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SEX DIFFERENCES IN SINGING AND DUETTING BEHAVIOR OF NEOTROPICAL RUFOUS-AND-WHITE WRENS (*THRYOTHORUS RUFALBUS*)

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ABSTRACT.—In many tropical bird species, males and females sing together in coordinated vocal duets. Although studies of duetting present unique opportunities for understanding conflict and cooperation between the sexes, very few investigations describe the similarities and differences between male and female singing behaviors. Here, we present the first detailed account of the singing behavior of Rufous-and-white Wrens (*Thryothorus rufalbus*), a resident tropical duetting songbird. Male and female songs share a similar structure, yet show pronounced sex differences. Male songs have lower frequency characteristics and more repeated trill syllables, and often sound louder than female songs. Males sing more than females, and only males show elevated song output at dawn. Both males and females have song repertoires. Males have an average repertoire size of 10.8 song types, whereas females have a significantly smaller average repertoire size of 8.5 song types. Although males share proportionately more of their song types with neighbors than females do, both sexes share more song types with nearby individuals than with distant individuals. Breeding partners combine their solo songs to create duets. Duets assume a variety of different forms, ranging from simple, overlapping male and female songs to complex combinations of multiple male and female songs. Most duets (73%) are created by females responding to male song. Males respond to female-initiated duets with shorter latencies than when females respond to male-initiated duets. Each pair sings certain combinations of song types in duets more often than can be explained by random association, which demonstrates that Rufous-and-white Wrens have duet types. The most common duet type was different for each pair. Our results show that Rufous-and-white Wrens have pronounced sex differences in song structure, singing activity, repertoire size, repertoire sharing, and duetting behavior. Received 1 March 2004, accepted 31 August 2004.

Key words: duet, Rufous-and-white Wren, sex differences, song repertoires, *Thryothorus rufalbus*.

Diferencias entre Sexos en el Canto y Comportamiento de Dueto en *Thryothorus rufalbus*

RESUMEN.—En muchas especies de aves tropicales, los machos y las hembras cantan juntos en duetos vocales coordinados. Aunque los estudios sobre estos duetos representan oportunidades únicas para entender el conflicto y la cooperación entre los sexos, muy pocas investigaciones han descrito las similitudes y diferencias en el comportamiento de canto entre machos y hembras. En este trabajo presentamos el primer estudio detallado sobre el comportamiento de canto de *Thryothorus rufalbus*, una especie de ave canora tropical residente que realiza duetos. Los cantos de los

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machos y las hembras presentan una estructura similar, pero existen diferencias marcadas entre ellos. Los cantos de los machos se caracterizan por ser de menor frecuencia y por presentar más sílabas en trino, y a menudo suenan más fuerte que los cantos de las hembras. Los machos cantan más que las hembras y sólo los machos presentan una mayor tasa de canto al amanecer. Tanto los machos como las hembras tienen repertorios de canto. Los machos tienen un tamaño de repertorio promedio de 10.8 tipos de canto, mientras que las hembras tienen en promedio repertorios significativamente más pequeños, de 8.5 tipos de canto. Aunque los machos comparten proporcionalmente más de sus tipos de canto con sus vecinos que las hembras, las aves de ambos sexos comparten más tipos de canto con individuos cercanos que con individuos distantes. Las parejas reproductivas combinan sus cantos individuales para crear duetos. Los duetos pueden ser de diversos tipos, desde una simple superposición entre los cantos del macho y la hembra, hasta combinaciones complejas de múltiples cantos de ambos sexos. La mayoría de los duetos (73%) son creados por hembras que responden al canto de los machos. Los machos responden a los duetos iniciados por las hembras con períodos de latencia más cortos que cuando las hembras responden a los duetos iniciados por los machos. Cada pareja canta determinadas combinaciones de tipos de canto en los duetos con más frecuencia de lo que podría explicarse por una asociación aleatoria, lo que demuestra que en *T. rufalbus* existen tipos de dueto. El tipo de dueto más común fue diferente en cada pareja. Nuestros resultados muestran que en *T. rufalbus* existen diferencias profundas entre los sexos en la estructura del canto, la actividad de canto, el tamaño del repertorio, el modo de compartir el repertorio y el comportamiento de dueto.

IN MANY BIRD species, songs are produced by males and are believed to evolve through male–male competition and female choice (Catchpole and Slater 1995). However, females of many species also sing (Langmore 1998); and in $\geq 3\%$ of avian species, paired males and females sing together in coordinated vocal duets (Hall 2004). Duetting birds offer a unique opportunity to explore the evolution of conflict and cooperation between the sexes. However, detailed investigations of the similarities and differences between male and female singing behaviors are rare. By quantifying male and female singing strategies, we can develop a better understanding of the selective forces driving the evolution of duetting.

The 27 species in the genus *Thryothorus* demonstrate a full spectrum of vocal behavior; there are species in which only males sing (Carolina Wrens [*T. ludovicianus*]; Haggerty and Morton 1995), species in which males and females sing independently (Banded Wrens [*T. pleurostictus*]; Molles and Vehrencamp 1999), and species in which males and females coordinate their vocalizations in precise antiphonal duets (Bay Wrens [*T. nigricapillus*]; Levin 1996; and Plain Wrens [*T. modestus*]; Mann et al. 2003).

Rufous-and-white Wrens (*T. rufalbus*) are a little-studied member of the genus (Farabaugh 1983). Brenowitz et al. (1996) conducted a comparison of the neuroanatomy of male and female Rufous-and-white Wrens and found that both sexes have well-developed brain nuclei associated with song production. Although the sexes have similar densities of androgen-receptors within those nuclei, the nuclei are larger in males than in females, which suggests a neural basis for sex differences in singing behavior (Brenowitz et al. 1996).

