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Report

Context-Dependent Functions of Avian Duets Revealed by Microphone-Array Recordings and Multispeaker Playback

Daniel J. Mennill[1,*] and Sandra L. Vehrencamp[2]
[1]Department of Biological Sciences
University of Windsor
401 Sunset Avenue
Windsor, Ontario N9B3P4
Canada
[2]Lab of Ornithology
Cornell University
159 Sapsucker Woods Road
Ithaca, New York 14850

Summary

In many tropical animals, male and female breeding partners combine their songs to produce vocal duets [1–5]. Duets are often so highly coordinated that human listeners mistake them for the songs of a single animal [6]. Behavioral ecologists rank duets among the most complex vocal performances in the animal kingdom [7, 8]. Despite much research, the evolutionary significance of duets remains elusive [9], in part because many duetting animals live in tropical habitats where dense vegetation makes behavioral observation difficult or impossible. Here, we evaluate the duetting behavior of rufous-and-white wrens (*Thryothorus rufalbus*) in the humid forests of Costa Rica. We employ two innovative technical approaches to study duetting behavior: an eight-microphone acoustic location system capable of triangulating animals' positions on the basis of recordings of their vocalizations [10] and dual-speaker playback capable of simulating duets in a spatially realistic manner [11]. Our analyses provide the first detailed spatial information on duetting in both a natural context and during confrontations with rivals. We demonstrate that birds perform duets across highly variable distances, that birds approach their partner after performing duets, and that duets of rivals induce aggressive, sex-specific responses. We conclude that duets serve distinct functions in aggressive and nonaggressive contexts.

Results and Discussion

Although vocal duets have long been known to occur in birds [1], insects [2], frogs [3], primates [4], and cetaceans [5], their function remains controversial [9]. Many competing hypotheses are invoked to explain the function of vocal duetting, some of which contend that duets arise through cooperation between pair members, whereas others propose that duets arise through conflict between the sexes [9]. The acoustic-contact hypothesis suggests that duets allow members of a mated pair to maintain contact in dense habitat where visual contact is obscured [6]. The territory-defense hypothesis suggests that duets allow pairs to cooperatively defend breeding territories against conspecific rivals [12]. The pair-bonding hypothesis suggests that duetting is a cooperative behavior that solidifies and maintains a social partnership [13], either by synchronizing reproductive physiology, coordinating reproductive activities, or signaling commitment between breeding partners [9, 14]. The mate-guarding hypothesis suggests that duetting is a noncooperative, intrasexually aggressive behavior in which male and female duet contributions advertise their partner's mated status to same-sex rivals [15]. These hypotheses lack resolution, in part because so many duetting animals live in densely foliated habitat where individuals cannot be monitored with conventional research techniques.

We used two innovative technical approaches to study duets: an acoustic location system (ALS), capable of triangulating the position of duetting animals on the basis of recordings of their vocalizations [10], together with the established technique of multispeaker playback, capable of simulating the voices of two animals in a spatially realistic manner [11, 16]. Combined, these techniques permit careful measurement of the relative position of duet partners, both during bouts of spontaneous duets and during duets sung in response to conspecific rivals. These technologies allow us to propose specific and novel predictions for each of the above hypotheses. Under the acoustic-contact hypothesis, we predict that males and females will perform duets when spatially separated from each other to provide information about their location, and we predict that birds may approach each other after a duet. Under the territory-defense hypothesis, we predict that duets will be given near territory boundaries, that duets will be associated with interactions with conspecific rivals or neighbors, and that animals will respond aggressively to duet playback. Under the pair-bonding hypothesis, we predict that pairs will perform duets while in close proximity to each other; that pairs will perform duets throughout their territory, but not preferentially near territory boundaries; and that during the breeding season, pairs may perform duets with a focus near their nest location to coordinate reproductive activities. Under the mate-guarding hypothesis, we predict strong responses to playback, and we predict that male and female playback subjects will respond most aggressively to the loudspeaker broadcasting the vocalization corresponding to their own sex.

