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Male and female rufous-and-white wrens do not match song types with same-sex rivals during simulated territorial intrusions

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In birds with song repertoires, song-type matching occurs when an individual responds to another individual's song by producing the same song type. Song-type matching has been described in multiple bird species and a growing body of evidence suggests that song-type matching may serve as a conventional signal of aggression, particularly in male birds in the temperate zone. Few studies have investigated song-type matching in tropical birds or female birds, in spite of the fact that avian biodiversity is highest in the tropics, that female song is widespread in the tropics, and that female song is the ancestral state among songbirds. In this study of rufous-and-white wrens *Thryophilus rufalbus*, a resident neotropical songbird where both sexes sing, we presented territorial males and females with playback that simulated a territorial rival producing shared and unshared songs. In response, both males and females sang matched song types at levels statistically equal to levels expected by chance. Furthermore, males and females exhibited similar levels of aggression and similar vocal behaviours in response to playback of both shared and unshared songs. These results indicate that rufous-and-white wrens do not use song-type matching in territorial conflicts as a conventional signal of aggression. We discuss alternative hypotheses for the function of song-type sharing in tropical birds. In particular, we point out that shared songs may play an important role in intra-pair communication, especially for birds where males and females combine their songs in vocal duets, and this may supersede the function of song-type matching in some tropical birds.

Keywords: acoustic behaviour, conventional signals, duets, female song, signal honesty, song, *Thryothorus rufalbus*, tropical birds

Introduction

In many different songbird species, individuals have distinct song types that form song repertoires, and these repertoires may serve a number of different functions. For instance, larger song repertoires in some species are a sexually selected trait that may be indicative of high-quality individuals (Dussourd and Ritchison 2003, Reid et al. 2004, Hesler et al. 2012), and may also be important in communicating aggression during territorial interactions with conspecific rivals (Falls et al. 1981, Falls 1985, Hughes et al. 2007). Many young birds learn their songs from nearby tutors

(Beecher et al. 2007, Mennill et al. 2018), and therefore often share song types with nearby conspecific animals (e.g. banded wrens *Thryophilus pleurostictus*, Molles and Vehrencamp 1999; winter wrens *Troglodytes troglodytes*, Camacho-Schlenker et al. 2011; tropical mockingbirds *Mimus gilvus*, Price and Yuan 2011; red-eyed vireos *Vireo olivaceous*, Moser-Purdy and Mennill 2016). The presence of shared song types allows birds to engage in complex vocal interactions (Todt and Naguib 2000, Akçay et al. 2013). In particular, song-type sharing allows birds to engage in a behaviour known as 'song-type matching', which occurs when two individuals sing the same song type during a vocal interaction. The principal hypothesis for the function of song-type matching is that it serves as a conventional signal of aggression, where a matched song type is a more aggressive signal than a non-matched song type, and communicates a threat of escalation (Krebs et al. 1981, Vehrencamp 2001, Akçay et al. 2013). Studies of diverse songbirds show that birds often match the song type of conspecific rivals during aggressive countersinging exchanges (e.g. great tits *Parus major*, Falls et al. 1981; western meadowlarks *Sturnella neglecta*, Falls 1985; song sparrows *Melospiza melodia*, Stoddard et al. 1992; tropical mockingbirds, Price and Yuan 2011).

One common experimental design for studies of song-type matching involves presenting a territorial bird with playback of both a shared song type and an unshared song type, and assessing whether the subject responds with a matched song type more often than expected by chance (chance expectation is usually calculated as the inverse of the animal's vocal repertoire size; Stoddard et al. 1992). In most studies, birds respond to a playback-simulated rival singing a shared song type by singing the same song type (i.e. a song match), although results are mixed when investigating the hypothesis that song-type matching is associated with aggression. Searcy and Beecher (2009) outline three criteria important for determining if a vocal signal should be considered an aggressive signal: 1) the signal must increase in frequency (i.e. rate) in aggressive contexts; 2) the signal must predict aggressive escalation; and 3) the receiver must respond differently to the signal in comparison to a control. One study in a western population of song sparrows found that song-type matching fulfilled the first two of these criteria: song-type matching was associated with attack, and song-type matching predicted escalation to more aggressive behaviours (Akçay et al. 2013). In contrast, an eastern population of song sparrows song-type matched at high frequencies, but song-type matching was not associated with aggressive behaviours (Searcy et al. 2013). Results of playback studies with other species have been equivocal, because some studies provide support for the hypothesis that song-type matching is an aggressive signal (Burt et al. 2001, Vehrencamp 2001) while others do not (Falls et al. 1981, Falls 1985). Further studies are needed in diverse species to determine the importance of song-type matching in aggressive contexts.

