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Seasonal variation in the duetting behaviour of rufous-and-white wrens (*Thryothorus rufalbus*)

Stephanie M. Topp · Daniel J. Mennill

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Abstract Seasonal variation in animal signalling behaviour has been well documented and has contributed much to our understanding of male signals. In contrast, we know little about seasonal variation in female signals or signals produced jointly by males and females, such as the vocal duets of birds. Here, we examine how singing behaviour changes in relation to time of year and breeding stage in rufous-and-white wrens (*Thryothorus rufalbus*), neotropical songbirds where both males and females sing and where breeding partners coordinate songs to produce vocal duets. We recorded a colour-marked population of birds over an extended time period encompassing multiple breeding stages. Across all time frames and breeding stages, males sang at higher rates than females and male solos were more common than duets or female solos. Males and females showed divergent seasonal patterns of singing. Females sang more often early in the year, during the pre-breeding season, and female song tapered off as the breeding season progressed. Duetting followed a parallel pattern, which resulted from females showing less duet responsiveness to their partner's songs later in the year. Male independent song rate peaked at the onset of the rainy season – a time when females become fertile – and males showed the highest level of duet responsiveness during this period. Our results suggest that early in the year, duets appear to be cooperative displays, functioning in joint territory defence and/or the coordination of breeding activities. When females are fertile, however, increased duet responsiveness by males is consistent with mate or paternity guarding.

Keywords Acoustic signals · Duets · Female song · Rufous-and-white wrens · Vocal communication

Introduction

Seasonal patterns of variation in animal signalling behaviour provide insight into the function of those signals. For example, patterns of annual variation in the vocal behaviour of male temperate songbirds provided some of the first evidence that song acts as a multifunctional signal in both mate attraction and territory defence (e.g. Catchpole 1973; Slagsvold 1977; Logan 1983; Lampe and Espmark 1987). Signals that are less prevalent, such as female song (Langmore 1998) or vocal duets (Hall 2004), have received less attention. Little is known about how duets or female song is used during different breeding stages or at different times of the year. To date, more than 222 mainly tropical species are known to duet, occurring in phylogenetically distinct groups (Farabaugh 1982). This suggests that selection for duetting behaviour is strong in the tropics, yet the function of duets and the relationship between duetting and breeding behaviour are still unclear.

Duets occur when two animals, usually the male and female of a mated pair, vocalize together in a coordinated fashion (Farabaugh 1982; Hall 2004). Hypotheses for the function of vocal duets fall into two broad categories based on (a) the intended receivers of the signals that comprise the duet and (b) whether duets are cooperative displays or

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S. M. Topp · D. J. Mennill (✉)
Department of Biological Sciences, University of Windsor,
Windsor, ON, Canada, N9B3P4
e-mail: dmennill@uwindsor.ca

occur as a result of conflicting interests between duetting individuals (Hall 2004). Duets result from individual singing strategies and are created when the second individual responds to the first individual's song (otherwise the first individual's song would be a solo; Hall 2004). By examining duets in this way – as a response to a partner's song – we can evaluate duet function by assessing seasonal variation in duetting behaviour based on changes in duet responsiveness (i.e. the proportion of partner songs that an individual answers to create a duet). For example, if duetting acts as a paternity guard when females are fertile (Sonnenschein and Reyer 1983), males should be more responsive to their partner's song by creating more duets (i.e. contributing the second portion of the duet) during the female fertile period (Hall 2004). If, on the other hand, duetting is a cooperative display of territory defence (Seibt and Wickler 1977), both sexes should be similarly responsive to their partner's songs by creating duets at times of increased competition for territories (Hall 2006).

Studies assessing the function and adaptive significance of duetting behaviour have largely used an experimental approach, simulating territorial intrusions using playback to test hypotheses for duet function (e.g. Levin 1996; Hall 2000; Seddon et al. 2002; Mennill 2006). Playback studies, however, only capture one moment in time and few studies consider the effect of different contexts (e.g. fertile versus non-fertile breeding stages) or time of year (e.g. dry versus rainy seasons) on behaviour (Hall 2004). It is important to analyse both time of year and breeding stage changes in singing behaviour, because both temperate and tropical species coordinate breeding to occur when food resources are available (Dawson et al. 2001). Periods of food availability have been argued to be more predictable for temperate species than for tropical species (Hau et al. 2000; Dawson et al. 2001; Hau 2001; Slater and Mann 2004), although generalizations about seasonality of tropical ecosystems need further investigation. Analysis of changes in singing behaviour with time of year in tropical species may shed significant insight into song function and the factors contributing to the evolution of female song and vocal duets in the tropics.

Both context and time of year are known to influence vocalizations of male and female temperate birds, reflecting the variable role that song plays in communication. For example, male blue grosbeaks, *Guiraca caerulea*, increase their song complexity, dawn chorus song rate, and number of song bouts during the female fertile period, suggesting that song functions as an assessment signal during this stage (Ballentine et al. 2003). Studies documenting female song have found that females vocalize early in the year before nest building, suggesting that the primary function of song for females is territory or resource defence (e.g. northern cardinals, *Cardinalis cardinalis*, Ritchison 1986; Vondrasek 2006; song sparrows, *Melospiza melodia*, Arcese et al. 1988; superb fairy wrens, *Malurus cyaneus*, Cooney and Cockburn 1995). Two recent studies on duetting have repeated simulated intrusions at different breeding stages or times of year. Hall (2000) repeated duet and solo playback trials to magpie-larks, *Grallina cyanoleuca*, during the non-breeding and pre-breeding seasons and found that response rates did not differ significantly between these stages. She proposed that this lack of variation was a consequence of year-round territoriality of this species. Fedy and Stutchbury (2005) performed playback to white-bellied antbirds, *Myrmeciza longipes*, during the dry (non-breeding) and rainy (breeding) seasons and found that birds responded more aggressively to simulated intrusion during the dry season, suggesting that time of year or breeding stage influences duet behaviour. Overall, few studies have examined the interplay of time of year or breeding stage on duetting behaviour or the individual singing strategies of males and females. As a result, little is known about how singing strategies change in duetting species or what roles males and females play in inter- and intrasexual communications.