We used an ALS and dual-speaker playback to test the functional significance of vocal duets in neotropical rufous-and-white wrens (*Thryothorus rufalbus*). Over a two-year period, we studied 19 territorial pairs of wrens living in the tropical humid forest of the Area de Conservación Guanacaste, Costa Rica. We monitored each pair of birds with an ALS and analyzed all recorded duets in two distinct contexts: a natural, unprovoked context and an aggressive context in which we used dual-speaker playback to simulate the solos and duets of rivals.

Duets Produced in a Natural Context

Recordings made with an eight-microphone ALS reveal a surprising degree of variation in the distance between male and female rufous-and-white wrens while they performed duets (Figure 1). Birds sang duets when they were as close together as 0.4 m and as far apart as 144.3 m (minimum and maximum distance across n = 525 duets from 19 pairs). Birds performed duets when separated by an average distance of 19.2 ± 2.2 m (n = 19 pairs; average of 27.6 ± 5.5 duets per pair).

*Correspondence: dmennill@uwindsor.ca

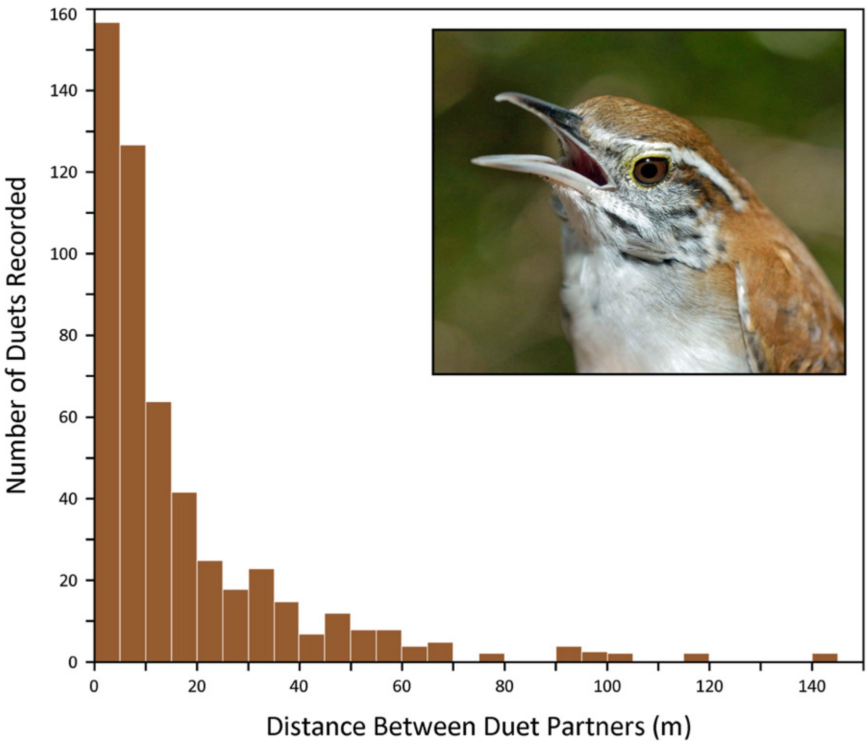

Figure 1. Rufous-and-White Wrens Perform Vocal Duets with Highly Variable Distances of Separation

Histogram showing distances between rufous-and-white-wren breeding partners while they are performing vocal duets in neotropical humid forest of Costa Rica, as measured with an eight-microphone acoustic location system (n = 525 duets recorded from 19 duetting pairs).

Breeding partners often performed duets in short bouts that contained two or more duets in rapid succession. During these duet bouts, birds approached their partner significantly more often than they retreated from their partner. In 45 of 65 duet bouts, the birds moved closer together (chi-square test, p = 0.002). The average distance moved by the male (18.7 ± 4.9 m) was similar to the average distance moved by the female (18.1 ± 4.9 m; paired t test: t = 0.3, p = 0.77). The bird that sang the first part of the duet moved significantly farther (18.4 ± 2.0 m) than the bird that sang the second part of the duet (14.5 ± 2.0 m; paired t test: t = 1.9, p = 0.05).

