

Duet singing and repertoire use in threat signalling of individuals and pairs

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Song-type switching rate and song matching have been shown to function as territorial signals in male solo song but, to our knowledge, seem not to have been previously studied in a duetting species. We studied the plain wren (*Thryothorus modestus zeledoni*), to test whether duets signalled threat through song-switching rates, or through phrase type or duet type matching. Increases in the rate of song switching appear to function as an anti-habituation device rather than as a specific signal of threat. Fitting with previous results that same-sex individuals share phrase types, but pairs do not share duet types, both males and females used duets to phrase type match to playback. Pairs, however, did not duet type match in response to playback, and this suggests that within the cooperative territory defence of the duet, each sex is targeting its aggression at same-sex competitors.

Keywords: canebrake wren; duetting; repertoire sharing

1. INTRODUCTION

Two distinct roles of song repertoires in territorial signalling have been described in male solo song. First, birds that sing with eventual variety (singing the same type several times before switching; Catchpole & Slater 1995) have the potential to alter the length of their song bouts (a series of songs of the same type), and hence also its converse, their song-switching rate. Second, in species where some or all of the repertoire is shared between males, rivals are able to match one another's song types, which may signal levels of threat (Krebs *et al.* 1981; Beecher *et al.* 1996, 2000).

Two theories propose that higher song-switching rates arise through physiological mechanisms. The anti-exhaustion hypothesis (Lambrechts & Dhondt 1988) proposes that switching prevents muscle fatigue from repetitive movements and therefore that, as song rate increases, so must song-switching rate, independent of context. The monotony threshold hypothesis (Hartshorne 1956) argues that switching prevents listener habituation and therefore switching must again increase with song rate. This is again independent of context, but focuses on receiver response. Alternatively, song switching may be an indicator of motivation to attack (Falls & D'Agincourt 1982; Kramer & Lemon 1983; Stoddard *et al.* 1988), and this predicts that

switching rates are affected by motivation and context rather than song rate.

Song matching during counter-singing is possible only when birds share some or all of their repertoires (Krebs *et al.* 1981; Beecher *et al.* 1994). Several studies support the theory first presented by Krebs *et al.* (1981), that song type matching is a signal of threat (Falls 1985; Beecher *et al.* 2000; Vehrencamp *et al.* 2003). No study of song matching in duetting appears, to our knowledge, to have previously been carried out but, as a joint performance by the pair, a duet has two potential levels of signal: individuals may use their phrases within the duet to signal to same-sex competitors, or the pair may use the duet to signal to other pairs.

Mann *et al.* (2003) give a description of the duets of a subspecies of the plain wren (referred to here as the canebrake wren, *Thryothorus modestus zeledoni*). Briefly, the basic duet structure is I(FM)*n*, with a male introductory phrase 'I' leading into a rapid cycle of *n* female 'F' and male 'M' duet phrases (see electronic Appendix A). Individuals have repertoires of 15–25 phrase types (males have repertoires of both I and M phrases), which pairs combine to form repertoires of 20–30 duet types. Singing shows eventual variety, and in previous work, song-switching rates were not correlated with song rates in pairs that were not interacting with others (I phrases: $R = 0.08$, $p = 0.11$, $n = 922$; duets: $R = 0.001$, $p = 0.99$, $n = 210$; nine pairs). Individuals within a population share a high proportion of their phrase repertoires, but pairs appear to rarely share duet types (L. Marshall-Ball and P. J. B. Slater, unpublished data). We examined whether song-switching rates relate to the level of intrusion threat, and tested the prediction that individuals would phrase type match during territorial interactions, but that pairs would not match duet types.

2. METHODS

Experiments were carried out at two field stations on the northeastern slope of Costa Rica (La Suerte: 10°26' N, 83°47' W; El Zota: 10°33' N, 83°44' W), in May–August and October–December 2002, involving 23 pairs and five territory-holding solo males.