In this study, we investigate variation in the singing strategies of rufous-and-white wrens (*Thryothorus rufalbus*) with respect to time of year and breeding stage. Rufous-and-white wrens are socially monogamous resident neotropical songbirds found from Mexico to Colombia and Venezuela (Brewer 2001). Rufous-and-white wren pairs hold year-round territories and males and females share parental duties (nest building and nestling provisioning; females alone incubate and brood). Both males and females have vocal repertoires and perform songs as independent solos or as coordinated duets (Mennill and Verehncamp 2005). Both sexes create duets (i.e. respond to their partner's songs), although females create more duets on average than males (Mennill and Verehncamp 2005). Responses to duet playback suggest that duets may function both as a cooperative territorial defence display and as a mate or paternity guarding display by males (Mennill 2006).

The goal of this study is to describe variation in rufous-and-white wren solo and duet singing behaviour using recordings collected from a colour-marked population over an extended time period and encompassing multiple breeding stages. We examine song function based on the relative use of duets and solo songs and the proportion of male versus female contributions to song with respect to time of year and breeding stage. We discuss patterns of variation in light of three hypotheses for the function of duets: the reproductive synchrony hypothesis, the mate/paternity guarding hypothesis, and the joint resource defence hypothesis.

Methods

Study species and population

We studied a population of rufous-and-white wrens in the humid forests of Santa Rosa National Park, Guanacaste Conservation Area, Costa Rica (10°40′N, 85°30′W). From 2004 through 2006, we monitored 15–20 breeding pairs per year. Birds were captured in mist nets using passive netting or brief periods of song playback. Each individual was given a unique combination of three plastic colour bands and one numbered aluminum band, and standard morphometric measurements were taken. Males and females were easily distinguished on the basis of morphometric measurements (Mennill and Verehncamp 2005), brood patches, and/or behavioural observations.

Sound recordings

We used Marantz digital recorders (model: PMD-670 or PMD-660) and Sennheiser directional microphones (model: MKH70 or ME67) to record all vocalizations produced by pairs during focal recordings. Recordings were collected between March and July of 2004 to 2006. This time period encompasses the end of the dry season (mid-December to mid-May) and the beginning of the rainy season (mid-May to mid-December) for the northwestern Pacific lowlands of Costa Rica. Each year, we recorded the date of the first prolonged rainfall marking the start of the rainy season. In 2006, we also deployed a temperature and humidity data logger (model: Onset Hobo Pro Series) to document the transition from the dry season to the rainy season; the data logger recorded temperature (°C) and relative humidity (%) every half hour throughout the entire field season.

We recorded 17 focal pairs (N=34 unique individuals) cyclically throughout the field season, revisiting each pair approximately every 10–15 days. To monitor how singing behaviour changed with time of year, we attempted to record each pair every fortnight between mid-March and mid-July. To monitor how singing behaviour changed with breeding stage, we attempted to record all pairs at least once during each of the following breeding stages: (a) pre-breeding period (the period before any nest-building activity was observed; N=12; recording range: March 23 to May 7), (b) nest-building period (including re-nesting attempts after nest failure; N=17; recording range: April 14 to June 17), (c) female fertile period (defined as the period of 4 days before first egg date and the first 2 days of egg laying; this period corresponds to the period when copulations were observed; N=11; recording range: April 27 to July 9), (d) incubation period (N=17; recording range: May 4 to July 13), (e) nestling period (N=7; recording range: May 18 to July 16), (f) fledgling period (after young had left the nest but were still accompanied by parents; N=1; recording date: July 1), and (g) post-predation events (defined as the period after nest predation, but before the pair began to construct a new nest; N=3; recording range: May 10 to June 11).

Focal recordings took place over a 2-h time period between 0500 and 0700 h encompassing the dawn chorus, a time when rufous-and-white wren song is common (Mennill and Verehncamp 2005). We collected 115 focal recordings, comprised of over 201 h of recordings from the 17 pairs. Continuous recording sessions lasted 104± 1.74 min (range 32–126 min) and, in total, each pair was recorded for an average of 11.88±0.002 h. During recording sessions, the recordist followed the focal male and female around their territory and dictated the singers' identities, the type of song (solo or duet), and in the case of a duet, which bird sang first, whenever this information was known. Male and female rufous-and-white wren songs have distinct frequency and fine structural characteristics (Mennill and Verehncamp 2005), therefore, experienced listeners are able to identity the sex of the singer based on song characteristics. Visual confirmation of the band combinations of recorded individuals was sought whenever possible.

To determine the breeding stage of each pair, from 0700 to 1100 h we carried out behavioural observations and checked nests. Whenever possible, we assessed breeding stage by observing each pair for 1 h on the day before collecting a focal recording. Nests were checked for eggs or, when active, observed during 1-h nest watches every 3 days to monitor for predation events and to determine the female's fertile period.

Song analysis

We visualized all focal recordings as continuous spectrographs using SYRINX-PC sound analysis software (J. Burt, Seattle, WA, USA). For each recording, we tabulated the following characteristics: time of first song, time of last recorded song, time at end of recording, and total number of songs produced. For each song, we noted the sex of the singer, whether the song was a solo or part of a duet, the song type (see Mennill and Verehncamp 2005), and, for songs produced during a duet, which bird sang first and which bird sang second. For each individual, we calculated independent song rate as the sum of all solo songs for that individual plus all duets where that individual sang first (i.e. times when an individual sang autonomously and may or may not have been joined by its partner). We calculated the independent song rate (per hour) for both individuals and the duet and solo rate (per hour) for the pair. We quantified the responsiveness of individuals to their partner's song as the proportion of their partner's total song output that they answered to create a duet. For example, female responsiveness was calculated as the number of duets where the male sang first and the female sang second, divided by this number plus the number of male solos (Mennill 2006). For comparison, we also calculated the proportion of total songs that pairs sang as duets or solos and the proportion of duets created by males and females to further examine the role each sex plays in shaping the patterns of duetting in this species.