Most song-type matching studies have focused on male birds in the north-temperate zone, including a heavy focus on song sparrows (Vehrencamp 2001, Akçay et al. 2013, Searcy et al. 2013), despite the fact that avian biodiversity reaches its peak in the tropics. Tropical birds exhibit many ecological and behavioural traits that differ from north-temperate birds, including prolonged-breeding seasons, year-round territoriality and the widespread presence of female song (Stutchbury and Morton 2001, Slater and Mann 2004). Recent comparative analyses have revealed that male and female song is the ancestral state among songbirds (Odom et al. 2014), highlighting the need for more thorough investigations of the function of song in both sexes. Studies of vocal matching in male and female tropical birds are rare, and those that have explored song-type matching did not measure the response of focal birds to shared and unshared songs (Rogers et al. 2006, Price and Yuan 2011, Templeton et al. 2013a). To our knowledge, no playback study to date has investigated how male and female tropical birds perceive shared and unshared songs in aggressive contexts.

In this study, we conducted a playback experiment to investigate song matching in both males and females in a tropical songbird: the rufous-and-white wren *Thryophilus rufalbus*. Rufous-and-white wrens are neotropical songbirds where males and females both sing solo songs as well as combine their songs to form duets. Rufous-and-white wrens have moderately sized vocal repertoires (males: 10.8 ± 0.7 song types, females: 8.5 ± 0.7 song types, Mennill and Vehrencamp 2005) that they sing with eventual variety. They exhibit a high rate of song-type sharing among males (6.7 ± 0.6 song types are shared between individual male neighbours, Mennill and Vehrencamp 2005, Harris et al. 2016) and a lower rate of song-type sharing among females (0.3 ± 0.6 song types are shared between individual female neighbours, Mennill and Vehrencamp 2005). We designed a playback experiment with two goals in mind: 1) we tested whether male and female rufous-and-white wrens song type match more frequently than expected by chance when presented with a playback-simulated rival singing a shared song type; 2) we tested whether rufous-and-white wrens interpret shared song types as more aggressive than unshared song types.

Material and methods

General field methods

We conducted playback experiments in Sector Santa Rosa of the Guanacaste Conservation Area in Costa Rica (10°51′N, 85°36′W) from 26 May to 28 June 2017. Playback subjects were 16 male and 13 female rufous-and-white wrens living in a population of birds that our laboratory group has studied since 2003. Every year, we band birds, map territories, record focal pairs and monitor nesting behaviour in this population (details in Woodworth et al. 2018). In the current experiment, all of the male subjects were colour-banded and five of the female subjects were colour-banded (females are more difficult to capture than males in this species). For unbanded females, we differentiated between individuals based on nest

location, territory position and the fine-structural features of songs in their vocal repertoires. All experimental subjects were paired at the time of playback. We had fewer female playback subjects (n = 13) than male playback subjects (n = 16) because two females disappeared after nest failures that occurred following the male playback session but prior to the female playback session for that pair, and technical difficulties with our recorder left us without a recording of one female's playback response.

Repertoire sampling and estimation

To sample the vocal repertoire of the playback subjects, we collected extensive recordings of each subject pair using both focal recording and automated recording approaches. We collected in-person focal recordings of spontaneous songs from each pair in the hour after dawn using a directional microphone (model: Sennheiser ME67/K6) connected to a solid-state digital recorder (model: Marantz PMD660, 44.1 kHz sampling rate, 16-bit encoding, WAVE format). We then placed autonomous recorders (model: SM2, Wildlife Acoustics, Concord, MA, USA) on focal birds' territories to acquire a greater sample of their songs. Autonomous recorders collected recordings from each pair over a period of 3–10 d. We could differentiate between male and female rufous-and-white wrens in these recordings because of sex-differences in acoustic features of their songs (Mennill and Vehrencamp 2005). We combined the focal recordings and autonomous recordings, and annotated them using SYRINX-PC (John Burt, Seattle, WA, USA), classifying each song from each individual as a specific song type, as in previous studies (Mennill and Vehrencamp 2005, Harris et al. 2016). Rufous-and-white wrens sing with eventual variety, repeating songs multiple times before switching to a different song type (Mennill and Vehrencamp 2005, Harris et al. 2016). Each song type can be readily distinguished from the next by distinct specto-temporal features, which we accomplished according to previously established protocol for this population (see Harris et al. 2016 for details).

From our field recordings, we created song libraries for each of our focal birds and estimated repertoire sizes for both males and females (see below, and Fig. 1). By referring to the song libraries for each male and female, we created playback stimuli that represented shared and unshared song-types relative to the repertoire of each of our subjects. We considered songs to be shared (matched) when they had highly similar time and frequency structures (see Fig. 2, for four examples of matched songs), using the same approach as previous studies in this species (Mennill and Vehrencamp 2005, Harris et al. 2016). To evaluate whether our assignments of song sharing were repeatable, the four authors conducted a test involving 10 arbitrarily selected pairs of songs and determined whether each pair represented a 'match' or a 'non-match' pair of songs; we found 100% agreement in these blind classifications.