(a) Playback experiments

Stimuli were constructed using AVISOFT SASLAB V. 5.2 (R. Specht, Berlin; see <http://www.avisoft-saslab.com>) from recordings made in 2001. They were constant in amplitude, length and timing of the duets, and the amount of singing time. The stimuli were assigned in a randomized block design. The samples of each stimulus were also randomized, never used more than twice, and subjects always heard non-neighbours. Replicate trials on the same pair were more than one week apart; different experiments on the same pair were separated by more than two weeks.

Playbacks were carried out using a 40 W amplifier (T1140), a portable Panasonic CD player (SL-SX228), and a 5' Visaton passive full range speaker, with amplitude calibrated (SPL meter, Beha 93411) to the level of wren song in the wild (*ca.* 75 dB at 5 m). Continuous sound recordings were taken throughout all trials, using a Sennheiser ME-66 gun microphone and a Marantz CP430 tape recorder (chrome tapes) placed 5 m from the speaker. Observations were made from concealed points, recording positions of birds (at 1 min intervals), and all songs and their structures.

The primary playback experiment tested responses to a high song-switching rate stimulus against a non-switching stimulus (each 6 min with three songs per minute). Both stimuli were presented in each trial, separated and followed by 10 min silent intervals. Song-switching rates of subjects in response to four other playback experiments are also presented; details of these are not discussed here (L. Marshall-Ball, unpublished data). The basic structure and set-up of all five experiments are shown in table 1.

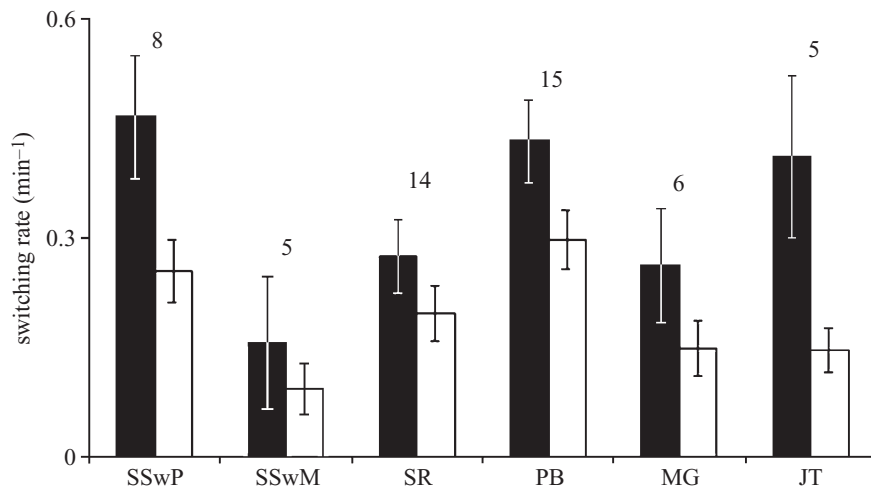


Figure 1. Mean song-switching rate \pm s.e. (number per minute) during playback (black bars) and intervals (open bars) for five experiments. Sample size above columns (number of pairs, except for SSwM which is number of solo males). Results of individual experiments: SSwP—song switching, pairs: $F_{3,59} = 5.44$, $p = 0.002$; SSwM—song switching, males: $F_{1,11.6} = 22.81$, $p < 0.0001$; SR—species recognition: $F_{1,61.8} = 14.03$, $p = 0.0004$; PB—pair-bond strength: $F_{7,184} = 4.39$, $p = 0.0002$; MG—mate-guarding: $F_{1,49.8} = 23.05$, $p < 0.0001$; JT—joint territory defence: $T = -3.46$, $p = 0.004$, d.f. = 14.

Table 1. The stimuli and design for five playback experiments.