Here, we present the first detailed account of sex roles in the singing and duetting behaviors of Rufous-and-white Wrens. We had three goals: (1) to describe the species' solo-singing and duetting behaviors; (2) to categorize the repertoire size, repertoire sharing, and singing mode of males and females for comparison with other *Thryothorus* wrens, including the sympatric Banded Wren and Plain Wren; and (3) to compare the vocal behaviors of male and female Rufous-and-white Wrens, to better understand which features of their song system may relate to their sexually dimorphic neuroanatomy as described by Brenowitz et al. (1996).

METHODS

GENERAL FIELD TECHNIQUES

Rufous-and-white Wrens are resident Neotropical songbirds found from Mexico to Colombia and Venezuela. Our study population inhabits the mature humid forest and late-successional regrowth forests in sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W).

In April through July 2003, we captured 27 birds with mist nets and banded each individual with a unique combination of three plastic color bands and one numbered metal band. We took standard morphometric measurements, including mass and the lengths of the culmen, wing chord, tarsus, and tail. We distinguished females from males by presence of a brood patch and by behavioral observations (in all pairs, one bird did all the incubating; we assumed that bird to be the female). Males and females were sexually dimorphic in all body measurements. Males were heavier than females (males: 25.8 ± 0.4 g, females: 23.7 ± 0.5 g; $F = 13.3$, $df = 1$ and 26 , $P = 0.001$). Males had longer bills (males: 13.1 ± 0.1 mm, females: 12.0 ± 0.1 mm; $F = 35.3$, $df = 1$ and 26 , $P < 0.0001$), longer wings (males: 70.4 ± 0.4 mm, females: 65.0 ± 0.5 mm; $F = 66.5$, $df = 1$ and 26 , $P < 0.0001$), longer tarsi (males: 21.2 ± 0.1 mm, females: 19.9 ± 0.2 mm; $F = 23.2$, $df = 1$ and 26 , $P < 0.0001$), and longer tails (males: 51.4 ± 0.4 mm, females: 47.4 ± 0.5 mm; $F = 43.0$, $df = 1$ and 26 , $P < 0.0001$). For all morphometric measurements, the smallest male was larger than the largest female.

FIELD RECORDINGS

We recorded songs from 16 breeding pairs of Rufous-and-white Wrens. Both the male and female of 12 of those pairs were color-banded; only the males of the remaining 4 pairs were color-banded. For all pairs, we conducted focal recording sessions, in which one recordist followed the male and female as they traveled around their territory between 0500 and 0700 hours (the first songs of the morning occurred at dawn, shortly after 0500 hours). During focal recordings, we spoke the identity of the singer into the microphone when it was known. Focal recordings were made with a directional microphone (model Sennhesier MKH-70), a

pre-amplifier (model Stewart BPS-1), and a tape recorder (model Marantz PMD-222). We digitized tapes using SYRINX-PC sound-analysis software (J. Burt, Seattle, Washington). In total, we collected 133 h of focal recordings; each of 16 pairs was recorded for 6.7 ± 0.9 h.

For 10 pairs, we made additional recordings using eight stationary microphones positioned around the focal pair's territory. Output from the eight microphones was recorded as eight-channel AIF files on a notebook computer using CHICKADEE multichannel recording software (J. Burt, Seattle, Washington). In total, we collected 170 h of eight-channel recordings; each of 10 pairs was recorded for 17.0 ± 0.1 h.

In addition to solo and duet songs, Rufous-and-white Wrens have several types of calls, including a genus-typical harsh chattering call, a low-pitched hollow hooting call, and a very quiet, high-pitched whistle. Those simple vocalizations are given by both sexes far less often than songs, which are the focus of the present investigation.

ANALYSES OF SOLO SONGS

We isolated all solo songs and duets contained in the 303 h of field recordings. We define a solo song as a series of notes produced by one individual and separated from that individual's previous or subsequent vocalizations by an interval ≥ 2.0 s. Both male and female Rufous-and-white Wrens have repertoires of distinct song types (i.e. songs containing a series of notes that are combined in a stereotyped order). Song types are easily distinguished by ear and by comparison of sound spectrograms. For each bird, we calculated repertoire size as the total number of different song types recorded. To test whether our sampling of song repertoires was complete, we plotted the cumulative number of song types detected against the number of songs recorded. Female repertoire size was more difficult to quantify than male repertoire size, because females sing less often (see below). Therefore, when comparing male and female repertoire sizes, we analyzed a subset of data that included only those song types realized in a sample of 35 changes in song type by each of 10 females and 12 males.

To describe the fine structure of Rufous-and-white Wren songs, we made detailed measurements of one representative song of each type for each bird. We measured the number of

distinct syllables (defined as continuous traces on a sound spectrogram) and the number of types of syllables (defined as syllables that share similar frequency and length characteristics). We measured the length of the entire song, length of the trill section of the song (all songs contained a series of repeated trill notes), and bandwidth of the terminal syllable (measurements made with frequency resolution 40 Hz and temporal resolution of 0.1 s using SYRINX-PC). We measured the frequency of maximum amplitude (FMA) for the entire trill and for the terminal syllable (measurements made with frequency resolution of 1 Hz using COOLEDIT 2000, Syntrillium Software, Phoenix, Arizona).