To ensure that unshared stimulus songs were truly unshared between the experimental subjects and the playback-simulated rivals, we attempted to record full repertoires
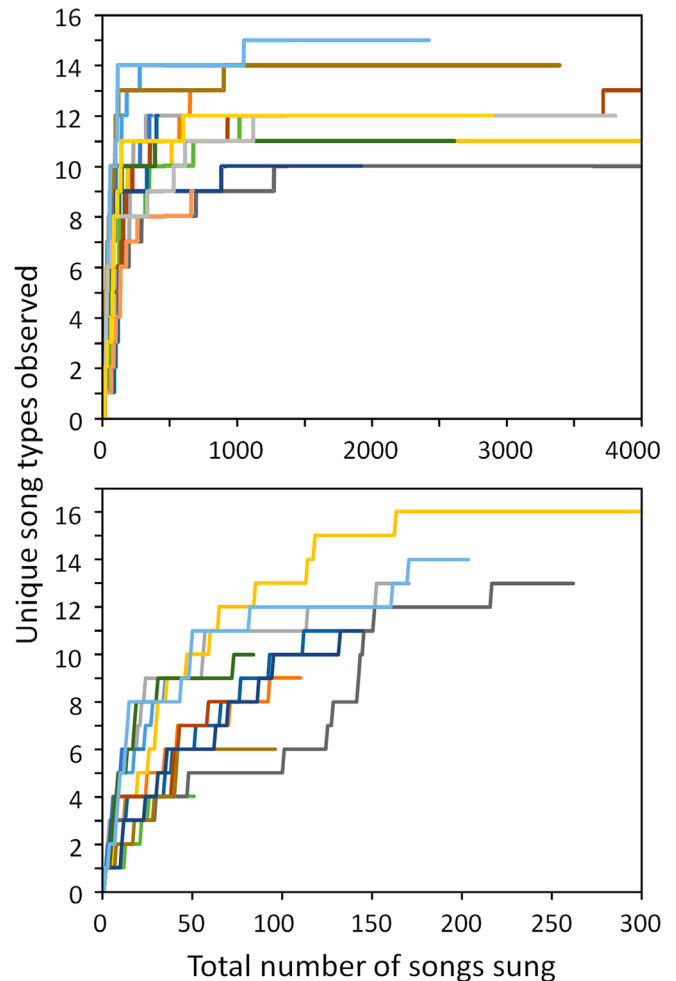

Figure 1. Rufous-and-white wren song repertoires for males (top) and females (bottom) showing the number of unique song types observed as a function of recording effort. For males 12 out of 16 birds reached a repertoire asymptote, indicating their full repertoires had been recorded, whereas for females only 3 out of 13 females reached a repertoire asymptote. Different scales are used on the x-axis in the top and bottom graphs because male song output is much higher than female song output.

of each individual. We estimated repertoire size by plotting the total number of songs sung on the x-axis and number of new songs sung on the y-axis (Fig. 1). When repertoire size is accurately estimated, this graph is expected to reach an asymptote. Most male birds (12 out of 16) reached a repertoire asymptote, indicating that we had recorded full repertoires for these birds (Fig. 1). Few female birds (3 out of 13) reached an asymptote, indicating that we did not record full repertoires for most females (Fig. 1). This is due to the low song rates of female rufous-and-white wrens (Mennill and Vehrencamp 2005). Nevertheless, we have confidence that our unshared songs used in female trials were unlikely to be in females' repertoires for several reasons: 1) song sharing is low in female rufous-and-white wrens (1.7 ± 0.3 song types shared, on average, across the study population; Mennill and Vehrencamp 2005), and we used songs that
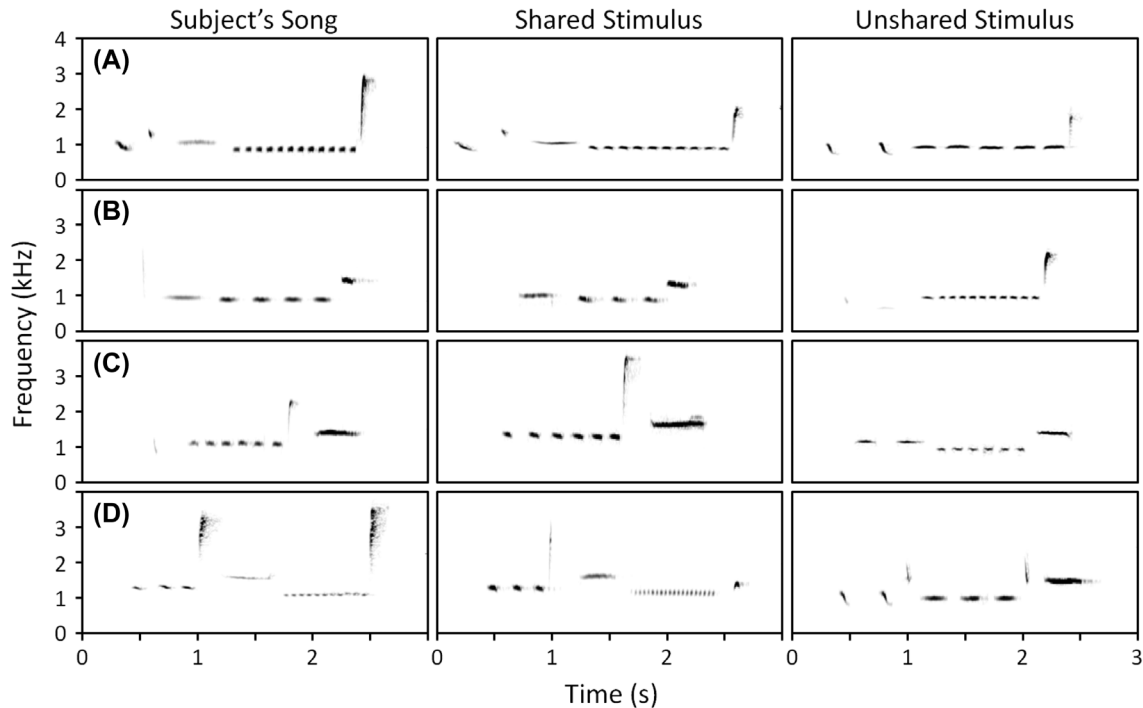
Figure 2. Sound spectrograms of the songs of four rufous-and-white wrens (left; (A) and (B) are male whereas (C) and (D) are female songs), shown next to an example of a shared, matching song (middle) and an unshared, non-matching song (right) used during their playback trials.

