m apart. I evaluated the responses of territorial pairs of wrens to the two speakers to test predictions of the three categories of hypotheses for duet function. If males and females communicate with opposite-sex outsiders through duets, I predicted that territorial males would respond more intensely to the female speaker and that territorial females would respond more intensely to the male speaker. If males and females communicate with same-sex intruders through duets, I predicted that territorial males would respond more intensely to the male speaker and that territorial females would respond more intensely to the female speaker. If duets function primarily in within-pair communication, I predicted that birds would respond weakly to playback, or with equally strong responses to the two speakers.

METHODS

General Field Methods

I gave stereo duet playback to mated pairs of rufous-and-white wrens living in humid evergreen forests in Sector Santa Rosa of the Area de Conservación Guanacaste (10°40'N, 85°30'W; $N = 16$ pairs) and along the Bajo del Tigre Trail of the Bosque Eterno de Los Niños (10°18'N, 84°48'W; $N = 8$ pairs) in northwestern Costa Rica. As part of an ongoing research project, birds were captured using mist nets and given one numbered aluminium band and three coloured leg bands in unique combinations. A total of 48 birds (24 breeding pairs) were involved in this experiment; 30 of 32 playback subjects in the Santa Rosa population were colour-banded and 2 of 16 playback subjects in the Bajo del Tigre population were colour-banded. Unbanded rufous-and-white wrens were easy to distinguish because pairs are territorial and rarely move beyond their territory boundaries. Although the sexes look alike, the songs of male and female rufous-and-white wrens show substantial differences (Mennill & Verehncamp 2005) and vocal cues allow experienced listeners to unambiguously distinguish between the sexes. The vocal repertoires of all playback subjects were catalogued before playback (see Mennill & Verehncamp 2005) and identities were confirmed by comparing birds' known repertoires to sound spectrograms of recordings made during playback.

Playback Technique

Playback trials were conducted between 24 April 2004 and 31 May 2004, early in the rufous-and-white wren breeding season. All playback subjects were monitored during the 2 days before playback to establish their territory boundaries and their stage of breeding. All pairs were actively nest building on the day that they received playback but none had completed nest building or commenced egg laying. Playback sessions were performed between 0700 and 1100 hours, a time of day when males have completed their dawn chorus song performance but when pairs often engage in bouts of duetting, male solo singing and female solo singing (Mennill & Verehncamp 2005).

The playback apparatus consisted of a pair of speakers (Sony SRS-A37) positioned within the boundaries of the subjects' breeding territory. The left and right speakers were separated by 16 m, a distance not atypical of duetting pairs of rufous-and-white wrens (personal observation). Speakers were oriented upwards and mounted on poles at a height of 1 m. After poles were put in position, a coin toss determined which pole would receive the left speaker versus the right speaker. Thus, speakers were positioned before determining which speaker would broadcast the male stimulus and which would broadcast the female stimulus. A flag was hung halfway between the two speakers as a reference point for measuring birds' positions during playback. Speakers were connected to a portable CD player (Sony D-SJ301), which was operated by an observer from a concealed position 30 m equidistant from both

speakers. Volume of speakers was held constant across playback trials at a natural sound pressure level (80 dB at 1 m horizontal distance from the upwards-oriented speaker using a Realistic 33-2050 sound level metre on slow setting).

The songs of playback subjects were recorded during playback trials using a directional microphone (Sennheiser MKH-70) connected to a solid-state digital recorder (Marantz PMD-670). The positions of the playback subjects relative to the playback speakers and the central flag were dictated quietly into the microphone during the trial.