Statistical analysis

We used mixed-model ANOVA to evaluate (a) combined solo and duet rates for pairs, (b) independent song rate and duet rate for individuals, (c) relative proportion of solo and duet songs, (d) relative proportion of duets created by males versus females, and (e) male and female duet responsiveness. We used this approach because our data set lacked independence because of repeated sampling of the same pairs and because our sample sizes were unbalanced (not all pairs could be recorded during all time periods or breeding stages because of inclement weather during the rainy season and very high levels of nest predation). This approach enabled us to incorporate both fixed and random effects in the analysis, so that the interdependence of data collected from the same bird or pair (random effect) was taken into account during the assessment of the fixed effects (dependant variables). For all models, variance associated with random effects was estimated using expected means squares method and fixed effects were estimated using standard least squares. Two separate models were fitted for each dependent variable to test the effect of (a) time of year and (b) breeding stage (independent variables) on singing behaviour. Models evaluating time of year were unrestricted by breeding stage, and models evaluating breeding stage were unrestricted by time of year. Song rate variables were normalized with square root transformation, and proportional variables were normalized with arcsine transformation. As expected, pair or individual (male or female) effects for most models were highly significant because of natural variation in singing behaviours of different individuals. We tested for significant differences between stages or time of year in each model using a Tukey–Kramer test.

We used a paired *t* test to compare male versus female responsiveness within each breeding stage. If individuals were recorded more than once in a breeding stage, we used the average song rate so that individuals were only represented once. Figures show non-transformed data, although transformed data were used in statistical analyses. All analyses were conducted in JMP 5.0 (SAS, Cary, NC, USA). Values are shown as means ± SE. All reported tests are two tailed.

Results

Singing behaviour and time of year

Regardless of time of year, rufous-and-white wren pairs sang a greater number of solo songs relative to duets and paired males sang at higher rates than paired females. However, singing and duetting rates varied substantially with time of year.

At our study site in Santa Rosa National Park, the average start date for the rainy season in 2004 to 2006 was 14 May, based on the date of when the first sustained rainfall was observed (18 May, 2004; 15 May, 2005; 10 May, 2006); this corresponded with dramatic changes in temperate and relative humidity (Fig. 1).

Rufous-and-white wren pairs produced more duets early in the year during the dry season, and duet rates decreased with the onset and progression of the rainy season. Overall, duet rates were highest in early April, more than a month before the start of the rainy season (Fig. 2a; ANOVA: $F_{23,92}$= 2.31, P=0.003; model effects—time period: $F_{1,7}$=3.68, P< 0.002, pair: $F_{1,16}$=1.49, P=0.12). During this peak in duet behaviour, duets comprised 13.8±2.7% of all recorded rufous-and-white wren vocalizations, whereas duets comprised only 0.9±0.3% of vocalizations in early July when duets were least frequent.

Rufous-and-white wren pairs produced the highest number of combined solo songs (i.e. male plus female solos) in late May, coinciding with the onset of the rainy season. Combined solo song rates peaked at this time of year and remained elevated for the duration of the study. Combined solo song rates during the dry season were significantly lower, with the lowest solo song rates occurring in late March (Fig. 2a; ANOVA: $F_{23,\ 92}$=9.57, P<0.0001; model effects—time period: $F_{1,7}$=24.83, P< 0.0001, pair: $F_{1,16}$=1.94, P=0.03). During the peak in solo-singing behaviour, duets comprised 3.2±1.0% of rufous-and-white wren vocalizations.

Females sang a greater number of songs early in the year. Female independent song rate peaked in early April and then declined throughout the remainder of the recording period (Fig. 2b; ANOVA: $F_{23,92}$=2.86, P< 0.0002; model effects—time period: $F_{1,7}$=5.00, P< 0.0001, female: $F_{1,16}$=2.19, P=0.01). During this peak in independent song, females sang on average of 45.0±8.6% of all recorded vocalizations. In contrast, males sang a greater number of songs later in the year. Male independent song rate peaked in late May and remained elevated into early July (Fig. 2b; ANOVA: $F_{23,\ 92}$=9.47, P<0.0001; model effects—time period: $F_{1,7}$=24.47, P<0.0001, male: $F_{1,16}$=2.16, P=0.01). During this peak in independent song, males sang on average of 93.1±2.2% of all recorded vocalizations.