Rufous-and-white wrens did not commonly perform duets at territory edges, but instead performed duets throughout their territories (Figure 2). The average distance to the territory edge was similar among duetting males and duetting females, and both sexes sang duets from positions significantly farther from their territory edge compared to randomly generated points (Figure 3; ANOVA: $F_{2,54}$ = 7.8, p = 0.001). Pairs frequently performed duets in the proximity of their nest; the average distance to the pair's nest was similar among duetting males and duetting females, and both sexes were significantly closer to their nest than were randomly generated points (Figure 3; ANOVA: $F_{2,54}$ = 8.7, p = 0.0005). This result may be a consequence of breeding pairs' focusing their activities around the nest and performing many duets at this time.

Our findings that breeding partners perform duets with such variable distances of separation, that duets are not focused at territory boundaries, and that breeding partners commonly approach each other between subsequent duets support our predictions of the acoustic-contact hypothesis. With their call-and-response duets, rufous-and-white wrens appear to play a version of the children's game "Marco Polo"; one individual sings, listens for a response from its partner, and moves toward its partner after hearing a response. That the bird who sings the first part of a duet moves farther than the bird who sings the second part reinforces the idea that the start of a duet is a request for locational information from a bird's partner. Other duetting animals are known to duet when visually separated [15, 17], and breeding partners in another wren species have been observed to approach each other after duets [18]. Given that so many duetting animals live in the vegetatively diverse, visually occluded habitats of the tropics [19], acoustic contact may be a widespread function of duets. Nevertheless, pairs also performed duets at very close distances (Figure 1), suggesting that acoustic contact is not the sole function of duets.

Results of the ALS-based spatial analyses provide some support for predictions of the pair-bonding hypothesis: Pairs often perform duets while in close proximity to each other, and duets are sung throughout the territory without a focus at territory boundaries, although they are sung closer to their nest than expected by chance. A recent temporal analysis of duetting behavior shows that rufous-and-white-wren duets are most common in the early part of the reproductive period and immediately after nest-predation events [20], findings that offer further support for the pair-bonding model.

Responses to Dual-Speaker Playback

In response to playback simulating territorial intrusion by neighboring birds, rufous-and-white wrens increased their song output. The average song rate before playback—including male solos, female solos, and duets—was 1.97 ± 0.33 songs/min compared to 3.34 ± 0.33 songs/min after playback (paired t test: t = 4.1, p = 0.0006, n = 18). Duet output increased dramatically after playback; in the 20 min prior to playback, pairs sang an average of 1.20 ± 2.00 duets, but after playback treatments, pairs sang a significantly higher average of 6.80 ± 2.00 duets per 20 min (paired t test: t = 2.9, p = 0.009, average across four playback treatments to n = 18 pairs).

We gave four playback treatments to each territorial pair of birds: male solos, female solos, duets in which the female sang first and the male responded to create the duet ("male-created duets"), and duets in which the male sang first and the female responded to create the duet ("female-created duets"). Territorial males sang significantly more solos in response to all four treatments compared with their preplayback solo song rate, and male solo song rate was consistently high across the four treatments (Figure 4A; ANOVA: $F_{21,68}$ = 9.6, p < 0.0001; model effects: playback type: F_4 = 5.3, p = 0.001, pair: F_{17} = 3.9, p < 0.0001). Male solos were plentiful after all playback treatments, outnumbering both female solos and duets