Playback began when the focal pair had been silent for at least 5 min. Playback lasted 10 min and occurred in two rounds. In round 1, six duet stimuli were broadcast at a rate of one duet every 10 s. The behaviours of the resident male and female were observed during playback and for 4 min following playback. In round 2, which immediately followed the end of the round 1, the six duet stimuli were broadcast again through the same speakers. Again the behaviours of the resident male and female were observed during playback and for 4 min following playback. During a pilot experiment in 2003, I found that many subjects responded strongly to the speaker nearest to them upon their initial approach (unpublished data). Birds may have responded more strongly to the nearer speaker because it seemed louder than the more distant one, because the position of the nearer speaker was easier to triangulate, or simply because the nearer speaker was the first one encountered. To overcome this potentially confounding pattern of behaviour, I incorporated a repeat of the playback stimulus. Although birds' responses in round 1 may have been influenced by the direction of their initial approach, birds in round 2 would already be near the playback apparatus and might be more likely to localize the two speakers and tactically choose which speaker to approach.

Playback Stimuli

Playback stimuli were stereo sound files where the male duet contribution was restricted to one channel and the

female duet contribution to the other channel (Fig. 1). All stimuli were recorded as monaural recordings (16-bit WAV files) from birds during spontaneous bouts of duetting in the 2 weeks before playback. The male and female duet contributions were separated using the 'frequency cursor filter' function of Syrinx-PC (J. Burt, Seattle, Washington, U.S.A.), which allows the user to apply multiple small-bandwidth filters and thereby remove either the male's song or the female's song from the original duet recording. The amplitudes of both the male and female duet contributions were subtly modified using the 'amplitude normalize' feature of CoolEdit 2000 (Syntrillium, Phoenix, Arizona, U.S.A.) so that all songs were broadcast at the same amplitude. The male and female duet contributions were then pasted separately into the left and right channels of a 16-bit stereo WAV file in CoolEdit 2000. The male and female duet contributions were given simultaneously so that they overlapped exactly (Fig. 1). Whether the male or female duet contribution was assigned to the left or right channel was alternated across trials. Sound files were burned to CD in Audio CD format using iTunes (Apple, Cupertino, California, U.S.A.).

Each pair of playback subjects received a different stimulus. The 24 stimuli were recorded from 24 pairs of birds. The stimulus pair was always a non-neighbouring pair to the playback subjects, where mean \pm SE distance between the territory of the stimulus pair and the subjects was 1.7 ± 0.2 km.

Response Measures

To measure birds' vocal behaviour, I used Syrinx-PC to visualize spectrograms of the recordings made during playback. I tabulated all songs produced during the 1-min playback periods and 4-min observation periods in both round 1 and round 2. Songs given by playback subjects were scored as belonging to one of five groups (see Mennill & Verehncamp 2005): (1) male solos, (2) female solos, (3) duets consisting of a male song followed by a female song ('male-initiated duets'), (4) duets consisting of a female song followed by a male song ('female-initiated

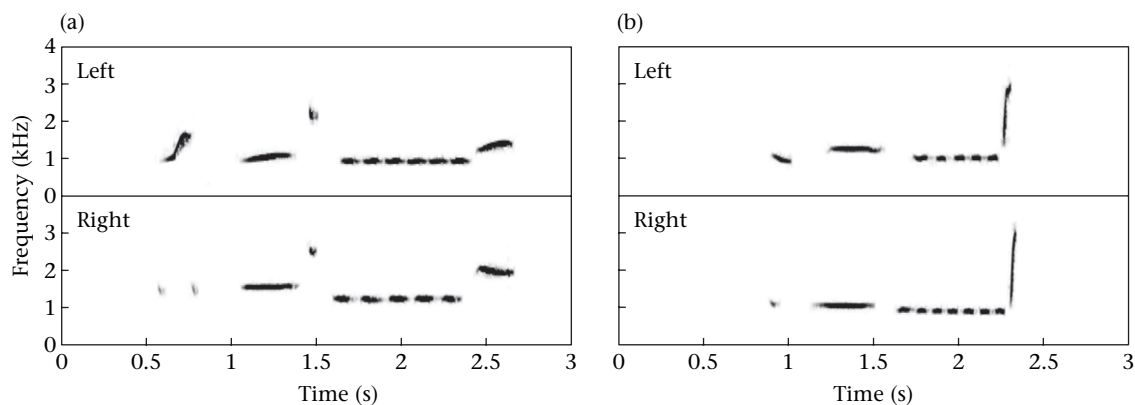


Figure 1. Stereo spectrograms of stimuli used to simulate the duets of rufous-and-white wrens. Male and female duet contributions were given in an exactly overlapping fashion through stereo loudspeakers positioned 16 m apart. (a) The male duet contribution is in the left channel and the female is in the right channel. (b) The female duet contribution is in the left channel and the male is in the right channel.