were not commonly sung in the population for our unshared stimuli; 2) we collected on average 9.8 ± 3.4 song types for each female (range 4–16) and average song repertoire size for female rufous-and-white wrens has been reported as 8.5 ± 0.7 song types (Mennill and Vehrencamp 2005), revealing that our repertoire sampling captured most of the females' repertoires; 3) previous research shows that, on average, 23% of a female's repertoire is unique, indicating that multiple female song types are specific to one individual (Mennill and Vehrencamp 2005).

Playback stimuli

We created stimuli that allowed us to simulate a territorial male or female rufous-and-white wren producing bouts of songs that were shared or unshared with the experimental subjects. The playback stimuli were collected from our focal field recordings. We extracted songs with low levels of background noise. We removed any excess low-frequency background noise by applying an 800 Hz high-pass filter, which was lower than the lowest frequency in all recorded songs. When background noise was present in other frequencies, we used the lasso selection tool and amplify functions to remove the noise using Audition (ver. 3.0, Adobe, San Jose, CA). We normalized all stimuli to -1 dB and standardized the amplitude of our loudspeaker (model: Scorpion X1B, FOXPRO) such that each playback stimulus had a peak amplitude of 75 dB at a distance of 1.0 m from the loudspeaker (sound level meter: Casella Cel-240; C weighting, fast response), a

normal singing volume for this species based on our auditory assessment in the field.

Each pair of rufous-and-white wrens received playback of four different stimuli: one shared song and one unshared song for each sex. Stimuli were constructed from recordings of birds from recent years (1–5 yr prior) or birds from the same year, but all songs were taken from birds that lived in distant parts of our study site, at least 2 km away from the focal bird in each playback. The purpose of this was to create stimuli from birds which, to our knowledge, had no previous interactions with the focal birds. Stimulus tracks were created by duplicating the same song repeatedly over a period of 3 min at a rate of one song played every 10 s (18 songs total). This methodology is similar to other studies of song-type matching where birds were given a chance to respond to 12 songs (Falls et al. 1981, Falls 1985) or 18 songs (Stoddard et al. 1992).

Playback trials

We conducted playback experiments between 06:30 h and 11:30 h, a time of day when rufous-and-white wren activity and song output is high. We conducted male trials first, and female trials approximately two weeks later. Female trials began after male trials because we required more time to sample female repertoires, given that females sing at lower rates than males (Mennill and Vehrencamp 2005). All trials were conducted when females were deemed to be not fertile (i.e. either incubating young or provisioning young).

We broadcast stimuli during our experiments using a FoxPro Scorpion X1B (FoxPro, Lewiston, PA, USA) loudspeaker, which we set up 20 m inside the territory boundaries of our focal pairs at a height of 1 m above the ground and at least 15 m away from active nests, thereby simulating a territorial intrusion by a bird near the edge of the subjects' territories. We set up flagging tape 2 m from the speaker in four directions to aid in distance estimates during playback. Playback trials began with a 1 min lure, consisting of playback of a conspecific rattle call to draw the birds near the speaker. This was followed by a 30-s period of silence, 3 min of the playback stimulus and 5 min of silent post-playback observation. The lure was necessary to attract the birds to the loudspeaker; during our preliminary trials, birds would rarely approach the loudspeaker during the trial without playback of calls beforehand. Shared and unshared playback trials were presented in a random order such that each treatment was presented first an equal number of times (across the 13 females, shared songs were presented first six times, and unshared songs were presented first seven times). We conducted shared and unshared playback treatments to each pair 1–3 d apart. We did not expose neighbouring pairs to playback trials on the same day.

The birds' vocal responses were recorded by a shotgun microphone positioned 20 m way from the loudspeaker, and the birds' behavioural responses were recorded by an observer whispering into the microphone while seated beside it. Recordings began at the start of the broadcast of the lure. We placed flags 2 m away from the loudspeaker in four cardinal directions to aid with estimation of subject distance from the loudspeaker. Later, we annotated the spoken commentary of each playback trial using SYRINX-PC, providing a timestamped record of each bird's physical and vocal behaviour.