Each Rufous-and-white Wren shared at least one song type in common with other birds in the population. We quantified repertoire sharing between pairs of individuals by calculating a song-type sharing coefficient ($S = 2 \times \text{number of song types shared between two individuals} / \text{sum of the repertoire sizes of those individuals}$) (McGregor and Krebs 1982, Molles and Vehrencamp 1999). We calculated repertoire sharing at three levels for each bird: (1) sharing coefficient between a bird and its partner, (2) average sharing coefficient between a bird and all neighboring birds in immediately adjoining territories, and (3) average sharing coefficient between a bird and all other birds in the population. To evaluate whether repertoire sharing decreased with distance between birds, we performed Mantel tests of the correlation between matrices of repertoire sharing between birds (sharing coefficient, S) and corresponding matrices of the distance between those birds' territories (meters between the closest edges of their territories) (Molles and Vehrencamp 1999). We conducted separate Mantel tests for male–male sharing and female–female sharing. To ensure that sex comparisons of repertoire sharing were not influenced by the lower song-output of females, we analyzed a subset of data that included only the song types realized in the first 35 changes in song type from 10 females and 12 males. Because results of those analyses were not different from the analyses of the entire data set, we here present results for all birds.

To quantify singing rate, we calculated the interval from the start of one song to the start of the next song. To avoid the influence of long pauses in song-rate calculations, we ignored between-song latencies >60 s. To quantify song

output, we calculated the number of songs per hour in each of the first four hours of the day ($n = 10$ pairs, each recorded for 4 h on two mornings) and compared the average number of songs per hour for each pair.

ANALYSES OF DUETS

We define duets as bouts of vocalizations given by a paired male and female in which the songs of the two individuals overlap or are temporally associated by an interval ≤ 1.0 s. For all recorded duets, we documented whether the duet was initiated and terminated by the male or the female. To evaluate whether one sex initiated duets more often than expected by chance, we conducted a binomial test for each pair. We measured precision of timing between male and female contributions to duets as the coefficient of variation ($CV = 100 \times \text{standard deviation} / \text{mean}$) in the delay between onset of the first song in the duet and onset of the second song.

In an intriguing study of Plain Wrens, Mann et al. (2003) found that males and females combine particular song types to create duet types. We followed the protocol of Mann et al. (2003) to test whether male and female Rufous-and-white Wrens combine their song types at random or whether they too have distinct duet types. For each pair, we entered the frequency of observed combinations of male and female song types into a matrix of all possible combinations. A series of successive duets that were composed of the same male and female song types were scored as a single occurrence of that duet type. We compared the observed frequencies of occurrence of each combination against the expected frequency of occurrence if males and females combined their songs at random. We calculated expected frequencies assuming a Poisson distribution with a minimum value of 0 (i.e. no occurrences of a particular combination of male and female song expected) and a maximum value ≥ 4 (Mann et al. 2003). We then compared observed and expected frequencies using a G -test. That procedure allowed us to evaluate whether pairs sang particular song types in combination more often than would be expected by chance; that is, whether Rufous-and-white Wren pairs have duet types. We included only those duets in which the male and female each contributed a single song type (the vast majority of recorded duets; see below).

STATISTICAL METHODS

For analyses of the fine structure of male and female songs, calculations of repertoire sharing at the population level, and calculations of duet precision, we used data from 30 birds. For analyses of repertoire sharing between neighbors, we used data from 24 birds that had one or more neighbors. For analyses of song rate and song output, repertoire sizes, and duet types, we used data from 10 pairs for which we had extensive recordings (i.e. >22 h per pair). We conducted G-tests and Mantel tests using POPTOOLS, version 2.5 (see Acknowledgments). For Mantel tests, we used 1,000 permutations per run. All remaining statistical analyses were conducted in JMP 4.0 (SAS Institute, Cary, North Carolina). We used nonparametric statistics when data could not be normalized. All tests are two-tailed. All values are reported as mean \pm SE.

RESULTS

SONG STRUCTURE

Solo songs of male and female Rufous-and-white Wrens share a similar structure (Fig. 1). Songs begin with a series of 1–6 introductory syllables (average number of introductory syllables: 2.9 ± 0.1). The middle section consists of a trill of 3–35 repeated syllables (average number of trill syllables: 8.2 ± 0.3). Songs end with an emphatic terminal syllable, which is often the loudest and highest-frequency part of the song.

Fine structural details of Rufous-and-white Wren songs show substantial sexual variation. The number of repeated syllables in male trills (8.3 ± 0.4 repeats) is significantly greater than that in female trills (6.4 ± 0.4 repeats) ($F = 10.6$, $df = 1$ and 29 , $P < 0.003$). Male songs have lower frequency characteristics than female songs, including a significantly lower average trill frequency (males: 922 ± 15 Hz, females: $1,037 \pm 15$ Hz; $F = 30.9$, $df = 1$ and 29 , $P < 0.0001$) and a significantly lower average terminal syllable frequency (males 776 ± 82 Hz, females: $1,044 \pm 82$ Hz; $F = 5.4$, $df = 1$ and 29 , $P = 0.03$). We found no difference in the number of types of syllables in male songs (4.2 ± 0.4) as compared with female songs (4.1 ± 0.3) ($F = 0.4$, $df = 1$ and 29 , $P = 0.5$) or in length of male songs (2.2 ± 0.1 s) as compared with female songs (2.2 ± 0.2 s) ($F = 1.0$, $df = 1$ and 29 , $P = 0.3$). Often, but not always, female songs appeared to be substantially

quieter than male songs; however, we did not quantify song amplitude in the field.

SINGING ACTIVITY

Males sing far more often than females: 93% of all songs recorded were given by males. Males have a peak of singing activity in the early morning (Fig. 2A; $F = 6.9$, $df = 3$ and 39 , $P < 0.001$). Females, on the other hand, sing at consistent low levels throughout the morning (Fig. 2B; $F = 2.0$, $df = 3$ and 38 , $P = 0.15$). Both sexes engage in bouts of solo songs interspersed with duets and punctuated by silent intervals. During song bouts, males sing at significantly higher rates, repeating their songs every 11.9 ± 0.3 s, whereas females repeat their songs every 16.4 ± 3.2 s ($F = 12.0$, $df = 1$ and 19 , $P = 0.003$).