duets'), and (5) duets consisting of a male and female singing in an exactly overlapping fashion ('simultaneous duets'). I calculated the duet responsiveness rate of females as the proportion of male songs with which the female duetted (i.e. the number of songs of group 3 divided by the sum of the number of songs of groups 1 and 3). Similarly, I calculated a responsiveness rate for males as the proportion of female songs with which the male duetted (i.e. the number of songs of group 4 divided by the sum of the number of songs of groups 2 and 4). I calculated the latency from the first playback stimulus to the first song sung by each of the playback subjects, regardless of whether their first song was given as a solo or as part of a duet.

I calculated two measurements of birds' physical behaviour: (1) the closest approach to each speaker by each member of the pair and (2) the relative proportion of the playback session spent closer to the male speaker versus the female speaker. Rufous-and-white wrens inhabit densely foliated humid forest; consequently, it was not possible to maintain visual contact with birds throughout the trials, and thus to accurately calculate the number of flights made by playback subjects or to determine which sex initiated movements towards the speakers. Birds were typically within the sight lines of the observer for at least 50% of each trial and the birds' vocalizations consistently allowed the observer to confidently identify their location relative to the speakers and the central flag.

Statistical Approach

I gave playback to 24 territorial pairs (i.e. 48 playback subjects). For 17 of 24 pairs, both the male and the female responded to playback, in four cases, only the male responded, and in three cases, neither bird responded. I compared the behaviour of males and females for 17 pairs where both the male and the female responded. In round 1, both the male and the female responded to playback in all 17 pairs, but in round 2, both the male and the female responded for 14 pairs, only the male responded for two pairs, and neither the male nor the female responded for one pair. Dense vegetation made it impossible to determine whether birds that did not respond were absent from the playback area or were present in the area but silent and still.

I used binomial tests to evaluate whether birds were more likely to approach the speaker broadcasting the male or female duet contribution. All analyses were conducted in JMP 5.0.1 (SAS, Miami, Florida, U.S.A.). All tests are two tailed. All values are reported as mean \pm SE.

RESULTS

Territorial pairs of rufous-and-white wrens responded to 17 of the 24 attempted stereo duet playback sessions by singing and approaching the speakers. In many trials, subjects gave harsh chattering calls and tail-wagging displays near the speakers. Both of these behaviours are often given in the presence of actual territorial intruders or predators (personal observation). Song rates were much higher in response to stereo duet playback (87.6 duets/h or

7.3 duets/5 min; Table 1) compared with spontaneous song rates (10.0 duets/h; Mennill & Verehncamp 2005). Therefore, the responses of males and females to stereo duet playback were consistent with aggressive reactions.

Vocal Responses

Birds responded to stereo duet playback by singing both solo songs and duets. In round 1, the first vocalization was a duet for 11 pairs (seven were male-initiated duets, four were female-initiated duets) and a male solo for the remaining six pairs ($N = 17$ responses to round 1). In round 2, the first vocalization was a duet for nine pairs (six were male-initiated duets, three were female-initiated duets), a male solo for six pairs, and a female solo for one pair ($N = 16$ responses to round 2). The first bird to sing in response to playback, either by singing a solo or the first part of a duet, was more often the male than the female in round 1 (binomial test: $P = 0.05$) and tended in the same direction in round 2 ($P = 0.08$). During both rounds of playback, male solos were the most common vocalization, followed closely by duets, whereas female solos were relatively rare (Table 1). Males gave significantly more solos than females in round 1 (paired t test: $t_{16} = 4.1$, $P < 0.001$) and round 2 ($t_{15} = 4.1$, $P < 0.0005$; Table 1).

