



Sing and do not stray: male rufous-and-white wrens use duets and physical behaviours to guard their mates

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In diverse animal taxa, breeding partners coordinate their vocalizations to produce vocal duets. One seldom-studied hypothesis for duets is the paternity guarding hypothesis, which states that male animals create duets to advertise their partner's mated status and minimize extrapair mating attempts between their partner and other males. We experimentally tested the paternity guarding hypothesis in rufous-and-white wrens, *Thryophilus rufalbus*, a neotropical duetting songbird. We designed a two-part playback experiment: males first experienced a simulated territorial intrusion by a rival male, and were then given opportunities to answer their female breeding partner's songs to create duets. We repeated this experiment during the female's fertile and nonfertile breeding stages. In support of predictions of the paternity guarding hypothesis, male wrens created more duets with their partner's songs during the fertile period compared to the nonfertile period. Additionally, male wrens appeared to physically guard their mates with greater intensity during the fertile period but did not increase their overall song rates, demonstrating that increased duetting rates during the fertile period were a result of a change in male duetting behaviour, rather than a change in song rate. Our study is among the first to experimentally test the paternity guarding hypothesis for duet function, and suggests that male rufous-and-white wrens use both vocal and physical behaviours to guard their paternity.

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In many animals, including diverse species in the tropics, elaborate vocalizations are often produced by both males and females, and in some species breeding partners combine their vocalizations into vocal duets (Geissmann, 2002; Hall, 2004; Slater & Mann, 2004; Stutchbury & Morton, 2001). Vocal duets are highly coordinated acoustic signals where one individual vocalizes and the partner creates a duet by vocalizing in response, either by overlapping the partner's vocalization or by producing a vocalization in quick succession (Hall, 2004). This behaviour occurs in primates (e.g. Caselli, Mennill, Gestich, Setz, & Bicca-Marques, 2015; Geissmann, 2002), frogs (e.g. Tobias, Viswanathan, & Kelley, 1998), insects (e.g. Bailey, 2003), and has been studied most extensively in birds (reviewed in Farabaugh, 1982; Hall, 2004; Tobias et al., 2016).

Vocal duets are multipurpose signals that serve functions in both cooperative and conflict-based contexts (e.g. Benedict, 2010; Mennill & Vehrencamp, 2008). The most widespread and well-

supported function for vocal duets is that they are used to cooperatively defend ecological resources (reviewed in Dahlin & Benedict, 2014; Douglas & Mennill, 2010). An alternative viewpoint is that duets can arise from intersexual conflict between breeding partners; an animal may perform a duet with its partner to prevent their partner from pairing or mating with other animals (Levin, 1996a, 1996b; Rogers, Langmore, & Mulder, 2007; Seddon & Tobias, 2006; Sonnenschein & Reyer, 1983; Tobias & Seddon, 2009). The importance of duets in intersexual conflict, however, remains poorly understood because few studies have used an experimental approach to study this idea (Baldassare et al., 2016; Hall, 2004).

One hypothesis for the function of vocal duets related to intersexual conflict is the paternity guarding hypothesis, which states that male animals answer their breeding partner's vocalizations to create duets in order to advertise their paired status and prevent them from mating with rival males (Hall, 2004; Sonnenschein & Reyer, 1983). Two important predictions arise from this hypothesis: (1) males should answer a higher proportion of female vocalizations to create duets during the fertile period in comparison to other breeding stages; and (2) duets should effectively reduce rates of extrapair offspring (i.e. offspring from males other than the social partner; Hall, 2004). Males in many species have been shown to use

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diverse paternity guarding strategies to reduce alternative breeding attempts during the fertile period, including increased vocalization rates (e.g. Holzman, 2012; Mace, 1987; McElligot & Hayden, 2001; Welling, Koivula, & Lahti, 1995), frequent mating attempts (reviewed in Møller & Birkhead, 1991) and physical mate guarding (reviewed in birds in Birkhead & Møller, 1992; Jormalainen, 1998; Schubert, 2009; Setchell, Charpentier, & Wickings, 2005). However, very few studies have investigated paternity guarding strategies in duetting species, particularly with respect to how duets may function as acoustic paternity guards.

To date, most studies of paternity guarding hypotheses in duetting animals have involved observational analysis of variation in duet rates across different breeding stages. For example, in four species of duetting birds (magpie-larks, *Grallina cyanoleuca*; buff-breasted wrens, *Cantorchilus leucotis*; purple-crowned fairy-wrens, *Malurus coronatus*; and red-backed fairy-wrens, *Malurus melanocephalus*), males do not create more duets with their females during the fertile versus nonfertile periods (Dowling & Webster, 2013; Gill, Vonhof, Stutchbury, Morton, & Quinn, 2005; Hall & Magrath, 2000; Hall & Peters, 2009), suggesting that duets do not function as acoustic paternity guards in these species. However, the paternity guarding hypothesis has only been tested experimentally in two duetting animals. In response to playback simulating the songs of a rival male during the female fertile period, male canebrake wrens, *Cantorchilus zeledoni*, produced more duet-initiation songs (i.e. male songs used to elicit polyphonal duet sequences with females), suggesting that males are more motivated to perform duets with females when they are fertile (Marshall-Ball, Mann, & Slater, 2006). In contrast, in response to playback simulating solo and paired intruders, male red-backed fairy-wrens did not sing more duets with their females in the fertile period compared to prefertile and postfertile breeding stages (Dowling & Webster, 2016), although, in another playback experiment with this species, males that sang more duets with their females had lower reproductive losses to extrapair paternity in their nests (Baldassere et al., 2016). In light of these conflicting results, further experimental investigation of the paternity guarding hypothesis in duetting species is warranted.

