

Duetting in space: a radio-telemetry study of the black-bellied wren

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In many birds, individuals ‘answer’ the songs of their pair-mates to produce vocal ‘duets’. One hypothesized function of song answering is that it prevents extra-pair birds from intruding into the duetting pair’s territory to obtain copulations or usurp one of the pair-mates. In this capacity, answering may signal that the pair-mates are close together, and so are prepared to defend against such an intrusion. Another functional hypothesis states that answering helps pair-mates maintain contact, and so predicts that a bird is more likely to approach its mate after a duet than after a solo song. I used radio-telemetry to monitor the distance between mated black-bellied wrens (*Pheugopedius fasciatoventris*). I found that birds of both sexes were more likely to answer their mate’s song when the mate was close, and that maximum duet length was negatively related to the distance between pair-mates. Furthermore, song answering positively affected the likelihood of one pair-mate approaching the other after a song. In a significant majority of the approaches after duet songs, the answering bird approached the initiator. I conclude that in the black-bellied wren, (i) the occurrence and duration of vocal duets covary with physical closeness and (ii) contact maintenance is a secondary function of duet participation.

Keywords: animal communication; vocal duet; radio-telemetry; *Thryothorus*; *Grallina*; contact maintenance

1. INTRODUCTION

In over 200 avian species, pair-mates vocalize together, producing ‘vocal duets’ (Farabaugh 1982). It has been hypothesized that duets convey information about a pair’s identity (Wiley & Wiley 1977) or tenure (Wickler 1980; Todt *et al.* 1981; Marshall-Ball *et al.* 2006; Hall & Magrath 2007), or the distance between the pair-mates (Todt *et al.* 1981; Hall 2006). The last of these is the focus of the present study.

Territory owners may send, and potential intruders may attend to, indicators of proximity in duets because pair-mates may be more effective territory defenders when they are in close proximity to one another (Hultsch & Todt 1984; Hall 2004; Hall & Magrath 2007; but see Rogers *et al.* 2004). Alternatively, pair closeness may prevent outsiders from sneaking into the territory for extra-pair copulations (Sonnenschein & Reyer 1983; Levin 1996a,b; Hall 2004). In the latter hypothesis, only the answering bird stands to benefit from signalling closeness.

Currently, Australian magpie-larks (*Grallina cyanoleuca*) are the only species in which duetting behaviour is known to covary with spatial proximity. Magpie-lark pairs are more likely to duet when the distance between pair-mates is small (Hall & Magrath 2000), and they produce faster duets when they are closer together (Hall 2006). These indicators of closeness may reveal the pair-mate’s proximity to extra-pair birds that are deciding whether to invade the territory (see §4). Under certain conditions, extra-pair birds may be able to localize sound sources with sufficient accuracy to estimate

the duetting birds’ proximity to one another. But when signal localization is complicated by large distances and/or high levels of signal degradation, these birds would be expected to attend to any reliable indicators of proximity that are available to them.

A little-tested hypothesis of duet function states that mated birds use duets to maintain contact with one another when visual contact is not possible (Thorpe 1973). There is ample evidence that contact maintenance is not the primary driver of the evolution of duetting (reviewed in Hall (2004)), but given the apparent ease with which duets could be used for this purpose, it is reasonable to ask whether birds use duets to maintain contact. In one of the few studies to address this hypothesis, Brown & Lemon (1979) observed that paired happy wrens (*Pheugopedius felix*) often approached one another after duetting. More recently, Mays *et al.* (2006) found support for a key prediction of the contact maintenance hypothesis when they discovered that female Steere’s liocichlas (*Liocichla steerii*) living in visually closed habitats answer their mates more frequently than females living in visually open habitats. To date, however, no study has quantified approaching behaviour as a function of song answering.