The majority of duets given in response to playback were male-initiated duets (i.e. duets created by females responding to male's song). Male-initiated duets were more common than female-initiated duets in round 1 ($t_{16} = 2.2$, $P = 0.04$) and round 2 ($t_{15} = 3.7$, $P = 0.002$; Table 1). However, because males sang more solo songs than females, the rate of duet responsiveness was similar for both sexes; both males and females responded to approximately half of their partner's songs to create duets (Table 1). Duet responsiveness of males and females did not differ in round 1 ($t_{16} = 0.4$, $P = 0.68$) or round 2 ($t_{15} = 0.1$, $P = 0.90$).

Table 1. The vocal responses of male and female rufous-and-white wrens to stereo duet playback, showing the mean \pm SE number of each type of vocalization sung by territorial playback subjects in response to two 5-min rounds of playback (percentage of total vocalizations shown in parentheses)

| | Round 1 | Round 2 |
|-----------------------------|---------------------------------|-----------------------------|
| Male solos | 7.7 \pm 1.3 (40 \pm 6) | 6.3 \pm 1.0 (50 \pm 8) |
| Female solos | 2.1 \pm 0.6 (12 \pm 4) | 1.2 \pm 0.4 (7 \pm 2) |
| Male-initiated duets | 5.3 \pm 1.0 (33 \pm 6) | 5.8 \pm 1.2 (34 \pm 6) |
| Female-initiated duets | 2.1 \pm 0.9 (13 \pm 6) | 1.5 \pm 0.5 (9 \pm 3) |
| Simultaneous duets | 0.06 \pm 0.06 (0.2 \pm 0.2) | 0.13 \pm 0.13 (1 \pm 1) |
| Male responsiveness rate* | 48 \pm 10 | 45 \pm 7 |
| Female responsiveness rate† | 57 \pm 11 | 43 \pm 8 |

*Percentage of female songs that male answered to create a duet.

†Percentage of male songs that female answered to create a duet.

The latency between the first playback stimulus and the first song sung by the playback subjects was shorter in round 2 than round 1. Measured from the beginning of the first stimulus, the average delay to the first male song was 40.6 ± 6.9 s in round 1 ($N = 17$) versus 23.1 ± 3.8 s in round 2 ($N = 16$; $t_{15} = 2.2$, $P = 0.05$). The average delay to the first female song was 67.3 ± 13.9 s in round 1 ($N = 17$) and 26.4 ± 4.1 s in round 2 ($N = 14$; $t_{13} = 3.0$, $P = 0.01$). Males tended to respond with shorter latencies than females in round 1 ($t_{16} = 2.0$, $P = 0.07$), whereas males and females responded with similar latencies in round 2 ($t_{13} = 0.6$, $P = 0.55$).

Physical Responses

Breeding partners consistently approached the speakers together and all birds approached the playback apparatus from the same direction as their partner. In round 1, birds tended to spend more time near the speaker that was closer to them on their initial approach. Fifteen pairs clearly approached from a direction that was unambiguously on one side of the two-speaker apparatus (the remaining two pairs approached along a path that was equidistant from both speakers); among these 15 pairs, 11 spent the majority of round 1 near the speaker on the side of their initial approach (binomial test: $P = 0.12$). Among these same 15 pairs, eight spent the majority of round 2 near the speaker on the side of their initial approach ($P = 1.0$). Therefore, although there was a nonsignificant tendency for birds to respond more intensely to the speaker nearest to them on their initial approach in round 1, this tendency disappeared in round 2.