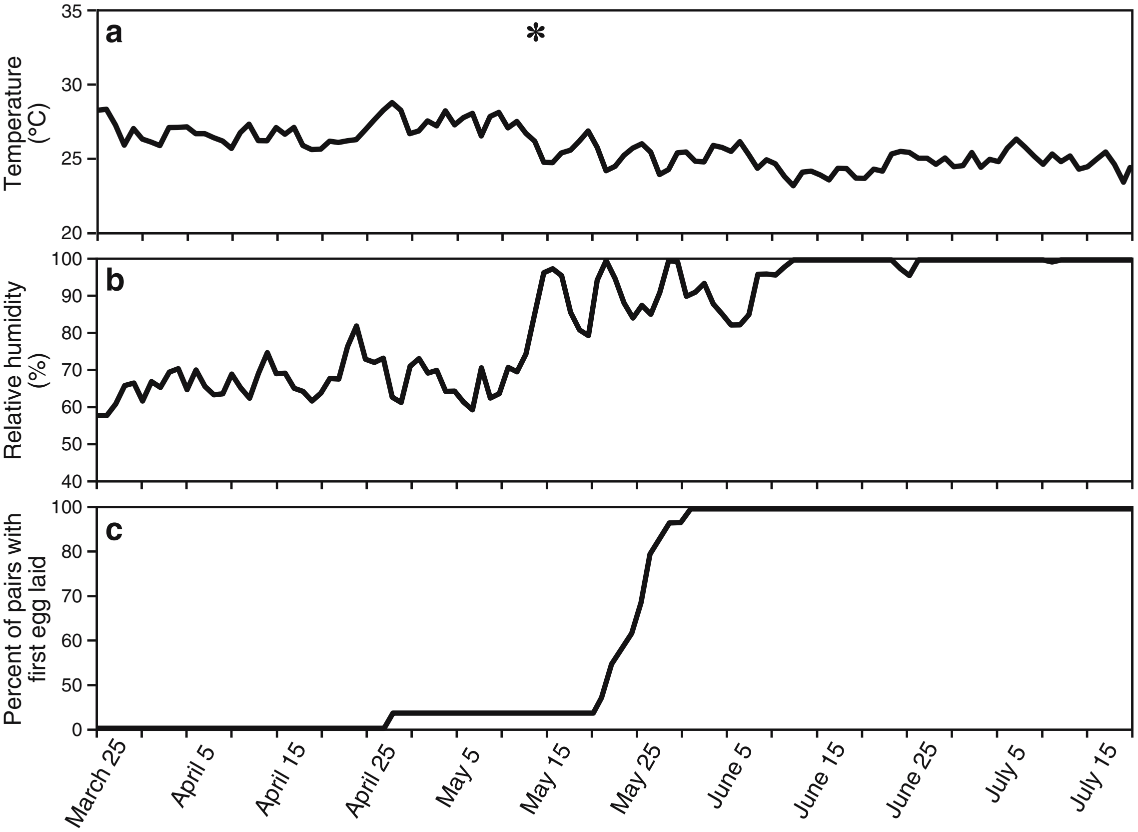

Fig. 1 Average daily temperature (**a**) and relative humidity (**b**) between mid-March and mid-July 2006 at Santa Rosa National Park, Costa Rica. The asterisk indicates the first prolonged rain of the year and the start of the rainy season. The proportion of pairs that had laid their first egg of the year (**c**) shows a dramatic increase at the onset of the rainy season, although most nests were soon depredated leading to ongoing, asynchronous cycles of re-nesting

Singing behaviour and breeding stage

Regardless of breeding stage, rufous-and-white wren pairs sang a greater number of solo songs than duets and paired males sang at higher rates than paired females. However, singing and duetting rates varied substantially with breeding stage.

Duet rates were highest in early stages of the rufous-and-white wren breeding cycle. Overall, duet rates were high in the pre-breeding stage and were lowest in the incubation and nestling stages (Fig. 3a; ANOVA: $F_{21,93}=2.62$, $P<0.001$; model effects—breeding stage: $F_{1,5}=5.50$, $P<0.0002$, pair: $F_{1,16}=1.69$, $P=0.06$). At their highest level, duets comprised 15.6±2.5% of rufous-and-white wren vocalizations, whereas duets comprised only 1.0±0.6% of vocalizations produced during the nestling stage.

Rufous-and-white wren pairs produced a higher number of combined solo songs (i.e. male plus female solos) in later breeding stages. Overall, combined solo rates were highest during the fertile, incubation and nestling periods and solo rates were lowest during the pre-breeding stage (Fig. 3a; ANOVA: $F_{21,\ 93}=5.19$, $P<0.0001$; model effects—breeding stage: $F_{1,5}=15.78$, $P<0.0001$, pair: $F_{1,16}=1.39$, $P=0.16$). During the peak in combined solo singing behaviour, duets comprised 3.5±1.1% of rufous-and-white wren vocalizations.

Female independent song rates were high in the pre-breeding stage and were lowest during the incubation and nestling stages (Fig. 3b; ANOVA: $F_{21,93}=3.37$, $P<0.0001$; model effects—breeding stage: $F_{1,5}=7.72$, $P<0.0001$, female: $F_{1,16}=1.92$, $P=0.03$). Male independent song rates peaked later than female rates and were highest during the fertile period (Fig. 3b; ANOVA: $F_{21,\ 93}=5.23$, $P<0.0001$; model effects—breeding stage: $F_{1,5}=15.86$, $P<0.0001$, male: $F_{1,16}=1.44$, $P=0.14$).

Comparison of male and female singing behaviour

Males sang more songs than females at all breeding stages (Sign test: $P<0.03$). Female rufous-and-white wrens contributed the greatest proportion of songs (solos and duets combined) during the pre-breeding period (ANOVA: $F_{21,\ 93}=8.11$, $P<0.0001$; model effects—breeding stage: $F_{1,5}=22.55$, $P<0.0001$, female: $F_{1,16}=2.96$, $P<0.001$). Male rufous-and-white wrens contributed the greatest pro-

