



## Timing isn't everything: responses of tropical wrens to coordinated duets, uncoordinated duets and alternating solos



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### ARTICLE INFO

#### Article history:

Received 29 January 2014

Initial acceptance 18 February 2014

Final acceptance 5 June 2014

Published online

MS. number: A14-00090R

#### Keywords:

duet  
duet coordination  
duet timing  
female behaviour  
territoriality  
tropical behaviour  
wren

The coordinated vocal duets of tropical animals often play a role in territorial signalling. Duet timing is dependent upon each animal's attentiveness to its partner and its ability or motivation to cooperate, and therefore precise coordination of duet elements could be an important signal to territorial rivals. We used a playback experiment to test the hypothesis that territorial animals distinguish between highly coordinated duets, poorly coordinated duets and alternating solos. We studied three related species of wrens that show natural variation in the coordination of their male and female songs: banded wrens, *Thryophilus pleurostictus*, occasionally perform loosely coordinated duets but more commonly sing solo songs; rufous-and-white wrens, *Thryophilus rufalbus*, regularly perform loosely coordinated duets; and plain wrens, *Cantorchilus modestus*, regularly perform highly coordinated duets. We used stereo duet playback to simulate highly coordinated duets, poorly coordinated duets, alternating solos and a heterospecific control. We played back these four treatments to 63 territorial pairs of wrens. Responses to experimental treatments were stronger than responses to control treatments. Response to the three experimental treatments varied among species. Banded wrens responded more strongly to both types of duets than to alternating solos, in terms of closest approach and number of passes over the speaker. Rufous-and-white wrens responded more intensely to alternating solos and coordinated duets than to uncoordinated duets, in terms of closest approach, number of passes over the speaker and number of songs initiated. Plain wrens responded most intensely to alternating solos in terms of closest approach, and no less intensely to alternating solos than to the other treatments in terms of other measures of response. Together, our results indicate that these three species of wrens distinguish between coordinated duets, uncoordinated duets and alternating solos. However, highly coordinated duets do not incite categorically stronger responses than uncoordinated duets or alternating solos in any of these species.

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Duets are the coordinated songs of two individuals, usually a mated pair, where the two animals' vocalizations alternate or overlap (Farabaugh, 1982; Hall, 2004, 2009). This phenomenon occurs in a variety of animals, including birds (Hall, 2009), primates (Haimoff, 1986), anurans (Tobias, Viswanathan, & Kelley, 1998) and insects (Bailey, 2003). Duetting behaviour shows a strong phylogenetic signal (Logue & Hall, 2014) and has evolved independently in multiple phylogenetic groups (Farabaugh, 1982). In spite of a growing body of research, the ecology and evolution of duetting behaviour remains poorly understood (Hall, 2009), possibly due to the multifunctional nature of duets both within and among species

(Benedict, 2010; Dahlin & Benedict, 2013; Grafe, Bitz, & Wink, 2004; Mennill & Vehrencamp, 2008). Our understanding of the functions of duets can be enhanced by careful attention to the dynamics of coordination in male and female duet contributions.

Hypotheses for the functions of duets can largely be grouped into two categories: those in which pair members cooperate with one another for mutual benefit, and those in which pair members compete to work towards conflicting goals (Hall, 2004). Cooperative functions include joint resource defence, maintaining the pair bond and ensuring reproductive synchrony (Armstrong, 1947), while competitive functions include mate guarding and paternity guarding (Levin, 1996; Sonnenschein & Reyer, 1983). Resource defence is a well-supported function of male song in north temperate songbirds (Catchpole & Slater, 2008), where songs are predominantly performed by males alone. Duets mirror male territorial song in that they are loud, easily localizable and used in interactions between neighbouring birds, and for this reason,

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resource defence is often considered a primary function of duets (Hall, 2009). Experimental research examining duetting as a mechanism for resource defence suggests that duets do function in this manner in many taxa (reviewed in: Dahlin & Benedict, 2013; Douglas & Mennill, 2010). However, previous studies have typically contrasted duet singing, male solo singing and female solo singing; this experimental design fails to control for the confounding difference in the number of intruders that are simulated. Differences in response to playback of duets and solos could be due to differences in the threat posed by a single intruder versus two intruders, rather than the coordination of songs into duets per se.

Temporal coordination is a defining feature of duetting behaviour, and as such, improving our understanding of the importance of coordination in animal duets is likely to shed light on their function and evolution. Duetting species can be grouped into two classes based on the form of their duets: those that answer their partner's song without fine-scale coordination of notes within the songs (e.g. polyphonal duetters) and those that coordinate the phrases within their synchronized songs (e.g. antiphonal duetters; Hall, 2009). Mechanistic studies of temporal coordination in antiphonal duetters indicate that duetting partners base their timing on the immediately preceding notes of their mate's song (Fortune, Rodriguez, Li, Ball, & Coleman, 2012; Logue, Chalmers, & Gowland, 2008). Coordinating songs requires attentiveness to the partner, and animals with higher levels of attentiveness may produce duets comprising a series of more precisely coordinated phrases. Therefore, duet timing could serve as a signal of attentiveness, which may be important both to the partner and to nearby territorial rivals (Hall, 2009). Male magpie-larks, *Grallina cyano-leuca*, for example, sing at a higher rate in response to playback of highly coordinated duets than to playback of poorly coordinated duets (Hall & Magrath, 2007), suggesting that precise timing can function as a more threatening territorial signal. In addition, magpie-lark pairs that have been together for longer periods sing more precisely coordinated duets, suggesting that duet coordination may indicate partnership length (Hall & Magrath, 2007). These results suggest that duet precision may be an index of a pair's ability or motivation to act collectively, where pairs that produce highly coordinated duets may cooperate to perform other behaviours successfully as well. Precision in temporal coordination seems to be important; black-bellied wrens, *Pheugopedius fasciatoventris*, will stop their songs short when performing duets that have large gaps or overlapping phrases, indicating that birds are sensitive to their own duet coordination (Logue et al., 2008). If other pairs use the duet coordination of rivals as a signal, they may be able to gain helpful information about the threat posed by a rival pair.