Male rufous-and-white wrens spent the majority of the playback observation period on the side of the male speaker in round 1 (binomial test: $P = 0.02$) and round 2 ($P = 0.004$; Fig. 2). Furthermore, most males approached the male speaker more closely than the female speaker in round 1 ($P = 0.05$) and round 2 ($P = 0.004$; Fig. 2). In round 1, the average male distance of closest approach was 8.6 ± 0.9 m to the male speaker versus 13.6 ± 1.3 m to the female speaker (paired t test: $t_{16} = 2.6$, $P < 0.02$), and in round 2, the average male distance of closest approach was 4.8 ± 0.8 m to the male speaker versus 14.5 ± 2.0 m to the female speaker ($t_{16} = 2.6$, $P < 0.02$). Males showed no tendency to spend more time on the side of the left speaker versus the right speaker (9 of 17 males spent more time on the side of the left speaker in round 1: $P = 0.31$; 9 of 16 males spent more time on the side of the left speaker in round 2: $P = 0.80$). Males also showed no tendency to approach the left speaker more closely than the right speaker (10 of 17 males approached the left speaker more closely than the right speaker in round 1: $P = 0.3$; 9 of 16 males approached the left speaker more closely than the right speaker in round 2: $P = 0.8$).

Female rufous-and-white wrens showed no significant tendency to spend more time on the side of the male speaker versus the female speaker, in either round 1 (binomial test: $P = 0.14$) or round 2 ($P = 0.18$; Fig. 2a). In round 1, the average female distance of closest approach was 14.0 ± 2.4 m to the male speaker and 15.4 ± 3.6 m to the female speaker (paired t test: $t_{16} = 0.5$, $P = 0.60$). In round 2, females showed a nonsignificant tendency to approach the male speaker more closely: the average female distance of closest approach was 8.5 ± 1.7 m to the male speaker and 13.0 ± 3.2 m to