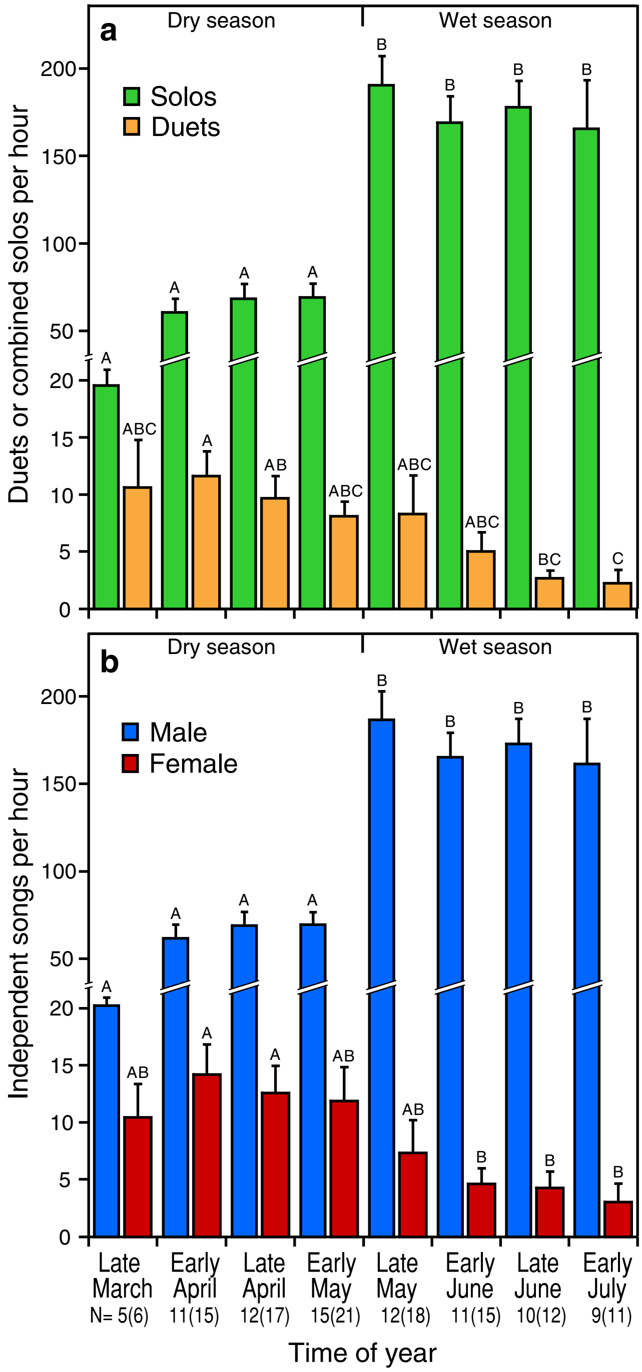

Fig. 2 Variation in song output of rufous-and-white wrens with time of year. **a** Combined male and female solo song output (*green bars*) and duet output (*orange bars*). **b** Male independent song output (*blue bars*; male solos plus duets where male sang first) and female independent song output (*red bars*; female solos plus duets where female sang first). Sample sizes show the number of pairs recorded with the total number of recording sessions in parentheses. *Uppercase letters* above bars show significant differences within each group (time periods not connected with the same letter are significantly different)

portion of songs during the female fertile stage, the incubation stage, and the nestling stage (ANOVA: $F_{21,93}$= 8.07, P<0.0001; model effects—breeding stage: $F_{1,5}$=21.91, P<0.0001, male: $F_{1,16}$=3.11, P<0.001).

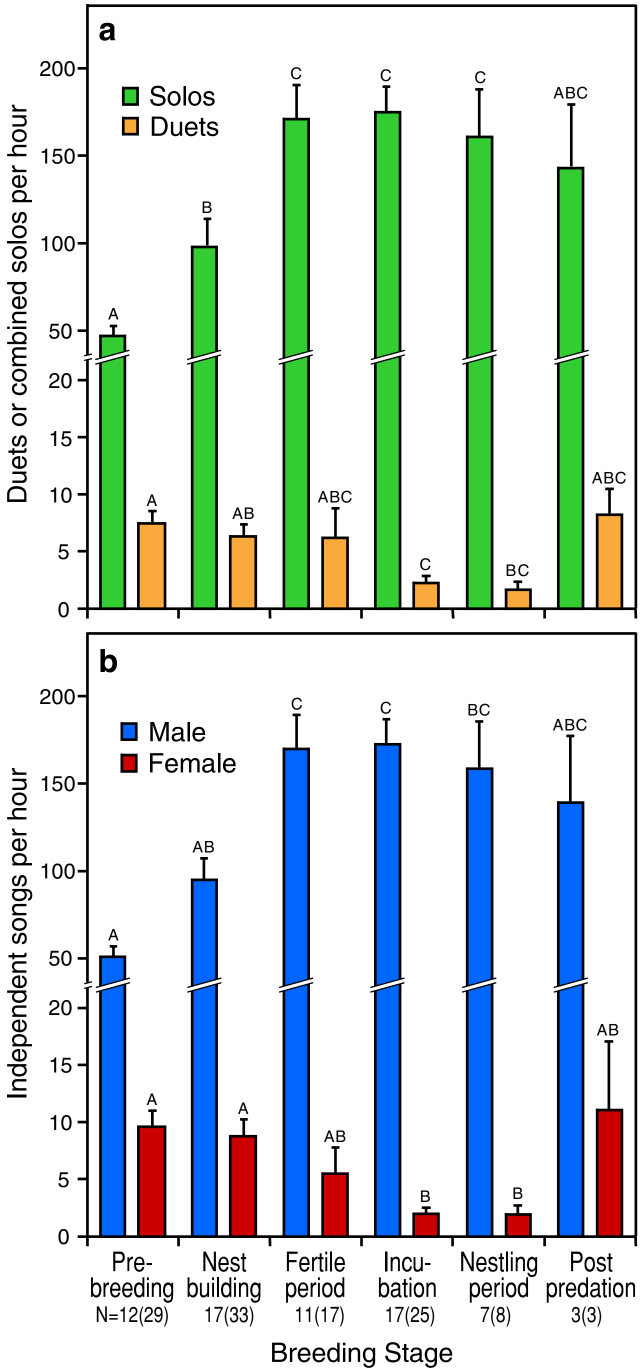

Fig. 3 Variation in song output (per hour) of rufous-and-white wrens with breeding stage. **a** Combined male and female solo song output (*green bars*) and duet output (*orange bars*). **b** Male independent song output (*blue bars*; male solos plus duets where male sang first) and female independent song output (*red bars*; female solos plus duets where female sang first). Sample sizes show the number of pairs recorded with the total number of recording sessions in parentheses. *Uppercase letters* above bars show significant differences within each group (breeding stages not connected with the same letter are significantly different)

Across all breeding stages, the majority of duets were created by females responding to their partner's songs (Fig. 4; Sign test: P<0.03). Females created a similar proportion of duets across all breeding stages (Fig. 4;