Statistical analysis

We used R (ver. 3.4.3, R Development Core Team) to analyze our data. We used an exact two-tailed binomial test to determine whether male and female rufous-and-white wrens song matched more frequently than expected by chance. Previous studies vary in how they assess song-type matching in response to playback: some studies assess whether the first song sung by the playback subject matches the playback stimulus (Falls et al. 1981), whereas other studies wait until the subject exhibits one change in song type and then assess whether that song type matches the playback stimulus (Stoddard et al. 1992). We felt it was prudent to include both types of analysis, and therefore we conducted one analysis where we assessed the first song type sung was a match or non-match, and a second analysis where we assessed the first song type sung after the subject changed song type (as in Templeton et al. 2013a). We used the inverse of the average repertoire size for the males (12) and females (9.8) as our expected values. In four matched song-type trials to females, the subject female did not sing. We included these trials in our analysis and considered them to have 0 song matches.

In these trials we ensured that the female was present in the territory during the playback trial by locating her after the experiment was over. We felt justified in including these trials in our analysis because the female was present, and had the opportunity to song type match with the speaker. We conducted a second test excluding these four females, and found that this did not influence our results (see Results).

To determine if rufous-and-white wren behaviour was influenced by whether they were exposed to shared or unshared songs, we conducted a principal components analysis (PCA) of seven behavioural and vocal variables: time spent within 10 m of the speaker, latency to approach within 10 m of the speaker, closest approach to the speaker, number of flights, number of songs sung, and duet responsiveness (i.e. proportion of partner's songs answered to create a duet), and number of song-type switches. We included the birds' behaviour during both the playback and post-playback periods combined. We conducted these analyses separately for each sex because we were interested in how females and males individually responded to shared and unshared playback. We ran a Kaiser–Meyer Olkin factor adequacy test (KMO test) on our male and female response datasets. The vocal response variables for males returned low scores (number of songs sung: 0.48, number of song switches: 0.47, duet responsiveness: 0.33) while the remaining variables all returned values of 0.59 or higher. While Kaiser (1974) recommends that variables with values below 0.5 not be included in a PCA, we elected to include these male variables because 1) we are interested in the vocal response of our male subjects, and 2) there is no difference in the significance of our results when these variables are included or excluded. In our female dataset, all variables returned values of 0.74 or higher. We also conducted Bartlett's test of sphericity on our dataset to ensure that our correlation matrices did not only contain zero values. This hypothesis was rejected for both males and females (males: $\chi^2 = 138.5$, $p < 0.001$; females: $\chi^2 = 219.2$, $p < 0.001$). We conducted our PCA using a correlation matrix of our data and then applied a varimax rotation using the package psych in R (ver. 1.8.12; Revelle 2018). Our male PCA produced two principal components with eigenvalues above 1. The first principal component for males explained 38% of the variance with an eigenvalue of 2.67 (Table 1), and had heavier loadings from the physical responses (time spent within 10 m of the speaker, closest approach to the speaker, and latency to approach the speaker; Table 1). Hereafter, we refer to this principal component as 'male physical response'. The second principal component for males explained 24% of the variance and had an eigenvalue of 1.69 (Table 1, and had heavier loadings from vocal response variables, (number of songs sung and number of song switches; Table 1). We refer to this principal component as 'male vocal response.' Our female PCA produced two principal components with eigenvalues greater than or equal to 1. The first principal component for females explained 41% of the variance and had an eigenvalue of 4.03 (Table 1), and had heavier loadings from physical responses (closest approach to the speaker, number of flights)

Table 1. Principal component loadings for male and female rufous-and-white wren playback responses, focused on physical responses and vocal responses.

	Male physical response (PC1)*	Male vocal response (PC2)*	Female response score 1 (PC1)†	Female response score 2 (PC2)†
Time spent within 10 m	0.84	0.00	0.32	0.83
Closest approach	−0.86	0.00	−0.71	−0.46
Latency to approach within 10 m	−0.91	0.15	−0.59	−0.70
Number of flights	0.58	0.47	0.79	0.42
Number of songs sung	0.16	0.73	0.80	0.28
Duet responsiveness	0.00	0.53	0.00	0.72
Number of song type switches	−0.12	0.79	0.80	−0.10
Proportion of variance explained	0.38	0.24	0.41	0.31
Eigenvalue	2.67	1.69	4.03	1.00

* Male PC1 scores showed high loading from physical response variables and we refer to this score as 'Male physical response', and male PC2 scores showed high loading from vocal response variables and so we refer to this score as 'Male vocal response'.
† Female PC scores did not show the same pattern of loading as male PC scores, and so we refer to female scores as 'Female response score 1' (loading is primarily from physical response scores but also number of songs sung) and 'Female response score 2' (loading is primarily from duet responsiveness and song type switches, but also time spent within 10 m of speaker).

but also two vocal responses (number of songs and number of song type switches; Table 1). We refer to this principal component as 'female response score 1.' The second principal component for females explained 31% of the variance and had an eigenvalue of 1 (Table 1), and had heavier loadings from two physical responses (time spent within 10 m of the speaker, latency to approach within 10 m of the speaker) as well as one vocal response (duet responsiveness; Table 1). We refer to this principal component as 'female response score 2.'