In this study, we test the paternity guarding hypothesis by conducting a playback experiment in a neotropical duetting songbird: the rufous-and-white wren, *Thryophilus rufalbus*. Rufous-and-white wrens provide an ideal species for testing the paternity guarding hypothesis for two reasons. First, unlike the aforementioned duetting species, males in this species answer a higher proportion of female songs to form duets during the fertile period, suggesting that duets may serve a paternity guarding function (Topp & Mennill, 2008). Second, rufous-and-white wrens exhibit low levels of extrapair paternity (2% of offspring in 6% of broods), indicating, given the previously stated observational evidence, that duets may play a role in acoustic mate guarding during the fertile period (Douglas, Heath, & Mennill, 2012). We used playback to simulate a rival male near the edge of a subject's territory, creating the impression that a male competitor had entered the subject male's territory. We then used playback to simulate the subject's breeding partner near the centre of the subject's territory, thereby giving males an opportunity to create duets with their breeding partner's songs.

We made a priori predictions about how male rufous-and-white wrens would respond to female songs in the second phase of this experiment. In accordance with the paternity guarding hypothesis, we predicted that males would answer a higher proportion of their female's songs to form duets (i.e. they would create more duets) during the fertile period compared to the nonfertile period. We also predicted that males would attempt to guard their paternity in two additional ways unrelated to duetting. We predicted that males

would increase their independent song rates (i.e. songs that were not part of a duet) during the fertile period compared to the nonfertile period, as has been observed in other studies of temperate songbirds (reviewed in Møller, 1991). We also predicted that males would exhibit a more intense physical response towards the loudspeaker simulating their breeding partner (i.e. they would physically guard the loudspeaker simulating their breeding partner by approaching more closely, more quickly, and remaining near to the loudspeaker for longer) during the fertile period compared to the nonfertile period.

METHODS

Study Species and General Field Methods

We conducted our experiment in 2016 and 2017 with a colour-banded population of rufous-and-white wrens in Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica (10°51'N, 85°36'W). Rufous-and-white wrens are neotropical, socially monogamous duetting songbirds found throughout many parts of Central America and northwestern South America in which breeding partners sing loosely coordinated polyphonal duets (details in Mennill & Vehrencamp, 2005). Members of our laboratory have studied this population since 2003; on an annual basis we band birds, map territories, find nests and record songs from most animals in the population (20–55 pairs per year). We banded all of the male playback subjects in this experiment with unique combinations of coloured leg bands to facilitate individual identification. We also banded 11 out of 21 of the females involved in this experiment (52%), and we were confident in our ability to differentiate between the remaining unbanded females based on their territory position and their unique vocal repertoires (see Mennill & Vehrencamp, 2005).

Playback Experiment

We conducted playback experiments to 21 different male rufous-and-white wrens between early May and mid-June across the 2 years of our study (7 pairs in 2016 and 14 pairs in 2017). This time of year coincides with the end of our subjects' nonbreeding season and the beginning of the breeding season (i.e. nest building and egg laying), coincident with the first large rainfall of the year (Topp & Mennill, 2008). Each male received playback on two occasions at different breeding stages. First, we delivered playback during the fertile period of the subject's partner, which we defined as the window from 5 days before to 2 days after females laid their first egg of a clutch (on average, we conducted fertile playbacks 3.7 ± 1.3 days before first egg date; Birkhead, 1998). Second, we delivered playback during the incubation period, which we defined as the period when females were incubating their completed clutch (females usually lay two to five eggs and incubate for 12–15 days; on average, we conducted playbacks on day 6.2 ± 4.4 of incubation). In 19 of 21 cases, we administered playback to focal males first during the fertile period and second during the incubation period. There were two pairs for which we first administered playback during the incubation stage and, due to nest predation, secondly during the fertile period while pairs were reneesting. We determined the breeding stage of each pair by finding and monitoring their nests, and by carefully observing the behaviour of birds in the weeks preceding playback.

Each playback experiment, both during the fertile and nonfertile period, included two stages of playback: the 'intrusion stage' and the 'duetting stage' (Fig. 1). During the intrusion stage, we used a loudspeaker placed within the territory to simulate a neighbouring male encroaching onto the subject's territory, potentially seeking

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