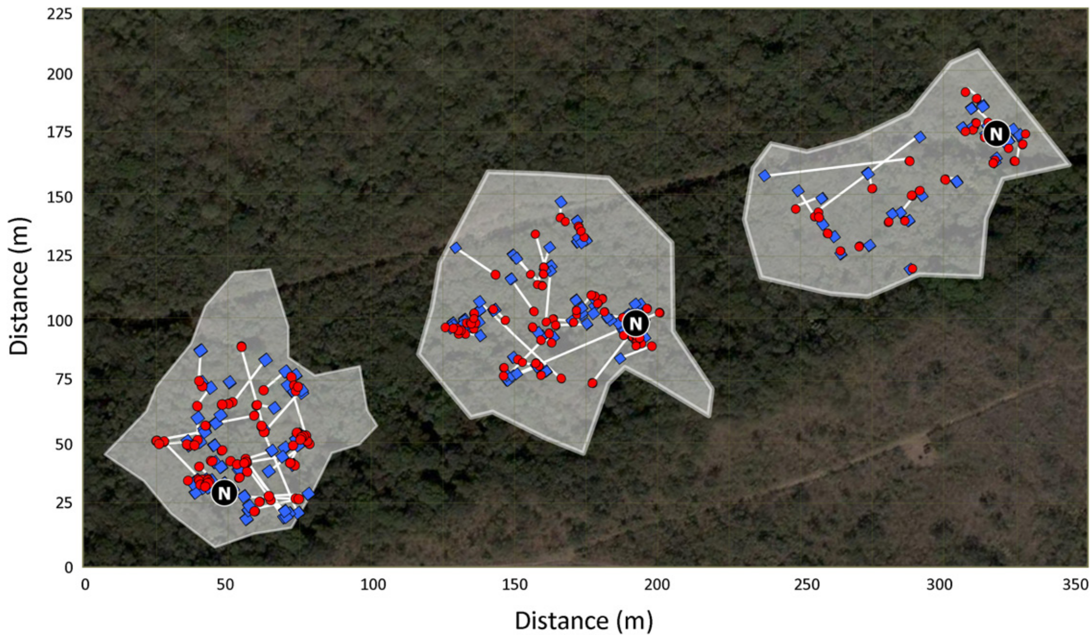

Figure 2. Map Showing the Positions of Duetting Male and Female Rufous-and-White Wrens in Guanacaste, Costa Rica

Duet positions of rufous-and-white wrens in three adjacent territories measured with an acoustic location system. Red circles show female positions, blue diamonds show male positions, and white lines connect the partners for each duet. Shaded regions show territories. Nest locations are indicated with black circles. Adjacent territories were recorded during successive 4-day intervals.

approximately ten to one (Figure 4). Females sang significantly more solos in response to female solos and male-created duets compared to their preplayback song rate, and they sang an intermediate level of solos in response to male solos and female-created duets (Figure 4B; ANOVA: $F_{21,68} = 6.1$, $p < 0.0001$; model effects: playback type: $F_4 = 4.2$, $p = 0.006$, pair: $F_{17} = 6.6$, $p < 0.0001$). Male-created duets were rare and occurred at similarly low levels across treatments (Figure 4C; ANOVA: $F_{21,68} = 1.9$, $p = 0.10$; model effects: playback type: $F_4 = 1.9$, $p = 0.16$, pair: $F_{17} = 2.1$, $p = 0.07$). Female-created duets were more common (Figure 4). Females created significantly more duets in response to all four treatments compared with their preplayback duet rate, and they created duets at similar levels across the four treatments (Figure 4D; ANOVA: $F_{21,68} = 6.8$, $p < 0.0001$; model effects: playback type: $F_4 = 4.6$, $p = 0.002$, pair: $F_{17} = 7.3$, $p < 0.0001$).

After playback, rufous-and-white wrens performed duets while closer together than during duets in a natural, unprovoked context. Duet partners were separated by 10.9 ± 2.0 m in the period after playback, significantly closer than their distance of separation outside of playback (19.2 ± 1.9 m; paired t test: $t = 4.8$, $p = 0.0002$, average across four playback treatments to n = 18 pairs). The distance between duet partners did not vary with playback type (ANOVA: $F_{21,68} = 0.7$, $p = 0.78$; model effects: playback type: $F_4 = 0.6$, $p = 0.61$, pair: $F_{17} = 0.8$, $p = 0.68$). It may not be surprising that the birds are closer together in response to playback, given that they are responding to the same intruder(s), but it is clear that both sexes respond intensely to territorial intrusion and that they may use duets to coordinate their response. In their approaches to the loudspeakers, the sexes did not show equivalent intensities of response; males exhibited closer approach responses overall and biased approach to the male loudspeaker, and females showed weaker approach responses and biased approach to the female loudspeaker after playback of female solos (see Supplemental Data, available online).