Vocal duets are relatively common among many birds in the tropics (Farabaugh, 1982). Tropical wrens, in particular, are well known for their ability to produce coordinated duets (Brewer, 2001; Mann, Dingess, Barker, Graves, & Slater, 2009). The 'Thryothorus wrens' are a group of tropical birds in which duetting is common, with highly variable degrees of temporal coordination (Mann et al., 2009). Formerly a single genus (i.e. *Thryothorus*), the group was recently split into four genera, and there is considerable variation in duetting behaviour and duet coordination between and within each of these new groups (Mann, Barker, Graves, Dingess-Mann, & Slater, 2006; Mann et al., 2009). Plain wrens, *Cantorchilus modestus*, sing highly coordinated antiphonal duets, where the male and female sing a series of rapidly alternating phrases with extremely small intervals of silence and very little overlap (Cuthbert & Mennill, 2007). Rufous-and-white wrens, *Thryophilus rufalbus*, show coordinated, polyphonal duets, in which the male and female songs are loosely associated in time and often involve overlapping (Mennill & Vehrencamp, 2005). Although male and female banded wrens, *Thryophilus pleurostictus*, both sing, they

historically have not been recognized as singing coordinated duets (Mann et al., 2009; Molles & Vehrencamp, 1999). However, recent detailed analysis demonstrates that males and females occasionally produce duets similar to the loosely coordinated duets of rufous-and-white wrens (Hall, Driscoll, & Vehrencamp, n.d.). This remarkable variation in acoustic coordination provides an intriguing model system in which to study the ecology and evolution of temporal coordination.

In this study, we tested the hypothesis that territorial animals respond differently to coordinated duets, poorly coordinated duets and alternating male and female solo songs. We presented temporally altered duets, as well as alternating male and female solo songs, to pairs of three species of tropical wrens that vary in their natural degree of coordination. We included three species of wrens in hopes of elucidating evolutionary mechanisms of coordinated displays. If birds distinguish between coordinated duets, uncoordinated duets and alternating solos, we predicted two possible outcomes: (1) wrens of all species would respond more intensely to highly coordinated duets than to poorly coordinated duets and alternating solos; or, alternatively, (2) wrens would respond more intensely to their species-typical form of song production (high-coordination duets for plain wrens, low-coordination duets for rufous-and-white wrens and banded wrens). Because these three species of wrens perform different types of duets, if all three species show strong responses to coordinated stimuli, this could provide evidence of a pre-existing bias towards perceiving highly coordinated duets as threatening signals.

## METHODS

### General Field Methods

We studied populations of three species of wrens in Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica (10° 40'N, 85° 30'W). Playback studies were conducted from 24 April to 2 June 2012, corresponding with the onset of the rainy season and the beginning of the breeding season (Topp & Mennill, 2008). We conducted playbacks in the morning, between 0600 and 1100 hours, when birds were most active. In total, we successfully completed trials with 63 pairs of wrens (126 unique birds): 21 pairs of plain wrens (42 unique birds), 22 pairs of rufous-and-white wrens (44 unique birds) and 20 pairs of banded wrens (40 unique birds), all of which were used in our analyses. The rufous-and-white wrens were part of an ongoing long-term study, and all males and most females were banded with unique combinations of coloured leg bands. Banded and plain wrens were not individually marked in this study, so we ensured that we sampled unique pairs by moving at least 60 m between adjacent same-species playback territories for plain wrens and banded wrens. For banded and plain wrens, we distinguished between sexes by careful attention to their songs, which are sexually distinct. Wren pairs tend to remain on stable territories throughout a season (plain wrens, approximately 400 m<sup>2</sup>; rufous-and-white wrens, approximately 10 000 m<sup>2</sup>; banded wrens approximately 3600 m<sup>2</sup>; Cuthbert & Mennill, 2007; Mennill & Vehrencamp, 2005; Molles & Vehrencamp, 2001).

### Playback Treatments

We used a stereo playback design (Douglas & Mennill, 2010) to simulate a pair of wrens singing inside the territory boundaries of our playback subjects. Subjects received four playback treatments: (1) highly coordinated conspecific duets, (2) poorly coordinated conspecific duets, (3) alternating male-and-female conspecific solo songs and (4) a control stimulus of highly coordinated duets of a

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