I tested the hypotheses that the occurrence and structure of duets covary with the distance between pair-mates, and that duets are used for contact maintenance, in the black-bellied wren (*Pheugopedius fasciatoventris*, recently revised from *Thryothorus fasciatoventris*; Mann *et al.* 2006). Black-bellied wrens are socially monogamous insectivores that defend all-purpose territories throughout the year. Duets in this species occur when one bird ‘initiates’ a vocalization and another bird ‘answers’ by

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rapidly producing a song of its own. Once a duet is begun, pair-mates may continue alternating phrases to extend the duet (I refer to songs that are part of a duet as 'phrases'). Black-bellied wrens are difficult to visually observe in the wild because they move furtively and spend most of their time in liana tangles and other dense vegetation (Ridgely & Gwynne 1989). For the present study, two observers simultaneously radio-tracked paired birds on territories marked with measured grids. Data on their locations and vocalizations were used to address the following four questions:

- (i) Is the distance between pair-mates independent of the probability of answering by males or females?
- (ii) Is the distance between pair-mates independent of duet duration?
- (iii) Are answered songs (duets) more likely than unanswered songs (solos) to be followed by a singer approaching the mate?
- (iv) If there is a reduction in the distance between pair-mates after duetting, is it the duet initiator or the answerer that moves towards the pair-mate?

2. MATERIAL AND METHODS

(a) *Species and study site*

Black-bellied wren territories include woodland or forest edges such as those caused by tree-fall gaps, ponds or roadways. Birds nest outside of, or on the edge of, the forest in grasses or sedges (Auer *et al.* 2007) and forage primarily in vines and foliage in the forest. Birds were sexed by size and song, both of which are strongly dimorphic (Logue *et al.* 2007). Both sexes sing solo (unanswered) songs, initiate duets and answer the songs of their mate.

This study was conducted in and around the village of Gamboa, Republic of Panama (9°07' N, 79°41' W). Of the five pairs that contributed to the study, two lived in a small woodlot known as 'The Gamboa Woods', two lived in the 22 000 ha Parque Nacional Soberanía (at the edges formed by the railway tracks to the north of Gamboa and Pipeline Road, respectively) and the remaining pair lived along the Old Gamboa Road, 8 km south of Gamboa. Observations took place in February, March and May 2003, and July and August 2004. Black-bellied wrens are known to nest from April to July (Auer *et al.* 2007). Females from two of the study pairs were incubating during this study.

(b) *Radio-tagging*

I conducted all of the fieldwork for this study with the help of an experienced field assistant. Mist nets and two-speaker playback were used to trap each pair. The birds were fitted with coloured leg bands, if they were not already banded, and radio transmitters (Model BD-2, Holohil Systems Ltd., Carp, Ontario). Transmitters weighed 0.72 g, equivalent to 2.6 and 3.2% of the mean weight of male and female black-bellied wrens, respectively (D. M. Logue 2007, unpublished data, maximum in this study was 3.5%). Transmitters were attached with a figure-of-eight leg harness fashioned from two strands of cotton embroidery thread (Rappole & Tipton 1991). Immediately after release, most of the birds exhibited laboured flight. I did not closely track birds on this first day, because I did not want to add to their stress. By the time observations began (1 or 2 days later), the tagged birds had

resumed normal mobility and were regularly observed making long flights to cross gaps in the forest (but see appendix A). When possible, birds were recaptured and their harnesses removed after observations (6 of the 10 birds). Given the hot and wet environment, I suspect that the thin cotton harnesses fell off of the remaining birds within a matter of weeks or months.