In accordance with our predictions of the territory-defense hypothesis, we found that pairs performed duets during interactions with simulated territorial intruders at more than five times their baseline rate. In addition, birds responded aggressively by approaching the simulated intruders. Although males approached the playback loudspeakers more closely than females in most treatments, both sexes approached and sang when presented with simulated territorial intruders. Other playback studies of duetting animals have supported similar conclusions [11, 12, 21]. Although the duets we recorded in a natural, unprovoked context were not associated with territory boundaries, birds' playback responses demonstrate that duets play a role in territory defense during aggressive interactions.

The birds' playback responses also provide support for the mate-guarding hypothesis. Birds showed strong responses to playback and, in some treatments, clearly responded with heightened intensity to same-sex stimuli. Females showed their closest responses to female-solo playback, and males to male-solo playback (see Supplemental Data). When facing a duetting pair of intruding birds, resident males responded more closely on the side of the male loudspeaker when the intruding male created duets, although they did not differentiate when rival females created duets. That both sexes of rufous-and-white wren created duets at similar levels in response to playback of solos and duets suggests that birds do not increase their responsiveness to their partner's songs when facing a same-sex rival. However, rufous-and-white wrens respond more aggressively to the vocalizations of their own sex, consistent with the idea of mate guarding or paternity guarding. The genetic mating strategy of rufous-and-white wrens is unknown, yet our field observations suggest that these birds

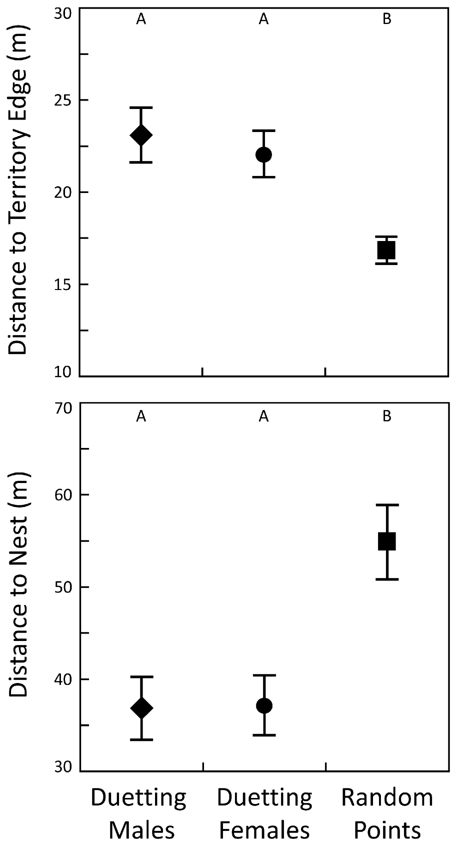

Figure 3. Duetting Rufous-and-White Wrens Perform Duets Farther from Territory Edges and Nearer to their Nest than Random Points

Average distances to territory features for duetting positions of male and female rufous-and-white wrens compared to randomly generated points (average male, female, and random point values across n = 19 territories). Symbols show means ± SE, and letters indicate significant differences (values not connected by the same letter are statistically different).

may engage in extra-pair copulations, like most birds investigated to date [22]. Moreover, rufous-and-white wrens frequently engage in divorce (unpublished data). Consequently, birds may show heightened response to same-sex rivals because those rivals may seek extra-pair copulations or new partnership opportunities.

Conclusions

Using the innovative technology of an ALS facilitates the visualization of the behavior of wild tropical animals in a way that no previous technology has permitted. Unlike radiotelemetry, which necessitates capture and modification of the study animal and often comes with undesirable consequences [18], ALS technology permits localization of unencumbered, free-living animals every time they produce a sound.