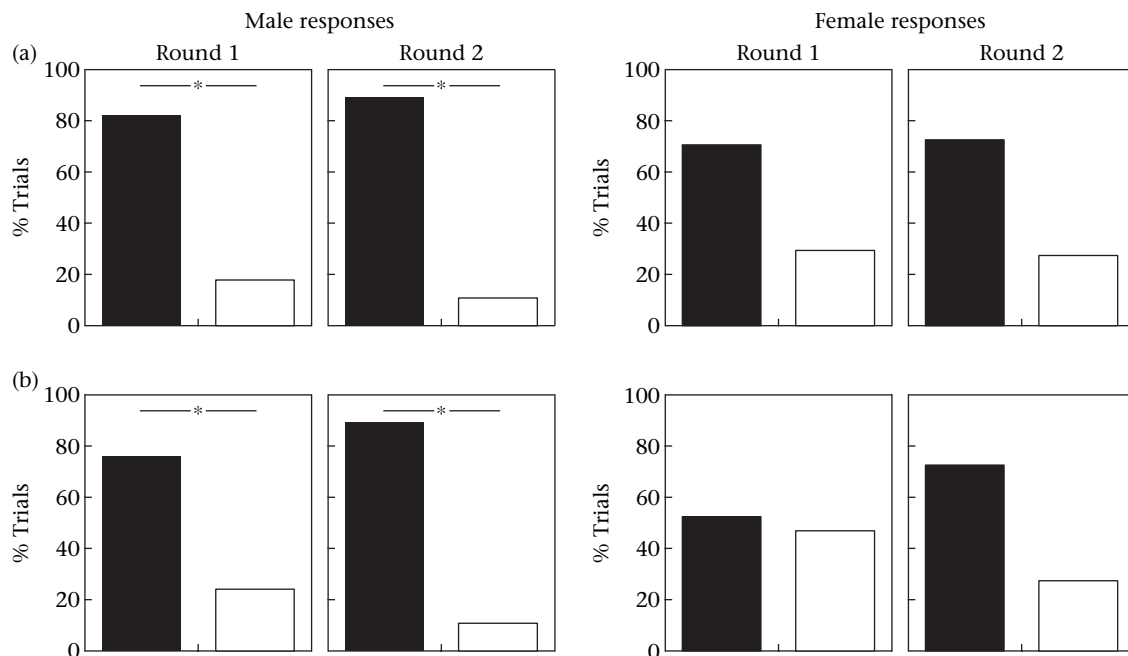


Figure 2. Responses of territorial male and female rufous-and-white wrens to two rounds of stereo duet playback of a non-neighbouring pair. In both rounds of each trial, one speaker broadcast the male duet contribution and the other speaker broadcast the female duet contribution. (a) Percentage of trials in which territorial birds spent more time near the male speaker (■) versus the female speaker (□). (b) Percentage of trials in which territorial birds more closely approached the male speaker (■) versus the female speaker (□).

the female speaker (paired t test: $t_{14} = 1.9$, $P = 0.08$). Females showed no tendency to spend more time on the side of the left speaker versus the right speaker (11 of 17 females spent more time on the side of the left speaker in round 1: $P = 0.33$; 8 of 14 females spent more time on the side of the left speaker in round 2: $P = 0.79$). Females also showed no tendency to approach the left speaker more closely than the right speaker (6 of 17 females approached the left speaker more closely in round 1: $P = 0.33$; 6 of 14 females approached the left speaker more closely in round 2: $P = 0.79$).

Most male and female rufous-and-white wrens responded on the same side of the two-speaker apparatus as their partner. Measured as the amount of time spent on each side of the playback apparatus, males and females showed the same side preference as their partner in round 1 (in 15 of 17 trials, the male and female spent the majority of round 1 on the same side; binomial test: $P = 0.002$) and they showed a similar tendency in round 2 (in 11 of 14 trials the male and female spent the majority of round 2 on the same side: $P = 0.06$). Interestingly, in all trials where males and females did not respond on the same side, the male responded more strongly on the side of the male speaker and the female responded more strongly on the side of the female speaker ($N = 5$ pairs).

DISCUSSION

Rufous-and-white wrens responded aggressively to stereo duet playback. Territorial males and females approached the playback speakers together and sang solos and duets at much higher levels than normal (Mennill & Verehncamp 2005). Playback responses suggest that rufous-and-white wren duets play a role in communication with outsiders. The aggressive behaviour and the increase in duet singing shown by both males and females indicate that duets are important in territory defence against conspecific rivals (Seibt & Wickler 1977).

The playback responses of males suggest further functions of rufous-and-white wren duets in addition to territory defence. Males clearly distinguished between speakers broadcasting male versus female stimuli, spending more time on the side of the male speaker and approaching the male speaker more closely. Male responses therefore matched the prediction of the second category of hypothesis for duet function, that male participation in duets is important in communication with same-sex outsiders. Two hypotheses fall within this category: the mate-guarding hypothesis (Stokes & Williams 1968) and the paternity-guarding hypothesis (Sonnenschein & Reyer 1983; Hall 2004). Under both hypotheses, males advertise their partner's mated status by duetting in the presence of same-sex outsiders. If mate guarding and paternity guarding are important behaviours for male rufous-and-white wrens, divorce and/or cuckoldry must be potential threats. Ongoing research exploring divorce rates and extrapair paternity in rufous-and-white wrens and other duetting species will be helpful for understanding the nature of the threat posed by rival conspecific males.

Female rufous-and-white wrens did not show a significant directional response to the two-speaker apparatus, in contrast to the pattern seen among males. Four interpretations may explain females' similar responses to the male and female speakers.

(1) Females may not be able to differentiate between male and female songs. This interpretation is unlikely because the songs of male and female rufous-and-white wrens show gross differences in fine structure (Mennill & Verehncamp 2005).

(2) Females may perceive male and female duet contributions as equally threatening. Although playback responses suggest that mate guarding and paternity guarding may be important to male rufous-and-white wrens (above), these behaviours may be unimportant to females. In many birds, divorce and mixed matings appear to be female-initiated reproductive tactics that entail a high cost for males (Dhondt 2002; Mennill et al. 2004). Thus, males may participate in duets to guard their mate and/or paternity, and males may respond most strongly to male rivals because they pose an additional threat. Females, in contrast, may participate in duets solely to defend their territory against conspecific rivals of both sexes.