SOLO REPERTOIRES

Both males and females have repertoires of distinct song types (Fig. 1). Males have a repertoire of 10.8 ± 0.7 song types (range = 6–14; $n = 10$). Plots of the number of song types detected versus the number of songs recorded show that we had complete sampling of male repertoires (Fig. 3A; the asymptote was reached after 653 ± 201 recorded songs; $n = 10$). Females had a repertoire of 8.5 ± 0.7 song types (range = 4–11; $n = 10$). Given that females sing far less often than males, sampling may not have been complete for all female repertoires (Fig. 3B). Cumulative repertoire plots suggest that our sampling was complete for only five females (among those females, the asymptote was reached after 111 ± 34 recorded songs; repertoire size was 8.4 ± 1.2 song types [range = 4–10, $n = 5$]). Male repertoires are significantly larger than female repertoires ($Z = 2.7$, $P < 0.01$, comparison of repertoires realized in the first 35 changes in song type for 10 females and 12 males).

Rufous-and-white Wrens sing with eventual variety (repeat-mode singing). During song bouts, males repeat the same song type 11.0 ± 0.9 times, on average, before changing to a different song type. Females, on the other hand, repeat the same song type 2.7 ± 0.9 times before changing to a different song type.

SHARING BETWEEN SOLO REPERTOIRES

All birds shared at least one song type with another bird in the population. Males shared

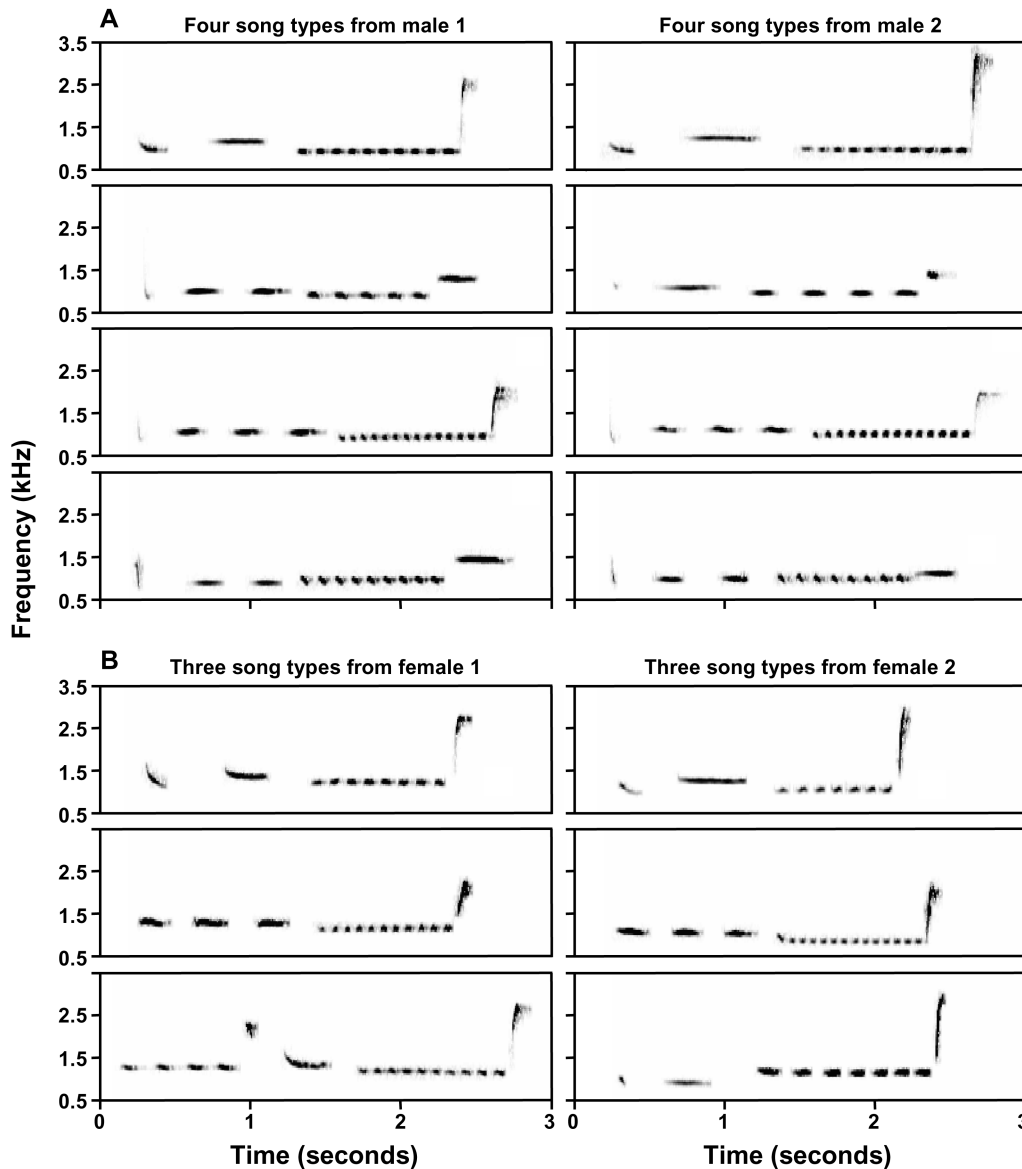


FIG. 1. Sound spectrograms of Rufous-and-white Wren solo songs. (A) Four song types for each of two males. Spectrograms are arranged showing matching song types between the male on the left and the male on the right. (B) Three song types for each of two females. The first two spectrograms are matches between the female on the left and the female on the right, whereas the bottom spectrograms show nonmatching song types.

an average of 5.9 ± 0.3 song types with one or more other males in the population (average male–male similarity index: $S = 0.59 \pm 0.03$). Females shared an average of 1.7 ± 0.3 song types with one or more other females in the population (average female–female similarity index: $S = 0.26 \pm 0.03$). Across the population,

female–female sharing was significantly lower than male–male sharing ($F = 65.7$, $df = 1$ and 29 , $P < 0.0001$).