We used linear mixed models to analyze our data using the 'nlme' package (ver. 3.1-137; Pinheiro et al. 2018) with male and female physical and vocal responses as our response variables in separate analyses. We input the interaction between type of playback (shared or unshared) and sex of playback (male or female) as our fixed effect and input individual and response of opposite sex as random effects.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mq427sp> (Moser-Purdy et al. 2019).

Results

Song matching

When exposed to a playback-simulated rival singing a shared song type, rufous-and-white wrens responded by singing, but neither males nor females showed a propensity to match the song type of the simulated rival. During playback simulating a male rival, males matched the rival's song type in 0 out of 16 trials with their first song type, and 1 out of 16 trials with their first song type after a song-type switch; both of these outcomes are statistically equal to the level of song-type matching expected by chance alone (binomial test, $p > 0.6$; expected proportion of matching: 1/12). During playback simulating a female rival, females matched the rival's song

type in only 2 out of 13 trials with their first song type, and only 1 out of 13 trials with their first song type after a type switch; again, both of these cases are statistically equal to the level of song-type matching expected by chance alone (binomial test, $p > 0.6$; expected proportion of matching: 1/9.8). When we excluded females who did not respond to playback but were confirmed to be present in their territory, we observed song-type matching in 2 out of 9 trials with their first song type, and 1 out of 9 trials with their first song type after a type switch; again, these results were statistically equal to the level of song-type matching expected by chance alone (binomial test, $p > 0.2$, expected proportion of matching: 1/9.8).

Response to shared and unshared playback

Rufous-and-white wrens responded to playback by approaching the loudspeaker, often approaching to within 10 m, and spending time near the speaker. Yet neither males nor females showed different intensities of response to shared versus unshared song types. Males responded similarly to playback of shared versus unshared song types, although they had a tendency to exhibit more intense responses to simulated male rivals compared to simulated female rivals (Table 2, Fig. 3). Females responded similarly to playback of shared versus unshared song types, although they exhibited a higher response to female playback versus male playback (Table 2, Fig. 4).

Discussion

Male and female rufous-and-white wrens sang songs that matched playback-simulated rivals at frequencies that did not exceed the levels expected by chance. Additionally, male and female wrens did not exhibit differences in aggressive behaviours when responding to shared versus unshared song types. Males and females showed heightened physical responses to playback of the same sex compared to the opposite sex,

Table 2. Results of a linear mixed model analysis comparing male and female rufous-and-white wren playback responses to rivals singing a shared or unshared song type. Playback type refers to shared or unshared song and sex of playback refers to whether the playback stimuli were songs from males or females. Playback was repeated to n = 16 males and n = 13 females.

	F	p
Male physical response (PC1)		
Playback type (shared or unshared)	0.09	0.78
Sex of playback	3.19	0.10
Playback type × sex of playback	0.04	0.86
Male vocal response (PC2)		
Playback type (shared or unshared)	0.07	0.80
Sex of playback	0.02	0.90
Playback type × sex of playback	2.54	0.17
Female response score 1 (PC1)		
Playback type (shared or unshared)	0.65	0.42
Sex of playback	3.30	0.07
Playback type × sex of playback	0.00	0.98
Female response score 2 (PC2)		
Playback type (shared or unshared)	0.40	0.53
Sex of playback	0.72	0.40
Playback type × sex of playback	0.01	0.91

presumably as a form of territory and mate defense against encroaching members of the same sex. We conclude that rufous-and-white wrens do not exhibit song-type matching behaviour during aggressive territorial interactions and that neither males nor females perceive shared songs as signals of aggression.

In several other studies of song-type matching, when birds were presented with shared playback they matched the song type of the playback (Falls et al. 1981, Falls 1985, Price and Yuan 2011). In some studies, song-type matching the playback stimulus was associated with more aggressive behaviours (Burt et al. 2001, Vehrencamp 2001; note: both

studies used interactive playback) while in other studies song-type matching was not associated with more aggressive behaviours (Falls et al. 1981, Falls 1985, Searcy et al. 2006, Ballentine et al. 2008). Our design was similar to other song-matching experiments (Falls et al. 1981, Stoddard et al. 1992) suggesting that our experimental design was not a factor inhibiting song-matching in our study. These results beg the question: why do rufous-and-white wrens share song types if they do not appear to be important for communicating aggression during territorial interactions? Several alternatives are possible.