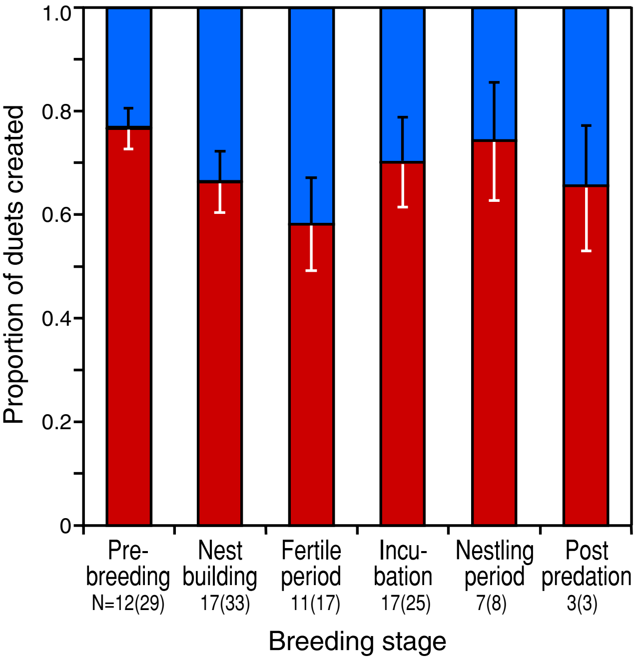

Fig. 4 Proportion of duets created by males (i.e. duets where female sang first and male sang second) in *blue*, versus duets created by females (i.e. duets where male sang first and female sang second) in *red*. Sample sizes show the number of pairs recorded with the total number of recording sessions in parentheses

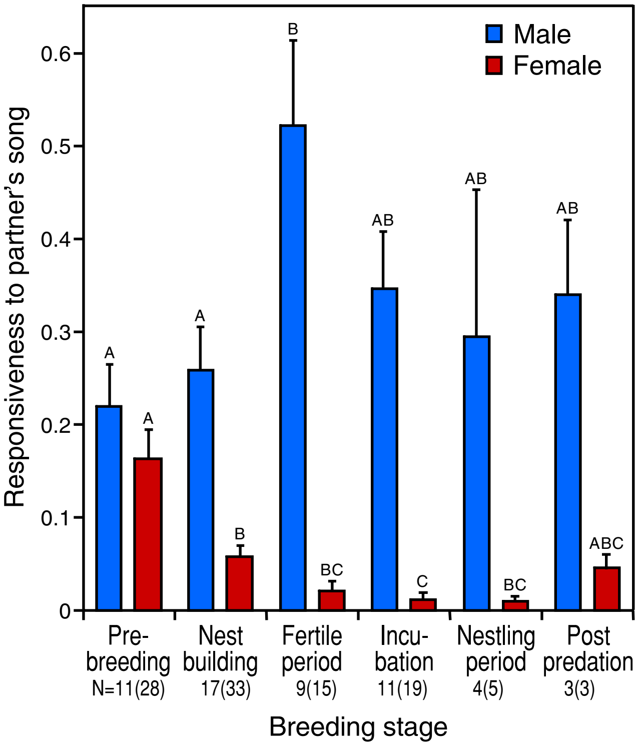

Fig. 5 Variation in male and female rufous-and-white wren duet responsiveness (proportion of partner's songs answered to create a duet) with breeding stage. Responsiveness of males to their partner's songs is shown in *blue* and responsiveness of females to their partner's songs is shown in *red*. Sample sizes show the number of pairs recorded with the total number of recording sessions in parentheses. *Uppercase letters* above bars show significant differences within each group (breeding stages not connected with the same letter are significantly different)

ANOVA: $F_{21,\ 76}$=0.90, P<0.59; model effects—breeding stage: $F_{1,5}$=0.78, P=0.57, female: $F_{1,16}$=0.89, P=0.58). Males created a similar but lower proportion of duets across all breeding stages (Fig. 4; ANOVA: $F_{21,\ 76}$=0.90, P=0.60; model effects—breeding stage: $F_{1,5}$=0.78, P=0.57, male: $F_{1,16}$=0.89, P=0.58). Sample sizes for this analysis are reduced because no duets were recorded for one pair in the pre-breeding stage, two pairs in the fertile stage, six pairs in the incubation stage, and four pairs in the nestling stage.

Despite the above results showing that females and males created similar proportions of duets across all breeding stages, the responsiveness of rufous-and-white wrens to their partner's song changed for both sexes because of dramatic seasonal variation in male and female song output. Overall, as the breeding season progressed, females became less responsive to their partner's songs while he increased his song output, whereas males became more responsive to their partner's songs while she decreased her song output. Female rufous-and-white wrens were most responsive to their partner's song in the pre-breeding stage and least responsive when incubating (Fig. 5; ANOVA: $F_{21,\ 93}$=4.67, P<0.0001; model effects—breeding stage: $F_{1,5}$=13.73, P<0.0001, female: $F_{1,16}$=1.46, P=0.13). For males, the tendency to answer their partner's song peaked during the female fertile period and was significantly higher than their tendency to respond to their partner's song during the pre-breeding period when males were least responsive (Fig. 5; ANOVA: $F_{21,\ 73}$=3.25, P<0.0001; model effects—breeding stage: $F_{1,5}$=3.88, P<0.01, male: $F_{1,16}$= 3.05, P<0.001).

Male and female rufous-and-white wrens exhibit different patterns of duet responsiveness across breeding stages (Fig. 5). Males and females were similarly responsive to their partner's song during the pre-breeding (paired t test: t_{10}=0.83, P=0.42), nestling (paired t test: t_3=1.17, P=0.33), and post-predation stages (paired t test: t_2 =3.56, P=0.07), although non-significant results during the nestling and post-predation stages could arise from smaller sample sizes during these stages. Males responded to their partner's songs significantly more than females during the nest-building (paired t test: t_{16}=2.37, P=0.03), fertile (paired t test: t_8= 4.98, P=0.001), and incubation periods (paired t_{10}=5.98, P=0.0001).

Discussion

Duet rates and solo song rates of rufous-and-white wrens change dramatically with time of year and breeding stage.

This suggests that duets and solo songs play different roles at different times of the year and breeding stages. Male song peaks with the onset of the rainy season in mid-May (Fig. 2), which immediately precedes the period when most females lay their first clutch (Fig. 3). Female song peaks in the dry season and tapers off throughout the rainy season (Fig. 2). Females drive the realized production of duets; regardless of season or nesting stage, females create the majority of duets by singing in response to their partner's song (Fig. 4). However, males are considerably more vocal than females, hence females answer proportionately fewer of their partner's songs to create duets (Fig. 5). Overall, duet rates are highest early in the year, during the pre-breeding stage, whereas solo song rates are highest at the start of the rainy season, during the female fertile period. The proportion of their partner's songs that individuals answer to create duets varies between the sexes and with breeding stage, suggesting that duetting behaviour may sometimes arise through cooperation and other times arise through attempted mate or paternity guarding by males.