Our analyses of vocal-duetting behavior in both natural and aggressive contexts provide strong support for the idea that duets are multipurpose signals that serve independent functions in different contexts. Our ALS recordings of duets produced in a natural, unprovoked context reveal that duets serve an important function in maintaining acoustic contact and perhaps in pair bonding. By contrast, our recordings of duets produced in an aggressive, confrontational context reveal that duets are involved in territory defense and perhaps in mate guarding. Behavioral ecologists have been unable to develop a single explanation for the functional significance of animal duets for several reasons. First, many duetting animals perform duets in such densely foliated habitat that direct observation is difficult. Increasingly sophisticated field technologies will help us to understand duetting behavior in the numerous duetting species that live in visually occluded habitats. Second, animals perform duets in many different situations. Our analyses of duetting in both passive and aggressive social environments, as well as complementary studies that demonstrate variation in duetting behavior across different situations [15, 23], emphasize that duet function varies with context. Third, and importantly, duetting is a phylogenetically diverse phenomenon that has evolved independently in many different animal taxa [1–5]. Consequently, it is naive to assume that one explanation will adequately address the adaptive significance of animal vocal duets. ALS recordings and multispeaker playback demonstrate that duets serve multiple independent functions in different contexts, and analysis of the social environment in which duets are produced is critical to understanding the ecology and evolution of this highly coordinated form of animal communication.

Experimental Procedures

Field Methods

Our ALS consisted of an array of eight omnidirectional microphones recording simultaneously to eight-channel sound files on a laptop computer [10]. Exploiting the slow speed of sound propagation through air, the ALS triangulates the position of birds on the basis of differences in sound arrival times at the microphones. We set up the microphones throughout the territories of rufous-and-white wrens, with an average intermicrophone distance of 75.2 ± 2.6 m. Territories were determined by visually tracking birds during focal recording sessions in the month prior to ALS recordings, collecting GPS coordinates of the positions where birds had been observed, and calculating minimum convex polygons around these positions. The ALS was capable of triangulating the distance between duetting partners with an accuracy of 2.12 ± 0.42 m. Full details on the ALS equipment and its locational accuracy are reported in Mennill et al. [10].

We collected ALS recordings of 19 color-banded pairs of rufous-and-white wrens in Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W). Each pair was recorded for the first five hours of the day on four consecutive mornings during the early part of the breeding season (May to June, 2003; April to May, 2004). Recording sessions were divided into two components: vocalizations recorded in a natural context and vocalizations recorded in response to playback. For one of the pairs, the female divorced her breeding partner after the second day of recording but prior to playback, resulting in a sample size of 18 pairs for the playback experiment.

We used multispeaker playback to simulate an intrusion by a neighboring pair of wrens on the third or fourth day of ALS recording between 0630 hr and 0930 hr. Each pair received four playback treatments: (1) male solos and (2) female solos (single-speaker stimuli), and (3) "male-created duets" in which the female sang first and the male sang second and (4) "female-created duets" in which the male sang first and the female sang second (two-speaker stimuli). All four treatments were given to a territorial pair on the same day with a 20 min silent interval between treatments. To rule out the possibility that order of presentation would influence playback responses, we followed a factorial design to determine the order of the four playback treatments and whether the left or right loudspeaker broadcast the male or female duet contribution. The twenty minutes preceding the first playback treatment was used to establish the birds' preplayback behavior.

Analytical Methods

Within ~400 hr of eight-channel ALS recordings, we identified duets with Syrinx-PC software (J. Burt, Seattle, WA). The positions of duetting birds were calculated with software written in MatLab (Mathworks, Natick, MA) on the basis of the GPS coordinates of the eight microphone positions and the delay in arrival times of the duet contributions at each microphone (details in Mennill et al. [10]). Using ArcView GIS v3.2 (ESRI, Redlands, CA),