The majority of song-matching studies in birds have been conducted in temperate-zone species, where it is primarily males that sing and defend territories during the breeding season (Slater and Mann 2004, Catchpole and Slater 2008). Many of these species experience highly condensed and intense breeding periods characterized by high densities of conspecific animals and heightened threats of territorial intrusions from conspecifics. Therefore, there may be a greater importance for temperate birds to be able to escalate aggressive contests to successfully defend territories and ward off rival males seeking extra-pair copulations. Many of these characteristics of the breeding ecology of temperate birds contrast those of rufous-and-white wrens, which may help to explain the lack of song-matching we observed during our playbacks. For example, rufous-and-white wrens at our study site have large breeding territories (Osmun and Mennill 2011), exhibit low rates of extra-pair paternity (2% of offspring in 6% of broods; Douglas et al. 2012), and defend territories year round (Mennill and Vehrencamp 2008, Kahn et al. 2018), suggesting that the intensity and prevalence of territorial conflicts in rufous-and-white wrens is lower than in temperate species studied to date. Additionally, both males and females sing in this species (Mennill and Vehrencamp 2005), and use duets during territory defense
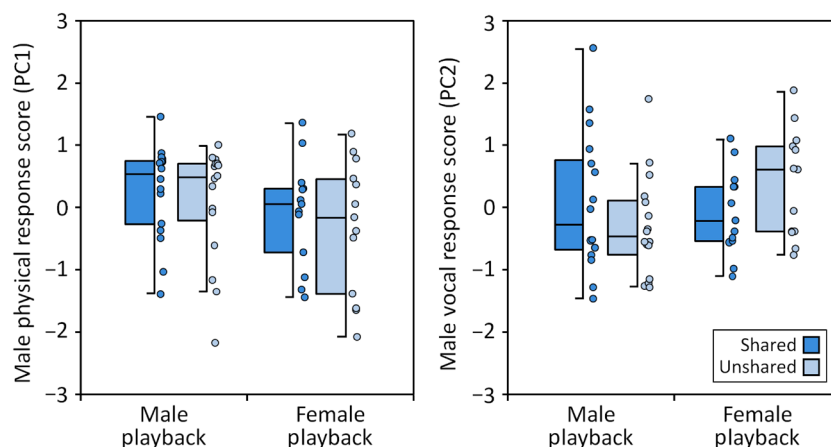

Figure 3. Male rufous-and-white wrens' physical responses and vocal responses to playback of shared and unshared song types by simulated male and female rivals. Physical and vocal response scores are principal component scores summarizing variation in male response data, where higher values indicate a more intense response (closer approach to loudspeaker, higher song output, etc.). Data are plotted as the raw data adjacent to box plots where the box shows the first quartile to the third quartile of the data, and the whiskers show 1.5 times the interquartile range beyond the first and third quartiles. Males showed higher physical response to male playback than female playback, but did not show different physical or vocal responses to playback of shared versus unshared songs.
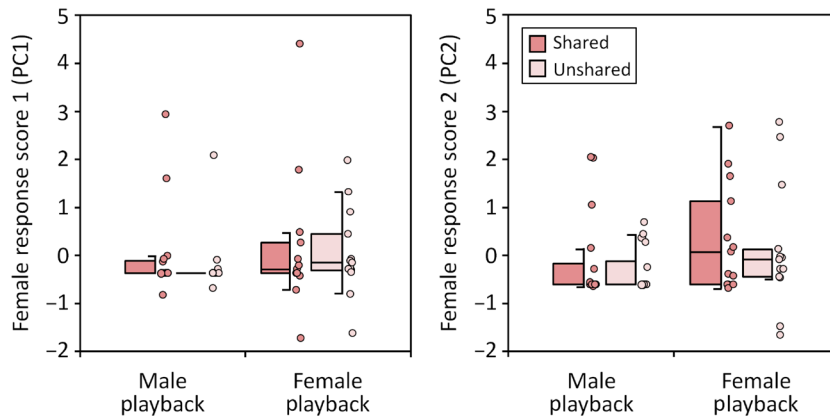
Figure 4. Female rufous-and-white wrens' physical responses and vocal responses to playback of shared and unshared song types by simulated male and female rivals. Responses are principal component scores summarizing variation in female response data. Data are plotted as the raw data adjacent to box plots where the box shows the first quartile to the third quartile of the data, and the whiskers show 1.5 times the interquartile range beyond the first and third quartiles. Females showed higher response scores to female playback than male playback for response score 1 (reflecting more time within 10 m, closer approaches, lower latencies of approach, more flights and more songs) but did not show different responses to playback of shared versus unshared songs. Female vocal output was low in response to male playback.

(Mennill 2006). It is possible that characteristics of duetting within or between pairs could be more important for escalating aggressive interactions than solo songs from one sex. Further studies are necessary to elucidate the ecological and behavioural factors that contribute to the lack of song-type matching observed in this study.