Males shared 6.7 ± 0.6 song types with males in neighboring territories ($S = 0.64 \pm 0.06$). Females shared 0.3 ± 0.6 song types with females in neighboring territories ($S = 0.26 \pm$

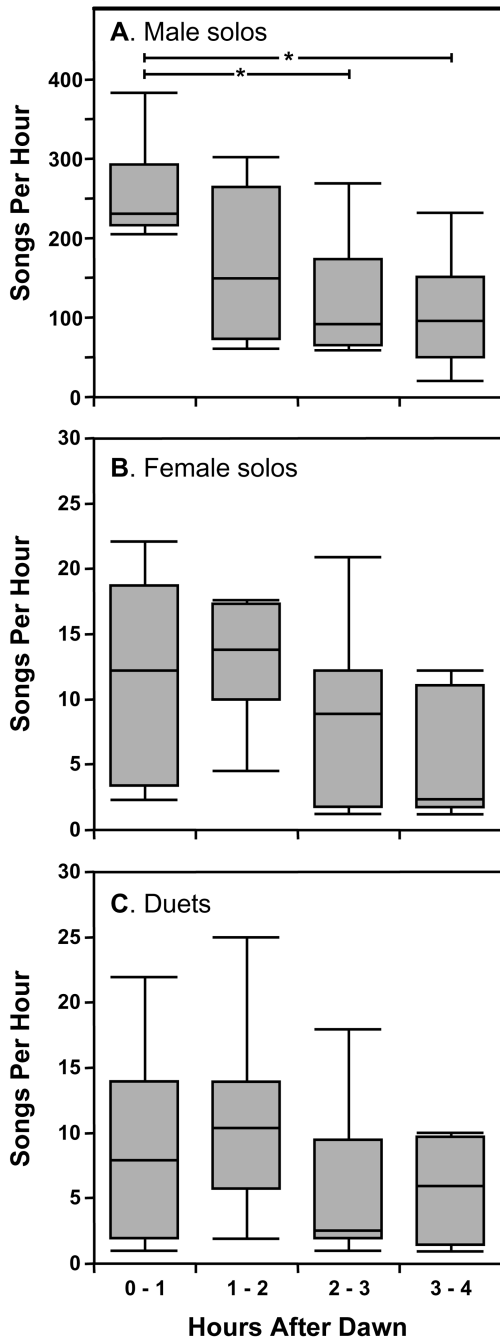


FIG. 2. Variation in song output of Rufous-and-white Wrens in relation to time of day. (A) Males have a peak in song output at dawn, singing significantly more in the first hour of the day (first light at ~0500 hours) than in the third and fourth hours of the day. Asterisks

0.06). Considering sharing between same-sex neighbors only, female–female sharing was significantly lower than male–male sharing ($F = 19.0$, $df = 1$ and 23 , $P < 0.0005$). Across the population, repertoire sharing declined with distance between birds’ territories, a pattern that held true for both males (Mantel $r = -0.24$, $P = 0.02$) and females (Mantel $r = -0.22$, $P = 0.03$). Therefore, both sexes share more songs in common with nearby birds than with distant birds.

Some song types were shared between the sexes, and others were sex-specific. Of 20 song types that were shared between two or more individuals, 12 were shared between both males and females, 4 were found exclusively in male repertoires, and 4 were found exclusively in female repertoires. Females’ repertoires contained more unique song types (i.e. song types not shared with any other bird in the population, male or female). Each female had 1.9 ± 0.4 unique song types ($23 \pm 4\%$ of their repertoire), whereas each male had only 0.7 ± 0.4 unique song types ($6 \pm 4\%$ of their repertoire) ($Z = 2.0$, $P = 0.04$).

Breeding partners shared 3.1 ± 0.7 song types ($S = 0.33 \pm 0.03$). On average, breeding partners did not have more songs in common than they did with all other opposite-sex birds in the population ($S = 0.29 \pm 0.03$; paired t -test; $t = 9.6$, $df = 15$, $P = 0.22$).

DUETS

Rufous-and-white Wrens create duets by combining their solo songs. Both males and females create duets by responding to their partner’s song. Most duets ($73 \pm 2\%$) are created by females responding to male song (e.g. Fig. 4A; binomial tests: all $P < 0.005$, $n = 10$ pairs), and the remaining duets are created by males responding to female songs (e.g. Fig. 4B). Of all male songs recorded, $6.4 \pm 3.3\%$ occurred in duets, whereas $79.1 \pm 3.3\%$ of all female songs recorded occurred in duets ($F = 250.1$,

← show significant differences by Tukey Kramer HSD. (B) Female song output and (C) female duet output do not vary with time of day. Note the different scales of vertical axes of top graph and bottom two graphs; male song output is much higher than female song output and duet output. Box plots show horizontal lines for the 10th, 25th, 50th, 75th, and 90th percentiles.