(c) *Gridding and tracking*

My assistant and I used a measuring tape, a compass and flagging tape to plot grid points at 20 m intervals on each territory. Beginning at least 1 day after trapping, pair-mates were simultaneously observed for 4 or 5 days in the 3 hours following sunrise. My assistant and I alternated days of observations of male and female birds. Birds were tracked with handheld three-element antennas and Telonics TR-4 radio receivers (Telonics, Inc., Mesa, AZ). Observers minimized their influence on the bird's behaviour by maintaining a 10 m distance from the subjects and avoiding loud exchanges. Observers noted the location of their focal bird on the grid at the beginning of each minute. When an observer did not know the bird's location, s/he noted that the bird was 'off record' until the next localization. Locations and notes on all vocalizations were recorded on paper timelines and subsequently transferred to spreadsheets. I applied the Pythagorean theorem to determine the horizontal distance between pair-mates (inter-bird distance or 'IBD') every minute. At times, one or both observers could see both birds and directly estimate the IBD. These estimates took precedence over the IBD's derived from grid locations. Five pairs were tracked over a total of 21 days, resulting in 126 tracking hours. Sample sizes varied among tests because some pairs did not produce all types of songs.

(d) *Data analysis*

(i) *Is the distance between pair-mates independent of the probability of answering by males or females?*

I addressed this question with Monte Carlo tests. The Monte Carlo permutation procedure uses an assumed model to generate a null distribution of test statistics, to which the observed test statistic is compared for significance testing (Manly 1997). Monte Carlo procedures offer several advantages over parametric or rank-based tests. For example, they produce exact (rather than asymptotic) *p*-values, allow the testing of more specific (and therefore more realistic) models and are substantially more robust with respect to small and imbalanced datasets, zeros and ties.

I describe the test comparing IBD during answered and unanswered male songs; the test using female song is functionally identical. I generated the test statistic by subtracting the average IBD during male solo song from the average IBD during male initiated duets for each pair, and then averaging these differences over all pairs that produced both male initiated duets and male solo songs. This test statistic gives equal statistical representation to each pair. The model was identical to the actual dataset, except that the indicator variable *female answer* was randomly shuffled within each pair. For example, if a particular female answered seven songs and left four songs unanswered, each iteration of the model would have her answering seven of the eleven songs, but which seven she answered would be randomly determined. Models were iterated 10 000 times to produce the expected distribution of test statistics, given the null hypothesis that female answering is random with respect to IBD.

(ii) *Is the distance between pair-mates independent of duet duration?*

Plotting the IBD versus the duration of duets revealed a triangular distribution, as would be expected if IBD limited duet duration. The statistical significance of a limiting relationship can be tested with an upper-bound regression, which is a regression that uses only those data points with the maximum y -axis value in each of several predetermined x -axis bins (Podos 1997; Ballentine *et al.* 2004). I divided the x -axis, IBD, into 10 m bins, and determined the maximum number of phrases in a duet from each bin. In cases where two or more duets in a bin shared the same maximum number of phrases, their IBD's were averaged. I then ran a linear regression on these upper boundary points using IBD as the independent variable, and *number of phrases* in the duet as a dependent variable. I was not able to control for among-pair variation in this analysis, so inferences apply to the population of duets rather than the population of pairs.

(iii) *Are answered songs (duets) more likely than unanswered songs (solos) to be followed by a singer approaching the mate?*

I addressed this question with a Monte Carlo test. I will describe the test examining male initiation and female answering; the converse test is functionally identical. An 'approach' is a discrete event, so it was necessary to develop a reasonable definition for that term prior to analysis. I assumed that birds do not use duets for localization when they are close together, so only vocalizations given when IBD was 10 m and above contributed to this analysis. I used 10 m as the cut-off distance throughout this definition because it is a round number and a distance at which visual contact is often limited (D. M. Logue 2004, personal observation). Estimating that 3 min is the maximum amount of time it would take for a reasonably motivated bird to cross its territory, I defined an approach as an IBD reduction of at least 10 m, resulting in a minimum $IBD \leq 10$ m, in the 3 min following a duet or solo song. I defined the test statistic as the average proportion of answered songs (duets) that resulted in an approach. Proportions were calculated separately for each pair and averaged over pairs, so all pairs contributed equally to the analysis. The model was the same as the dataset, except that the indicator variable *female answer* (0 = female did not answer, 1 = female answered) was shuffled within each pair. Models were iterated 10 000 times to produce the expected distribution of test statistics, given the null hypothesis that the probability of approach after a male initiation is independent of whether or not the female answers.