(Experiments other than that on 'song-switching rate' are not discussed fully here (L. Marshall-Ball, unpublished data). All stimuli are presented in each trial in a randomized block design, see § 2a for details.)

experiment	stimuli	number of subjects	number of trials per subject	time of day
song-switching rate	3 phrase types (2 switches) 1 phrase type (no switches)	8 pairs, 5 solo males	2	07.00–08.30
species recognition	canebrake wren duet black-bellied wren duet	14 pairs	2	05.30–07.00
pair-bond strength	long duet short duet fast duet slow duet	15 pairs	2	05.30–07.00
mate-guarding	male solo song female solo song	6 pairs	4	15.30–17.30
joint territory defence	male solo song female solo song duet	5 pairs	1	17.30–07.00

(b) Data analyses

All song recordings taken during the experiments were processed in AVISOFT SASLAB; song types were identified by eye from spectrograms. Responses to playbacks used in the analyses were: *male distance to speaker*, *male-female distance*, *duet rate*, *mean duet length*, *I phrase singing rate* (for solo males), and *song-switching rate*. These were compiled as means per minute for each experimental section (stimulus 1 playback, interval, stimulus 2 playback and interval, etc.), for each subject pair and trial. A repeated-measures GLM was used to overcome the effects of variation between days and pairs, allowing the data to be tested for relative differences in response within each trial (subject: *pairs/solo males*; repeated measures and effects: *experimental section* and *trial*). In the song-switching-rate experiment, solo male subjects and paired subjects were analysed separately. Wherever multiple comparisons were being analysed, the critical probability value was taken as $p_{crit} = 0.01$ (including *post-hocs*); in tests involving a single comparison, $p_{crit} = 0.05$.

(c) Phrase and duet matching to playback

Occurrence of subject birds matching I, F and M phrases, and whole duet types, to those in the playback, were scored from responses to simple duet stimuli (song-switching-rate experiment: *non-switching stimulus*; species-recognition experiment: *canebrake wren stimulus*; table 1), and (phrase matching only) from responses to both male and female solo song stimuli in the mate-guarding experiment (table 1).

The probability of phrase matching occurring by chance was calculated from the subject's repertoire size, and the number of different phrase types sung in response to playback. This predicted rate of chance phrase matching was compared to the observed rate for both males and females. Data are presented from 32 trials on 11 males, and 31 trials on 13 females (phrase matching was possible in all trials).

Duet type matching in response to playback of duets was calculated from 21 trials on nine pairs (duet matching possible in all). Potential duet matches were where the subject pair possessed, in their repertoire, all three (I, F and M) phrases used in the playback. The probability of duet matching by chance was calculated from the numbers of duet types sung and subject duet repertoire sizes, and thus it was assumed that subject responses were restricted to their duet type repertoire and that they would not form new duet types in response to playback.

3. RESULTS

Individual repertoires were counted from all recordings made during 2002, and only those individuals with more than 70 song bouts recorded were included in the analyses. This approximated the point at which new duet discovery rates levelled off (L. Marshall-Ball, unpublished data).

Table 2. A repeated measures GLM.

((a) and (b) demonstrate the change to non-significance of the effect of experimental section (playback period or interval) on song-switching rate when song rate was taken into account. See § 3a for details.)

(a) song-switching rate				
null model	d.f.	χ^2 -value	<i>p</i> -value	
song-switching rate	1	7.42	0.0065	
effect	effect d.f.	error d.f.	<i>F</i> -value	<i>p</i> -value
trial	1	59	0.20	0.655
experimental section	3	59	5.44	0.002

(b) song-switching rate per duet of pairs in response to playback				
null model	d.f.	χ^2 -value	<i>p</i> -value	
song switches per duet	1	3.22	0.073	
effect	effect d.f.	error d.f.	<i>F</i> -value	<i>p</i> -value
trial	1	46	0.41	0.525
experimental section	3	46	0.77	0.516

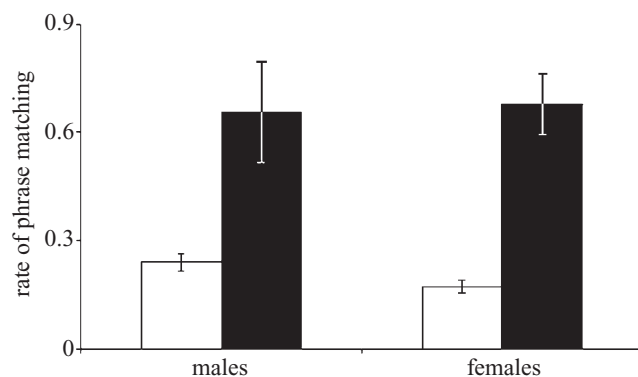


Figure 2. Observed (filled bars) and predicted (open bars) rates of phrase matching to playback. Paired *t*-tests of mean rates per individual: males: $t = 2.42$, $p = 0.036$, $n = 11$; females: $t = 5.61$, $p < 0.001$, $n = 13$.