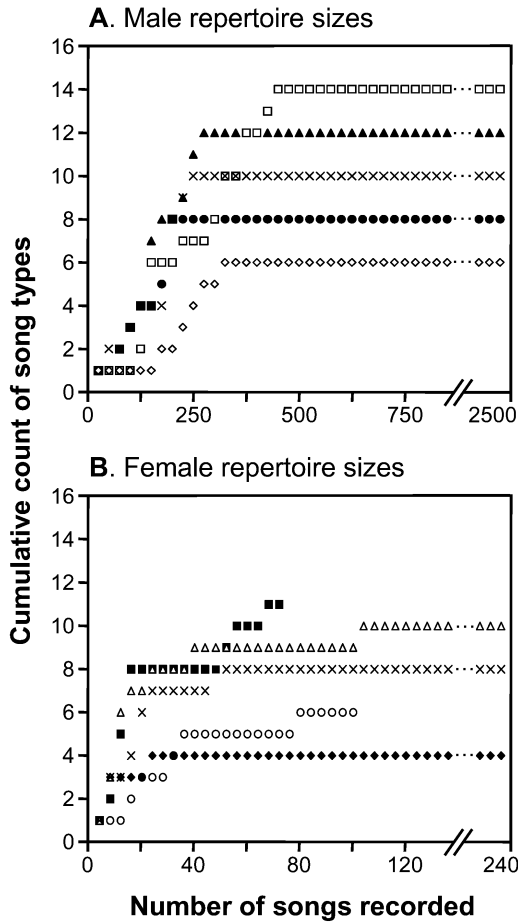


FIG. 3. Repertoire sizes for male and female Rufous-and-white Wrens. (A) Examples of cumulative repertoire plots for five different males. Sampling was complete for all five males shown. (B) Because females sing less often than males, repertoire sampling was often incomplete for females. Cumulative repertoire plots are shown for three females for which repertoire sampling was complete and two females for which sampling was incomplete. Note the different scales of horizontal axes of top and bottom graphs.

df = 1 and 19, $P < 0.0001$). That asymmetry in the proportion of male and female songs that occur in duets, taken together with the fact that males have higher song output than females, demonstrates that males sing duet responses to proportionately more of their partners' songs than do females. In most duets (60%), the duet initiator's song is overlapped by the partner's

response (e.g. Fig. 4A). In the remaining 40% of duets, there is a short break between the initiator's song and the partner's response (e.g. Fig. 4B). Rufous-and-white Wren pairs duet throughout the morning at a consistent rate (Fig. 2C; $F = 0.8$, $df = 3$ and 27 , $P < 0.50$).

We classified duets into three types. "Simple duets" are initiated by one bird and terminated by its partner (Fig. 4A, B). Simple duets constituted $78.8 \pm 4.0\%$ of recorded duets (average for $n = 10$ pairs). "Sandwich duets" are those initiated and terminated by two songs from the same bird, whose partner sings the middle section (Fig. 4C). Sandwich duets constituted $18.2 \pm 2.9\%$ of recorded duets. "Complex duets" are those in which both birds contribute two or more songs in various combinations (Fig. 4D). Complex duets were rare and constituted the remaining $3.0 \pm 1.2\%$ of recorded duets.

DUET PRECISION

The delay between the duet initiator's song and the responder's song was 2.03 ± 0.21 s. When males initiated duets, females responded after 2.15 ± 0.25 s. When females initiated duets, males responded after only 1.62 ± 0.31 s, which was significantly faster than the female responses to male-initiated duets (paired t -test: $t = 3.2$, $df = 16$, $P = 0.005$). We found substantial variation in duet precision: the delay between the duet initiator's song and the responder's song had a CV of 45.3%. Duet precision was similar for male-initiated duets (CV = 44.0%) and female-initiated duets (CV = 48.8%; paired t -test: $t = 0.6$, $df = 16$, $P = 0.56$).

DUET REPERTOIRES

Rufous-and-white Wrens have distinct duet types. Certain combinations of male and female song types were associated more often than would be expected if birds combined their song types at random (Table 1). On average, the most common duet type for each pair constituted $17.1 \pm 2.2\%$ of all of the duets sung by that pair ($n = 10$). We recorded an average of 26.4 ± 3.7 duet types for each pair. Our sampling of duet repertoires was not complete even for the most extensively recorded pair ($n = 53$ duet types detected from 173 duet bouts).

We tested whether the most common duet types involved song-type matching between the