(iv) *If there is a reduction in the distance between pair-mates after duetting, is it the duet initiator or the answerer that moves towards the pair-mate?*

I observed 12 events in which a duet was followed by an approach. I used a Monte Carlo test to determine whether the identity of the pair-mate that moved following these putative 'localizing duets' was random with respect to the identity of the duet initiator. I defined the test statistic as the average proportion of localizing duets in which the duet initiator moved. The proportion was determined for each pair, and averaged over pairs, so all pairs contributed equally. The model was the same as the dataset, except that the indicator variable *moving individual* (0 = song answerer, 1 = song initiator) was a random binomial ($p=0.5$). The model was iterated 10 000 times to produce the expected distribution of test statistics, given the null hypothesis that the identity of the

bird that moves towards its mate is independent of the identity of the song initiator.

I calculated two-tailed p -values for questions (i), (ii) and (iv). For the Monte Carlo tests used to address questions (i) and (iv), two-tailed p -values were defined as twice the proportion of the null distribution beyond the observed test statistic. This definition assumes that the tails of the distributions are symmetrical. The mate-localization hypothesis generates the directional prediction that the probability of approach after an answered song is greater than the probability of approach after a solo song, so I calculated one-tailed p -values for the tests of question (iii). Monte Carlo tests were conducted in Microsoft EXCEL (2007, Microsoft Corporation, Redmond, WA) equipped with POPTOOLS v. 2.7.5 plug-in (Hood 2006). The regression was conducted in SPSS v. 15.0 (2006). Distributions are summarized as mean \pm s.d. Percentiles are represented as P_N , where N is the percentage of values below the stated value.

3. RESULTS

On average, pair-mates were within 10 m of each other in $33.8 \pm 15.0\%$ of observations, and $38.0 \pm 31.2\%$ of songs were answered. I found a negative relationship between the IBD and the females' probability of answering the songs of their mates ($N=4$ pairs, 232 male initiations; IBD difference = -23.7 ± 12.5 m; $p=0.0002$; figure 1*a*). Male answering was also significantly associated with shorter IBD's ($N=3$ pairs, 48 female initiations; IBD difference = -20.6 ± 4.7 m; $p=0.01$; figure 1*b*). From the point of view of an extra-pair bird that hears a vocalization, the occurrence of a duet was a good predictor that the pair-mates were close together ($P_{90}=35.4$ m, $P_{50}=10.0$ m), when compared with the occurrence of male solo song ($P_{90}=71.6$ m, $P_{50}=52.5$ m) or female solo song ($P_{90}=77.5$ m, $P_{50}=24.6$ m). The upper-bound regression of IBD against phrase number was negative and significant, indicating that the maximum number of phrases in a duet decreases with increasing IBD ($r^2=0.81$, $F_{1,6}=21.95$, $p=0.005$; figure 2).

When IBD was 10 m and above, male initiations were four times more likely to be followed by an approach if the female answered ($N=4$ pairs, 199 male initiations; proportion of male initiations followed by approach: unanswered = 0.07 ± 0.08 , answered = 0.28 ± 0.36 ; $p=0.007$). Likewise, female initiations given from at least 10 m away were significantly more likely to be followed by an approach if the male answered ($N=3$ pairs, 29 female initiations; proportion of female initiations followed by approach: unanswered = 0 ± 0 , answered = 0.34 ± 0.06 ; $p=0.048$). When duets were followed by an approach, the duet initiator was significantly more likely to approach the answering bird, than the converse ($N=4$ pairs, 12 approaches after duetting; proportion in which initiator approaches = 0.83 ± 0.24 ; $p=0.035$). In all 10 cases in which the initiator approached the answerer, the answerer sang the last phrase in the duet. A significance test would give the same result as the previous test, but since initiating and ending a duet are not independent (Logue 2004), I have not conducted this test.