(3) The sample size in the current investigation may have been inadequate to detect a difference in female responses to male versus female duet contributions. Although nonsignificant, there was a tendency for females to respond more strongly to the male speaker, a tendency which was stronger in round 2 than round 1.

(4) Female responses may be influenced by male responses. In most playback sessions, males were the first birds to respond to playback. If the male leads the territorial pair's confrontation with a rival pair, and pairs benefit by remaining in close contact during aggressive territorial encounters, differential responses of females to the two speakers may have been overshadowed by females' drive to remain close to their partner. In all five cases where the male and female did not respond on the same side of the playback apparatus, the female responded more strongly on the side of the female speaker. This anecdotally supports the idea that females respond aggressively to other females, but future research should test this idea specifically by conducting stereo duet playback to females in the absence of males.

Using a similar two-speaker design, Rogers et al. (2004) showed that duetting magpie-larks respond to stereo speakers as a pair, where both the male and female respond most strongly to the same speaker. Similarly, my results show that rufous-and-white wrens respond to territorial intruders as a pair, approaching the same speaker in playback round 1 and tending to do the same in playback round 2. Logue & Gammon's (2004) stereo duet playback to black-bellied wrens, a congener of rufous-and-white wrens, revealed several differences in territorial birds' responses to playback of rivals' duets. Male black-bellied wrens did not approach the male speaker more closely than the female speaker, whereas females approached the female speaker more closely (Logue & Gammon 2004). Black-bellied wren duets involve alternating duet contributions by males and females, and playback order

effects may have contributed to the differences observed by Logue & Gammon (2004). Indeed, the female-directed responses of female black-bellied wrens resulted from playback sessions where the female stimulus was broadcast first (i.e. female-initiated duets). The differences in responses of these two closely related species of duetting wrens suggest that male-initiated duets, female-initiated duets and exactly overlapping duets may serve separate functions and communicate distinct signals of threat to territorial males and females.

Stereo duet playback offers several unique advantages for the study of duetting. Duets, by definition, are acoustic events that originate from two point sources. Birds are highly adept at localizing the distance and direction to conspecific singers (e.g. Naguib 1997). Duets broadcast through a single speaker may be perceived by birds as a single rival producing both male and female components of a duet. In at least one duetting bird species, the eastern whipbird, males are capable of producing both the male and female duet contributions (A. Rogers, personal communication); duets of this species played through a single speaker probably simulate a male solo instead of a duet. Stereo duet playback facilitates simulation of duets in a spatially realistic way. This may be more important to some duetting species than others. In some animals, males and females duet from side-by-side positions (e.g. magpie-larks: Hall & Magrath 2000; tropical boubou: Grafe & Bitz 2004), and a duet played through a single speaker might simulate a realistic duet in such species. In other animals, males and females often duet when they are separated by highly variable distances (e.g. rufous-and-white wrens: personal observation; eastern whipbirds: Watson 1969). In these species, stereo duet playback seems preferable to single speaker playback. Importantly, with duet contributions broadcast through separate speakers, the responses of territorial birds to male versus female duet contributions can be tested separately.

For rufous-and-white wrens, stereo duet playback demonstrates not only that duets play a role in joint territory defence, but also that males respond more strongly to the male contribution of duets whereas females respond with similar strength to both sexes of opponents. These results underscore the idea that duets serve multiple functions (Sonnenschein & Reyer 1983), and also that males and females may produce signals targeted for specific and potentially different receivers within their coordinated vocal displays. Although the responses of rufous-and-white wrens to duet playback demonstrate a territory defence function of duets, these results do not refute the idea that duets also serve some importance in within-pair communication. Ongoing research will clarify male and female communication strategies by evaluating the responses of territorial pairs to playback of male and female solos as well as to stereo playback of male-initiated and female-initiated duets.

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