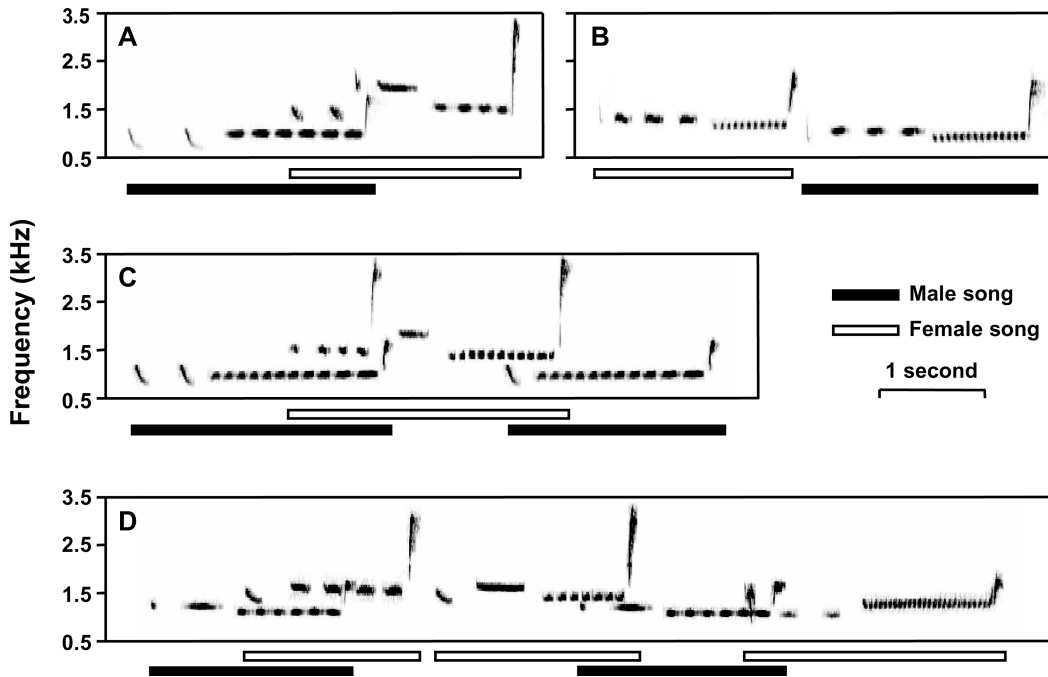


FIG. 4. Sound spectrograms of Rufous-and-white Wren duets. Simple duets (A and B) involve one song contributed by each partner. The songs of the partners may (A) overlap or (B) follow in direct succession, and either sex can play the role of duet initiator or responder. Sandwich duets (C) occur when one bird initiates and terminates the duet, whereas the partner sings the middle section. Complex duets (D) involve more than two songs contributed by each partner.

TABLE 1. Associations between specific male and female song types in the duets of Rufous-and-white Wrens. Recorded combinations of male and female song types were tabulated in a matrix. Observed frequencies of occurrence for each combination of male and female song type were compared against expected values derived from a Poisson distribution using a G-test (Mann et al. 2003). Significant deviations from the expected frequencies indicate associations that occurred more often than would be expected if males and females combined their song types at random.

Pair	Number of duets analyzed	Cells with frequency score ≥ 4		Phrase types randomly associated?		
		Observed	Expected	G_{adj}	df	P
A	173	16	9.94	58.1	3	<0.0001
B	79	5	0.69	28.6	3	<0.0001
C	69	5	0.93	47.9	3	<0.0001
D	66	4	0.30	37.9	3	<0.0001
E	60	8	3.87	41.2	3	<0.0001
F	52	4	0.16	43.0	3	<0.0001
G	39	1	0.17	16.5	3	<0.0050
H	37	3	0.02	37.1	3	<0.0001
I	36	3	0.03	42.0	3	<0.0001
J	33	1	0.04	6.7	3	<0.0500

duetting partners (e.g. Fig. 4B). Only 16% of the most common duet types involved a type match between the male and female ($n = 50$ duet types that occurred $\geq 4\times$ among the 10 pairs in Table 1). Thus, Rufous-and-white Wrens do not routinely match the song type of their partner while duetting. Across all pairs, we found no patterns of similarity in common duet types. The most common duet type was different for each pair. Therefore, although Rufous-and-white Wrens have formalized duet types, those duet types appear to be pair-specific and there appears to be no significant duet-type sharing across the population.

DISCUSSION

Male and female Rufous-and-white Wrens sing independent solo songs as well as coordinated vocal duets. Male solo songs are more common than female solo songs or duets. Songs of both sexes share a similar structure with varied introductory syllables, a long trill, and an emphatic terminal syllable. Males and females have repertoires of song types, which they combine to create duets. Duets can be created by either sex in response to the partner's song. Duets usually involve overlapping male and female songs, though the delay in onset between male and female contributions is quite variable. Rufous-and-white Wrens have pair-specific duet types, in which they combine particular song types more often than can be explained by random association.

We found pronounced sexual differences in the solo singing and duetting behaviors of Rufous-and-white Wrens. Male songs are lower in frequency and have more repeated trill syllables than female songs. Males sing more often than females, and only males show a peak in singing behavior at dawn. Males have larger song repertoires than females, males share more song types in common with other birds in the population, and males are less likely to have novel song types. In approximately three-quarters of all duets, a male is the duet initiator and a female the responder. Males respond after a significantly shorter delay in female-initiated duets than females do in male-initiated duets.

Farabaugh (1983) conducted a comparative analysis of several *Thryothorus* spp. wrens in Panama. Although her research focused on Buff-breasted Wrens (*T. leucotis*), she presented

a basic description of Rufous-and-white Wren songs. She reported an average male repertoire size of 14.0 ± 1.0 ($n = 10$) and an average female repertoire size of 6.0 ± 0.6 ($n = 6$). Farabaugh's (1983) repertoire estimate for females was an underestimate, based on a relatively small number of recorded songs (75 bouts of female song vs. ~ 750 bouts of female song in the present study). For Rufous-and-white Wrens, the relative rarity of female song means that females must be recorded extensively before accurate repertoire measurements can be made. In the present study, we had complete repertoire sampling for only five females, despite an average of >22 h of recording per pair. Farabaugh's analyses of duetting behavior in Rufous-and-white Wrens also suffered from problems associated with a small sample size. Although she suggested that males and females combine their song types randomly during duets, that was based on ~ 20 recorded duets from each of three pairs (Farabaugh 1983). Our extensive recordings demonstrate that pairs contribute songs to duets nonrandomly, with certain combinations of male and female song types occurring more often than expected. Like Farabaugh (1983), we found that most female songs are given in duets, whereas most male songs are given as solos. Our calculated rates of song output among Costa Rican birds are similar to Farabaugh's (1983) calculations for Panamanian birds. Farabaugh's (1983) description of Panama wrens and Ahumada's (2001) notes of Colombian wrens suggest that the asymmetry between male and female song output is common across this species' range.