Examining the context of localizing duets revealed two interesting patterns. Although significance tests would be inappropriate here (I discovered these patterns by examining the data), these observations may be useful for designing

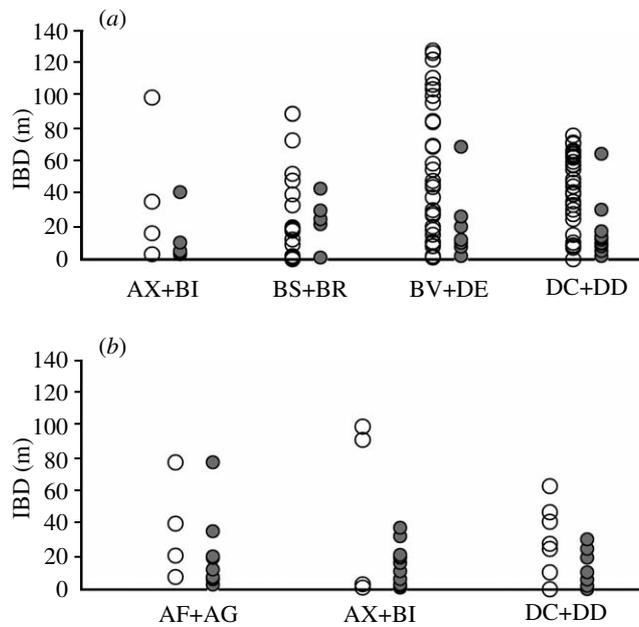


Figure 1. Dot plots showing the distance between pair-mates (IBD) during unanswred (open circles) and answered (filled circles) songs sung by (a) male and (b) female black-bellied wrens. The x-axes indicate pair identity. Males and females that did not initiate songs did not contribute to their respective graphs.

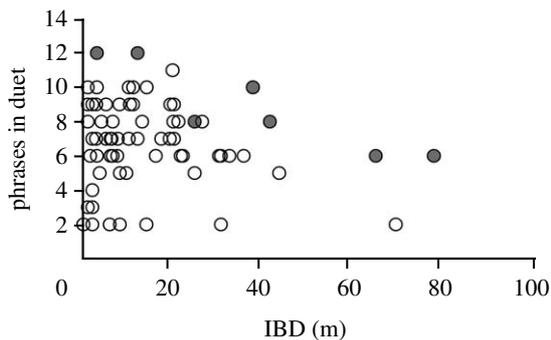


Figure 2. A plot of the total number of phrases in a duet versus the distance between pair-mates (IBD) when the duet was sung. Filled circles indicate points that contributed to the upper-bound regression (see text).

future studies. First, five localizing duets occurred shortly after a vocalization from a neighbour, but none of these involved a solo singing neighbour followed by an approach from the same-sex pair-mate. Second, on three occasions, the female answered the male from the nest, the male approached to join her there for 6–9 min and then left.

4. DISCUSSION

In the black-bellied wren, song answering (i.e. duetting) indicates that the singing pair-mates are close to each other, and are likely to be closer still over the ensuing minutes. Long duets are particularly indicative of close pairs, because they are rare or absent when pair-mates are separated by long distances. These findings raise two questions: (i) do other birds attend to the IBD information present in these songs? and (ii) is the covariation of IBD and answering rate adaptive?