Seasonal variation in song and territory defence

Our analysis of seasonal variation suggests that rufous-and-white wren duets play a role in joint territory defence early in the year, corroborating the findings of a previous playback study. Using stereo duet playback during the nest-building period, Mennill (2006) demonstrated that male and female rufous-and-white wrens sing duets and solos at higher rates than normal when interacting with simulated territorial intruders. In addition, Mennill (2006) compared male and female duet responsiveness during playback trials and found that the sexes were equally responsive to their partner's song during the playback-simulated intrusions. Equal levels of duet responsiveness have been suggested to be a sign of cooperation between the sexes (Hall 2004, 2006). In the present study, we found that duet responsiveness varied with breeding stage. During the pre-breeding stage, males and females showed an equal level of duet responsiveness to each other's songs. This suggests that duetting at this stage is a cooperative display, allowing pairs to defend resources from conspecific rivals.

Seasonal changes in female song have been documented for a number of north-temperate birds (e.g. northern cardinals, Ritchison 1986; Vondrasek 2006; song sparrows, Arcese et al. 1988; white-crowned sparrows, Baptista et al. 1993), tropical birds (e.g. red-shouldered blackbirds, *Agelaius assimilis*, Whittingham et al. 1997), and south-temperate birds (e.g. magpie-larks, *G. cyanoleuca*, Tingay 1974; Hall 2006; bar-throated apalis, *Apalis flavida*, Harcus 1977; superb fairy wrens, Cooney and Cockburn 1995; bellbirds, *Anthornis melanura*, Brunton and Li 2006). In most cases, female song, whether sung as a solo or as part of a duet, peaks before the start of the breeding season, before nest building has begun (e.g. Vondrasek 2006; Hall 2006). In this study, we also found that female independent song rates were highest early in the year, before breeding. For example, in March, females sang approximately half of all recorded vocalizations, whereas in late May, females sang only one sixteenth of all recorded vocalizations; during the pre-breeding period, females sang just under a third of all recorded vocalizations, whereas during the nestling stage, they sang only one fiftieth of all recorded vocalizations.

In non-duetting species, a peak in female song before nesting appears to result from an increase in female aggression during the defence of a territory or resource (Langmore 1998). For example, female white-crowned sparrows only respond aggressively to playback before nest building (Baptista et al. 1993). In female superb fairy wrens (Cooney and Cockburn 1995) and female northern cardinals (Vondrasek 2006), female song rates were highest when birds were reasserting or defending territorial boundaries against intruders before nesting, but rates dropped once the breeding season commenced. In tropical species, few studies have addressed how duet and female song rates change seasonally. However, playback studies provide evidence that female song and duets are important in territory and resource defence, both for tropical species in general (Hall 2004) and rufous-and-white wrens in particular (Mennill 2006). In most cases, both males and females respond aggressively to playback-simulating intrusion by duetting rivals, increasing solo song and duet rates (e.g. bay wren, *Thryothorus nigricapillus*, Levin 1996; magpie-larks, Hall 2000; eastern whipbirds, *Psophodes olivaceus*, Rogers et al. 2006; rufous-and-white wrens, Mennill 2006).

Only two studies to date have assessed seasonal changes in song using playback in the tropics (Hall 2000; Fedy and Stutchbury 2005). In both cases, duets and solo songs were used in territorial displays. In magpie-larks, pairs exhibited strong responses to male and female intruders, but responses did not vary seasonally (Hall 2000). This suggests that some resources may be limited year round, requiring equally aggressive responses to conspecific rivals regardless of the season (Hall 2000). In white-bellied antbirds, pairs responded more aggressively during the dry (pre-breeding) season than the rainy (breeding) season, suggesting that resource competition varies seasonally (Fedy and Stutchbury 2005), as is the case for temperate females that sing (e.g. Arcese et al. 1988; Baptista et al. 1993).

The combination of year-round territoriality, low adult mortality, long periods of fledgling care, and delayed dispersal in tropical species (Skutch 1985; Martin 1996; Slater and Mann 2004) contribute to a heightened need for territory defence in the tropics. However, there may be periods where the pressure for resource or territory defence is unusually high, and during such periods duets may be a more effective territorial display than solo songs (Hall 2004). We observed the highest number of non-territorial birds (floaters) in March and early April, suggesting that competition for breeding territories is highest at this time of year. Coupled with the observed peak in duetting at this time of year, this observation lends support to the idea that duets are important in territory defence.

With the initiation of the rufous-and-white wren breeding season, male independent song increases, while duetting decreases, which may imply that once territory re-establishment has occurred and neighbourhoods have become relatively stable, males take over the role of territory defence. As male independent song rate peaks and remains high after the female's fertile period, it is likely that male solo song may be used to defend territories from rival males while the female is incubating and brooding the young. In temperate regions, a peak in dawn song during the female's fertile period or at the onset of incubation has been observed in many species (reviewed in Kunc et al. 2005). For species in which a peak in song is not limited to the female's fertile period, it is suggested that continued dawn singing is used to maintain territories (e.g. Staicer et al. 1996; Liu 2004; Kunc et al. 2005). In our study population in 2006, one unusual rufous-and-white wren pair had no surrounding neighbours within 1.0 km, and we observed reduced male independent song rates throughout the breeding season, lending support to the idea that continued male song is important for intersexual interactions and territory defence.