We used playback to simulate songs of strangers instead of neighbours. It is possible that rufous-and-white wrens interpret shared and unshared stranger songs as equally threatening due to the high threat associated with an intrusion by a stranger (Temeles 1994), and therefore respond equally aggressively to both types of song. However, this explanation fails to explain the lack of song-type matching during trials that involved shared song types. If singing a shared song type is an aggressive signal in rufous-and-white wrens, we would expect that during a high-threat intrusion, wrens would respond with highly aggressive signals to repel intruders. Other species, including western meadowlarks, song sparrows, and great tits (when controlled for familiarity), show higher levels of song-type matching to playback of stranger song than to neighbour song (Falls et al. 1981, Falls 1985, Stoddard et al. 1992), indicating that stranger song should readily elicit song-type matching if it is important in communicating aggression. It is still possible that shared song types are only used in neighbour interactions in rufous-and-white wrens and an experiment testing response to shared and unshared neighbour songs may yield interesting results. Such a study would also be able to investigate repertoire matching, wherein focal birds respond to neighbour shared song stimulus with a different song that is found in both of their repertoires (Beecher et al. 1996). This may be a less aggressive signal than song-type matching and may facilitate de-escalation of territorial conflicts (Beecher et al. 1996). Rufous-and-white wrens may attempt to avoid costly territorial conflicts by de-escalating aggressive interactions with neighbours through repertoire matching. However, under this hypothesis

we would still expect that rufous-and-white wrens would respond by matching the song type to a highly aggressive stranger intrusion if they interpret song-type matching as an aggressive signal.

Shared song may not be used for intrasexual conflict in rufous-and-white wrens, and instead shared songs may play a different role in duets or intrapair communication. Like other duetting songbirds (e.g. black-bellied wrens, *Pheugopedius fasciatoventris*, Logue 2006; happy wrens, *Pheugopedius felix*, Templeton et al. 2013b), rufous-and-white wrens exhibit duet codes where males and females combine songs from their vocal repertoires non-randomly (Mennill and Vehrencamp 2005). It is possible that during territorial interactions, male and female rufous-and-white wrens choose song types relative to their duet code and the song-type choice of their partner, rather than choosing a song relative to the song type produced by their rival. Song-type matching appears to be important within the duet codes of rufous-and-white wrens; Osmun (2010) showed that 5 out of the 10 most common duet types in rufous-and-white wrens involved matched songs produced by the male and female. Furthermore, in happy wrens when females are given the choice between song-type matching female playback or forming the appropriate duet with their mate, they choose the latter (Templeton et al. 2013a) which suggests that song sharing in duetting species has an important function in pair communication. Song-type matching between breeding pairs in aggressive contexts has not been studied in rufous-and-white wrens and may provide an explanation for song sharing in this species. Furthermore, male rufous-and-white wrens use more of their repertoire when paired than when unpaired, (Hennin et al. 2009) suggesting that different song types may have more function within pairs than between same-sex rivals. Across duetting species, it is conceivable that repertoire selection to achieve duet codes is more important than repertoire selection in the context of intrasexual aggression.

Another alternative explanation for our negative results is that our sample size (n = 16 males and n = 13 females) was too small to detect song-type matching. Song-type matching in most studies occurs at high rates (Falls et al. 1981, Burt et al. 2002) and song-type matching is regularly found in temperate birds with sample sizes of 20 (Falls et al. 1981, Burt et al. 2001) and even with sample sizes as low as 10 and 14 (Stoddard et al. 1992). Song-type matching rates were very low in our study (males: 6.3% of trials, females: 16.7% of trials). If rufous-and-white wrens interpreted shared and unshared songs as different signals but our sample size was too small to detect this, we would have expected to have observed more than a single song match for males and three song matches for females during our playbacks (Table 2, Fig. 3, 4). Perhaps with a much larger sample size we would detect a small effect, however if we require a large sample size to detect a difference in response to shared and unshared stimuli it is unlikely that song-type matching plays a major role in communicating aggression for rufous-and-white wrens.

We were motivated to study song-type matching in rufous-and-white wrens given the high level of repertoire sharing found in this species, particularly for males but also for females (Mennill and Vehrencamp 2005, Harris et al. 2016). In contrast to our initial idea that this pattern might be associated with song-type matching, it is possible that song type sharing is simply a by-product of the pattern of song learning and dispersal in our study population. A recent study found that birds in this population exhibit limited breeding dispersal, suggesting that male rufous-and-white wrens learn songs from their fathers as well as nearby neighbours (Graham et al. 2017). Young males share more songs with their fathers the closer their breeding territory is established near their natal territory (Graham et al. 2017). By comparison, the song tutors of female rufous-and-white wrens are less apparent. Female rufous-and-white wrens exhibit no relationship between song-sharing with their mother and dispersal distance from natal territories. The lower song-sharing observed in females may reflect the fact that females exhibit greater dispersal than males (Graham et al. 2017), and thereby learn from a larger pool of tutors (Graham et al. 2018).

We found that male and female rufous-and-white wrens do not match song types with playback simulating a same-sex rival intruding on their territory. Additionally, we found that rufous-and-white wrens react with similar aggression to both shared and unshared song stimulus. These results add to a small body of research on song-type matching in tropical birds which, to this point, lack any consensus on the importance of song-type sharing in birds of the tropics. Taken together, these studies suggest that song sharing may have a different function in tropical birds than in temperate birds such as communication within pairs instead of aggressive interactions between same-sex rivals.

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