This study indicates that vocal signals from the territory holders provide information that extra-pair birds could

use to increase their chances of encountering a lone territory holder. This information would be valuable to potential intruders if they stand to gain greater fitness from interacting with a lone territory holder than with a mated pair. There are at least three realistic scenarios where this is likely to be the case. First, when a bird is intruding to gain an extra-pair copulation, it will tend to derive greater net benefits if it encounters only the opposite sex pair-mate. The remaining scenarios assume pair-mates cooperate to defend and secure shared resources (reviewed in Logue 2005). Second, when a bird is intruding to gain residency on a territory, it will tend to derive greater net benefits if it encounters only the same-sex pair-mate. Third, when a pair of birds is intruding to expand their territory, they would derive the greatest net benefit if they encountered only one territory holder. Thus, duets indicate IBD, and information about IBD is likely to be valuable to extra-pair receivers in a variety of contexts, suggesting the prediction that extra-pair birds preferentially invade territories emanating solo songs rather than duets, and short duets rather than long duets.

The associations I report between IBD and song answering may be the products of adaptation or constraint. The adaptive explanation states that birds benefit from answering their mates and participating in extended duets only when the mate is nearby. This could be because answering when IBD is high produces poorly coordinated duets (e.g. due to the finite speed of sound in air) or an overtly stereophonic signal, which reveals the high IBD to potential intruders. A playback experiment on Australian magpie-larks showed that tightly coordinated duets provoked stronger responses than did poorly coordinated duets (Hall & Magrath 2007), indicating that answering only when IBD is small may be adaptive. Furthermore, both sexes of black-bellied wren adjust the timing of their duet contributions to increase the temporal coordination in their duets (D. M. Logue *et al.* 2007, unpublished data), suggesting that coordination benefits both pair-mates. An alternative to the adaptive explanation is that birds are constrained in their ability to answer songs from a distant mate because they cannot hear the song, or they cannot recognize the singer. Although this explanation may contribute to the phenomena described in this paper, a strictly constraint-based explanation is probably inaccurate because human observers could often (but not always) hear the distant unanswred bird, and because it fails to explain the limiting effect of IBD on duet duration.

Approaching the mate after a vocalization was significantly associated with answered songs (as opposed to solo song) from both sexes. In 10 of the 12 approaches that followed a duet, the initiating bird flew to join the answering bird. These findings constitute the first quantitative evidence that birds use duets to maintain contact. Only a fraction of duets stimulated an approach, confirming that contact maintenance is a secondary function of duet song in the black-bellied wren. The finding that the answering bird emitted the final phrase in 10 of the 12 duets that preceded approaches is predicted by the hypothesis that the initiator uses acoustic cues to locate the mate. The interpretation of this finding, however, is complicated by the fact that duet termination is negatively related to duet initiation (Logue 2004).

I found preliminary evidence that localizing duets are used in the contexts of cooperative resource defence and

incubation. Approaches after a neighbour's song may function to prevent the mate or territory from being usurped. Notably, I did not observe any approaches in response to same-sex solo song from a neighbour, as would be expected if mate localization was used to prevent the mate from copulating outside the pair bond. Finally, I observed several approaches following duets when one individual was at the nest, suggesting that answering may function to summon the mate to the nest (e.g. for an incubation feeding).

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APPENDIX A

(a) Note on ethics, sample size and efficacy of methods

I offer three points of caution to researchers considering radio-telemetry on territorial tropical forest birds. First, and most importantly, the radio-tags adversely affected some birds. One bird's antenna coiled around vegetation, necessitating a rescue. Three females and one male lost their territories within 48 hours of being fitted with radio-tags. They were all replaced by same-sex conspecifics, suggesting that the radio-tags influenced the subjects' ability to maintain their position on the territory. Generally, the usurped birds stayed on or near their former territories, but did not sing. None of the pairs to which they had belonged contributed to the dataset. Thus, a second point of caution is that the ratio of investment to data for this study was very high. In all, 6 of the 11 pairs that were caught, tagged and mapped did not contribute to the dataset, resulting in lost radio-tags, wasted work days and a lower-than-anticipated sample size. Finally, it proved quite challenging to track the birds through their dense habitat, while keeping detailed notes and carrying all of the necessary equipment.

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