Seasonal variation in song and reproductive coordination

High duet rates early in the year and high male independent song during the breeding season could also result from song being used cooperatively to coordinate breeding activities (Dilger 1953). Few studies have tested this hypothesis. However, a peak in duet behaviour before nest building and again after predation events suggests that duets may be used to synchronize the breeding activities of a pair (Dilger 1953; Hall 2004). We found that rufous-and-white wren breeding partners were equally responsive to each other's song during the pre-breeding and nestling stage and after predation events, but not during nest building, the female fertile period, or incubation stages. After predation events, we also found a tendency for duet rates to peak again, although this trend was not supported statistically. Increases in duet behaviour after predation events have been documented in slate-coloured boubous, *Laniarus funebris* (Sonnenschein and Reyer 1983), and a resurgence in male song after predation has been documented in mockingbirds, *Mimus polyglottos* (Logan 1983). In addition, we observed rufous-and-white pairs performing duets close together, and in association with choosing alternate nest sites, after predation events. However, our results could be an artifact of few recordings of pairs after nest predation events ($N=3$).

Additionally, a peak in male independent song with the onset of the rainy season and the female fertile period may also be the stimulus needed to fine tune reproductive activities to coincide with the time of year when resources are most plentiful. Tropical species are able to detect slight changes in photoperiod and use this cue to initiate breeding activities (e.g. nest building; Hau et al. 1998; Wikelski et al. 2000; Hau 2001), however, there are fewer environmental cues of seasonality in the tropics than the temperate zone (Hau et al. 2000), and the onset of the rainy season is variable from year to year in some tropical ecosystems (Ahumada 2001). Both temperate and tropical species time reproduction for when conditions are optimal (reviewed in Slater and Mann 2004). The timing of optimal conditions is argued to be less predictable in the tropics, such that tropical species may remain in a state of 'readiness to breed' for substantial portions of the year (Hau et al. 2000; Dawson et al. 2001). Male vocalizations are known to play an important role in stimulating females to reproduce, both in songbirds (e.g. Kroodsma 1976; Morton et al. 1985) and in other taxa (e.g. red deer, *Cervus elphus*, McComb 1987; midwife toads, *Alytes muletensis*, Lea et al. 2001; crickets, *Gryllodes sigillatus*, Bateman et al. 2005). Because male rufous-and-white wren song rate peaks at the onset of the rainy season and there is a trend for duetting to increase after predation events, it may be that duets and an increase in male independent song are important for synchronizing reproductive activities in rufous-and-white wrens. In this case, duets may be important for coordinating joint activities, such as nest building, while high rates of male independent song may provide a mechanism for stimulating and fine tuning the reproductive activities of females (Logan 1983; Lea et al. 2001). This has been suggested as an explanation for the cyclical pattern of song use that occurs in mockingbirds during the breeding season (Logan 1983). Further investigation into both the territory defence and reproductive synchrony hypotheses is warranted, although it is likely that duets for rufous-and-white wrens are used cooperatively in both contexts.

Duet responsiveness and mate/paternity guarding

Seasonal patterns of variation in male song provide evidence that duets and solo songs also function in intrasexual communication among male rufous-and-white wrens. Evidence for this is twofold: (a) male responsiveness to his partner's song peaks when females are fertile, yet at the same time female song rate is decreasing; (b) male independent song rate shows a dramatic increase when females are fertile. The peak in male responsiveness during the fertile stage suggests that duets may act as a mate or paternity guard (Sonnenschein and Reyer 1983; Hall 2004). That is, males may sing solo songs and create duets with their partner's songs to advertise their partner's mated status. Variation in male song with time of year and breeding stage has been well documented for temperate songbirds (e.g. Slagsvold 1977; Logan 1983). In numerous temperate species, male dawn song rate peaks during the female's fertile period (e.g. European blackbird, *Turdus merula*, Cuthill and MacDonald 1990; European starlings, *Sturnus vulgaris*, Pinxten and Eens 1998). A peak in song rate during this breeding stage has been interpreted by some as evidence that male song plays a role in mate guarding (e.g. Cuthill and MacDonald 1990) and/or paternity guarding (e.g. Greg-Smith 1982).

For duetting species, mate guarding and paternity guarding have recently been proposed as alternative functions for duets (reviewed in Hall 2004). In assessing these hypotheses, it is important to assess the likelihood of an individual joining its partner's song to create a duet. For mate guarding to occur, individual males or females are expected to respond to more of their partner's songs when their position in a partnership is threatened (Levin 1996; Hall 2004). For acoustic paternity guarding, males are expected to respond to more of their partner's song when she is fertile to discourage extra-pair copulations (Levin 1996; Hall 2004). Evidence from stereo duet playback with rufous-and-white wrens suggests that duets function in communication with same-sexed intruders for males, acting as a mate and/or paternity guard (in addition to the role of duets in joint territory defence); male rufous-and-white wrens respond with a higher level of aggression to a speaker playing the male duet contribution than the female duet contribution, suggesting that intruding males are perceived as a greater threat than intruding females (Mennill 2006). Female response, in contrast, did not vary with the sex of the intruder (Mennill 2006). The genetic mating system of rufous-and-white wrens is still unknown, although we have documented females making forays into neighbouring male territories before laying and males following females at a close range when they are fertile, suggesting that this species follows a mixed reproductive strategy (D. J. Mennill, personal observation). Future analyses of the genetic mating system of this and other duetting species will help elucidate the possible function of duets in paternity guarding. Evidence from other studies examining duet function as an acoustic mate and/or paternity guard are equivocal (Hall and Magrath 2000; Seddon et al. 2002; Gill et al. 2005; Rogers et al. 2006). Therefore, further research using stereo duet playback to assess singing strategies and responsiveness of males and females during different breeding stages will be beneficial for understanding the degree to which duetting birds use duet song in same-sex communication.

Conclusion

Our results highlight the need for a greater understanding of how individuals and mated pairs contribute to variation in solo and duet song during different seasons and breeding stages in duetting animals. This study demonstrates that duets act as multifunction signals for rufous-and-white wrens, where the contribution of males and females to both solo and duet song output changes with time of year and breeding stage. On the one hand, rufous-and-white wren duets appear to act as cooperative signals between members of a mated pair, facilitating territory defence and/or breeding synchrony, early in the breeding season. On the other hand, rufous-and-white wren duets appear to arise through the competitive interests of males, with male duet responsiveness discouraging opportunities for rival individuals to usurp his partnership or paternity. Further research into seasonal variation in vocal behaviour will help yield a deeper insight into sexual conflict and cooperation in animals.

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