(a) Song-switching rate

There were no differences in song rates, song-switching rate or approach behaviour of the subjects to the switching and non-switching playback stimuli. The switching rate of subjects was significantly correlated with I phrase singing rate in solo males (Pearson's correlations. $R = 0.421$, $p = 0.017$, d.f. = 31) and with duetting rate in pairs ($R = 0.377$, $p = 0.001$, d.f. = 71), but not with any other response variable. Both pairs and solo birds showed greater song-switching rates during playback relative to the subsequent interval, and this pattern was consistent across all experiments that were carried out regardless of the stimuli involved (see figure 1). However, phrase switching rate per duet (for pairs) or per I phrase (for solo males) did not change significantly between experimental sections ($p > 0.1$), and thus the increases in switching rate were proportional to increases in song rate. Table 2 shows GLM results from paired subjects for the effect of playback on song-switching rate and on song-switching rate per duet.

(b) Phrase matching to playback

Both males and females showed a strong tendency to phrase match to playback more often than expected by chance (see figure 2). There were no differences between males and females either in the predicted (chance) rate of

phrase matching, or in the observed rates (two-sample *t*-test on means per individual: predicted phrase matching: $t = 0.76$, $p = 0.46$, d.f. = 22; observed phrase matching: $t = 0.27$, $p = 0.79$, d.f. = 22).

(c) Duet matching to playback

The predicted rate of duet matching was 2.6 matches in the 21 trials analysed, but only one match actually occurred. *G*-test comparisons of the rate predicted by chance and the observed duet matching showed no significant difference ($G_{\text{adj}} = 1.97$, $p = 0.25$, d.f. = 1).

4. DISCUSSION

If song-switching rate in canebrake wrens was indicative of the motivation level, and the threat posed by a simulated intruding pair, subjects were predicted to respond more strongly to a stimulus with two song switches in 6 min than a stimulus with no switches in 6 min (with the same song rate). Neither pairs nor solo males showed any difference in response, thus the higher song-switching rate was not perceived as a greater threat.

Subjects increased their song-switching rates in line with their song rates, in response to playback. This suggests that rather than being a specific signal of threat, an increase in song switching may serve a less direct purpose. Despite not correlating with any other measured response, song-switching rate was correlated with I phrase singing rate in solo males and duetting rate in pairs. This contrasts with results from an observational study carried out in 2001, where song rate did not normally correlate with song-switching rates in undisturbed birds (L. Marshall-Ball and P. J. B. Slater, unpublished data). If song switching functioned to prevent muscle fatigue as suggested in the anti-exhaustion hypothesis (Lambrechts & Dhondt 1988), it would be correlated to song rate even when there was no direct interaction with extra-pair receivers. As this was not the case, it seems most likely that faster song switching in this species is used during territorial interactions to prevent receiver habituation (Hartshorne 1956), and maintain the level of threat represented by the song.

The occurrence of phrase sharing in this species meant that the wrens had the potential to match both phrase types and duet types to playback. Duet matching was

extremely rare in the experiments, in line with the lack of duet sharing. By contrast, both male and female wrens phrase type matched to playback, and did so at an equal rate. This was possible owing to high song switching rates that were driven by both members of the pair, and that enabled both sexes to independently phrase match to the playback. This strongly suggests an intrasexual aggressive function within the apparent joint performance of the duet. This study has demonstrated for the first time, to our knowledge, two very different uses of phrase and duet repertoires in territorial interactions: cooperative signal strengthening through song switching, and defence against same-sex competitors through phrase type matching.

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