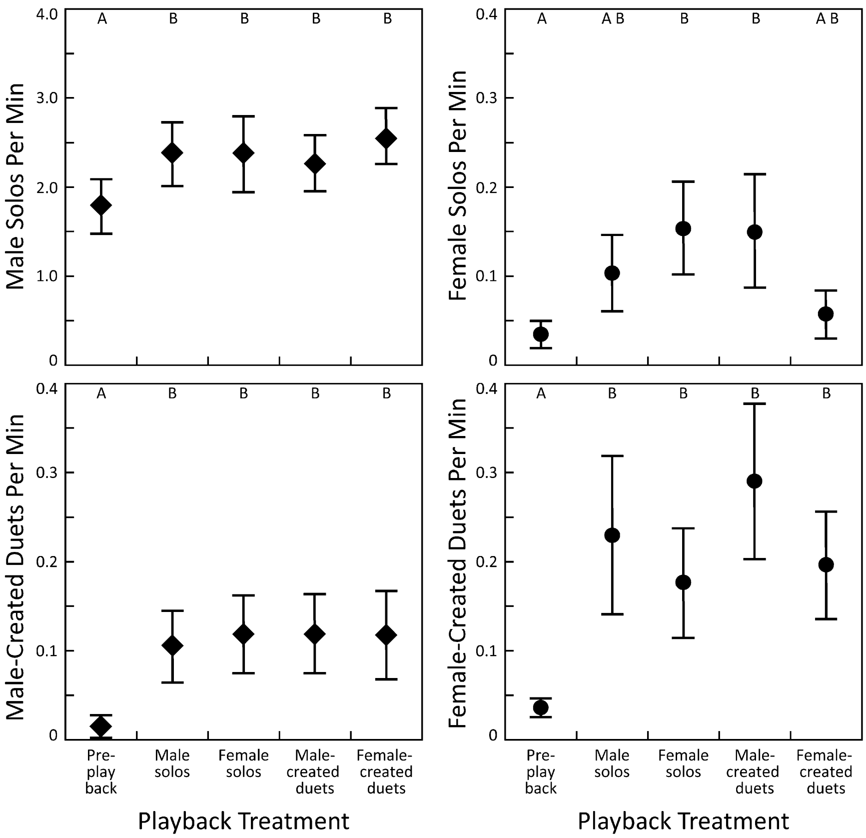

Figure 4. Male and Female Rufous-and-White Wrens Show Different Responses to Four Playback treatments

Solo and duet song rates of male and female rufous-and-white wrens in response to playback of male solos, female solos, male-created duets (duets in which the female sang first and the male responded to create the duet), and female-created duets (duets in which the male sang first and the female responded to create the duet). Symbols show means ± SE, and letters indicate significant differences (values not connected by the same letter are statistically different).

we calculated the distances between the positions of the duetting partners, between duetting individuals and the nearest edge of their territory, and between duetting individuals and their nest by using the "Nearest Feature" extension (Jenness Enterprises, Flagstaff, AZ). We compared these to measurements for 100 points randomly positioned within each pair's territory by using the "Random Point Generator" extension (Jenness Enterprises, Flagstaff, AZ). For duets recorded in response to playback, we calculated the distance between duetting partners, as well as the distance between each of the responding birds and the two loudspeakers broadcasting the components of the simulated duet.

To evaluate whether birds approached or retreated from one another during bouts of duetting in an unprovoked context, we analyzed all song bouts that contained two or more duets in close succession (separated by <60 s of silence). Of 87 duet bouts recorded, we found a total of 65 bouts during which the distance between the pair changed by more than 2.12 m (the minimum detectable distance for our ALS [10]). Our analysis of duet bouts is based on n = 17 pairs in which we recorded one or more bouts.

We analyzed responses to playback in terms of birds' vocal and physical responses. For vocal responses, we measured the number of male and female solos and the number of male-created and female-created duets given in response to each playback treatment. For physical responses, we measured the Euclidean distance between the resident male and female and the two loudspeakers during all songs sung in response to playback (see Supplemental Data).

We used mixed-model ANOVA to compare solo and duet rates across the playback treatments, incorporating pair as a random effect. As expected, pair effects for most models were highly significant because of natural variation in the singing behavior of different pairs (i.e., some birds sing more than others). Song-rate measures were log transformed to achieve normality. All analyses were conducted in JMP 5.0 (SAS Institute, Cary, NC). All values are presented as mean ± SE. All tests are two-tailed with a significance threshold of $p = 0.05$.

Supplemental Data

Supplemental Data include Supplemental Results and Discussion, Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at http://www.current-biology.com/cgi/content/full/18/17/1314/DC1/.

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