The sex differences we describe in singing behavior mirror differences observed in the neuroanatomy of males and females. Male and female Rufous-and-white Wrens have well-developed brain nuclei involved in song production and song learning, including song nuclei HVC, RA, area X, IMAN, Rt, Pt, and nXII (Brenowitz and Arnold 1986, Brenowitz et al. 1996). Both sexes have similar proportions of androgen receptors in their HVC and IMAN, consistent with levels observed in male brains for species where only males sing (Brenowitz et al. 1996). However, male Rufous-and-white Wrens have significantly larger HVC, RA and area X nuclei (Brenowitz and Arnold 1986). Brenowitz and his colleagues suggest a correspondence between this neural dimorphism and sex differences in repertoire

size (Brenowitz and Arnold 1986). Here, we show that, in addition to sex differences in repertoire size, Rufous-and-white Wrens show many other dramatic differences between the sexes. Sexually dimorphic brain nuclei may be related not only to repertoire sizes, but also to patterns of song sharing, patterns of song learning, and patterns of song performance.

Our analyses confirm Ridgely and Tudor's (1989) assertion that Rufous-and-white Wren songs are unlike any others in the genus *Thryothorus*. Four features are common among the songs of duetting *Thryothorus* wrens: (1) songs are short, (2) they usually lack long trills, (3) they often have terminal syllables with sharply rising or falling frequency sweeps, and (4) male and female songs are given in a rapid and precisely coordinated interchange during duets (Brown and Lemon 1979). In accordance with the third pattern, the terminal syllable of Rufous-and-white Wrens is often a sharply rising frequency sweep (Fig. 1). Contrary to the other three patterns, however, Rufous-and-white Wrens sing relatively long songs with long trills, given in a slow and loosely coordinated fashion during duets. Furthermore, Rufous-and-white Wrens sing in a dramatically lower frequency range (0.75–3 kHz) than all other *Thryothorus* species that have been examined in detail, including Banded Wrens (2–9 kHz), Bay Wrens (2–6 kHz), Black-bellied Wrens (1–4 kHz; *T. fasciatoventris*), Buff-breasted Wrens (2–5 kHz), Carolina Wrens (2–6 kHz), Happy Wrens (1–5 kHz; *T. felix*), Plain Wrens (2–8 kHz), Rufous-breasted Wrens (2–6 kHz; *T. rutilis*), and Sinaloa Wrens (1–6 kHz; *T. sinaloa*) (Brown and Lemon 1979, Farabaugh 1983, Simpson 1984, Morton 1987, Levin 1996, Molles and Vehrencamp 1999, Mann et al. 2003). The low frequency of Rufous-and-white Wren songs may be adapted to maximize sound transmission in a songbird that sings from low perches in a heavily forested environment (Bradbury and Vehrencamp 1995). Future research on other *Thryothorus* species will confirm whether Rufous-and-white Wrens are truly unique, or whether there is an unexplored spectrum of variation in *Thryothorus* wren songs. The voice of the critically endangered Niceforo's Wren (*T. nicefori*) is of particular interest; although Niceforo's Wren may be the closest relative of the Rufous-and-white Wren, its voice is undescribed.

Among 27 species of *Thryothorus* wrens, all species that have been investigated have vocal

repertoires. The repertoires of Rufous-and-white Wrens are the smallest reported in the genus: >8 (present study), as compared with >15 for Plain Wrens (Mann et al. 2003), >15 for Bay Wrens (Levin 1996), ≥ 17 for Sinaloa Wrens (Brown and Lemon 1979), 20 for Banded Wrens (Molles and Vehrencamp 1999), 29 for Happy Wrens (Brown and Lemon 1979), and 32 for Carolina Wrens (Morton 1987). Rufous-and-white Wrens sing with eventual variety, repeating each song type before moving on to a different song type. Across the genus, all duetting species are repeat-mode singers (Happy Wrens, Brown and Lemon 1979; Buff-breasted Wrens, Farabaugh 1983; Bay Wrens, Levin 1996; Plain Wrens, Mann et al. 2003), whereas both of the tropical species, which do not duet, are serial-mode singers (Sinaloa Wren, Brown and Lemon 1979; Banded Wrens, Molles and Vehrencamp 1999). Repeat-mode singing may provide a basis for the evolution of duetting, allowing one member of a pair to anticipate songs from its partner.

Repertoire sharing has been investigated carefully only in three other species of *Thryothorus* wren, the duetting Bay Wren and the non-duetting Banded Wren and Carolina Wren. In Bay Wrens, 20% of each male's repertoire is individually unique, whereas 0% of each female's repertoire is individually unique (Levin 1996). We found the opposite pattern in Rufous-and-white Wrens; 6% of each male's repertoire is individually unique and 23% of each female's repertoire is individually unique. In Banded Wrens and Carolina Wrens, repertoire sharing decreases with distance between males (Morton 1987, Molles and Vehrencamp 1999). The repertoire sharing between neighboring Banded Wrens plays an important role in male–male countersinging interactions. Type matching (responding with the same song type as an opponent) is a more aggressive signal than repertoire matching (responding with a different song type that is shared with the opponent's repertoire), which is a more aggressive signal than nonmatching (Molles and Vehrencamp 2001). All male Rufous-and-white Wrens share multiple song types with their neighbors, and song-type sharing decreases with distance between males and females. Consequently, type matching and repertoire matching may play a similar role in territorial interactions between neighboring males. Type matching is likely to be less important for females, however, who

share very few song types in common with their neighbors. Future research evaluating the countersinging dynamics between neighboring birds and differences in the spatial and temporal production of song types will evaluate whether male and female Rufous-and-white Wrens follow similar singing strategies.

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