



The behavioural mechanisms underlying temporal coordination in black-bellied wren duets

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(Received 18 June 2007; initial acceptance 6 August 2007;
final acceptance 16 October 2007; published online 25 March 2008; MS. number: A10798R)

Duetting is a form of animal communication in which two individuals produce temporally coordinated vocal signals. Describing the individual-level patterns of behaviour that structure duets is an integral step towards understanding the adaptive function(s) of duet participation. We investigated the fine scale timing of duet contributions in male and female black-bellied wrens, *Pheugopedius fasciatoventris*, by analysing recorded duets and by stimulating birds to 'duet' with recorded songs in the field. Previous research on this species revealed that most duets consist of alternating male and female phrases, and that females abide by individually distinctive 'duet codes', which link each male phrase type with a specific answer from the female's repertoire. In the present analysis, we found that the timing of male duet phrases was primarily influenced by the time that the prior female phrase began, and secondarily influenced by an internal tempo. Female phrase timing, however, was most strongly influenced by the time that the prior male song ended, and secondarily influenced by the female's internal tempo. The average answering time for both sexes was less than 0.08 s before the end of the mate's prior phrase. Coordination at the beginning of the duet appears to limit duet length; duets with large gaps or overlapping phrases were always short. We conclude that both sexes make 'on-the-spot' adjustments in timing that function to minimize gaps and overlap between duet phrases. Overall, our results are consistent with the hypothesis that well-coordinated duets benefit both partners by communicating that their shared territory will be defended by a high-quality defensive coalition.

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Keywords: answering rule; antiphonal song; behavioural mechanism; black-bellied wren; bird song; sexual dimorphism; cooperative territory defence; coordinated behaviour; *Pheugopedius (Thryothorus) fasciatoventris*

Vocal duetting is a phylogenetically widespread phenomenon in which two animals vocalize with temporal coordination. Birds, in particular, have evolved a tremendous variety of complex, highly coordinated duet songs. The functional significance of duet participation remains controversial, although it is widely agreed that duets are involved in territory defence (reviewed in Logue 2005), and that duet participation serves multiple adaptive functions (reviewed in Hall 2004). We suggest that progress on questions of function may be hastened by an improved understanding of the behavioural mechanisms (i.e. the individual-level patterns of behaviour) that

produce duets. It is important to examine behaviour at the level of the individual because the individual is the fundamental unit of selection and the two birds that produce a duet may follow very different behavioural programmes. For example, female black-bellied wrens, *Pheugopedius fasciatoventris* (previously *Thryothorus fasciatoventris*; Mann et al. 2006) adhere strictly to individually specific 'duet codes' linking the phrase types that they sing to specific male phrase types, but males do not adhere strictly to duet codes (Logue 2006, 2007a). Describing the behavioural mechanisms that produce duets furthers the goals of understanding the function of duet participation (Hall 2004, 2006; Rogers 2005) and of reconstructing the evolution of duetting (Mann et al. 2006).

Three recent studies use novel analytical approaches to reveal surprising patterns underlying temporal coordination in duetting birds. First, Laje & Mindlin (2003) report

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that the male rufous hornero, *Furnarius rufus*, begins a duet by singing an accelerating trill, over which the female sings a series of notes. Defining a 'coincidence' as a moment in which male and female notes occur simultaneously, the authors determined the ratio of female notes to male notes between each coincidence. They discovered that throughout the course of a duet, the ratio increases nonlinearly, in a manner well characterized by a step function known as the 'Devil's Staircase'. This function occurs when one oscillator forces a second oscillator, suggesting that the female's timing is a response to the male's inherent rhythm. In a study of Australian magpie-larks, *Grallina cyanoleuca*, Hall (2006) found that singing tempos were positively correlated among pairs, which is consistent with the hypothesis that at least one pairmate adjusts its behaviour to coordinate with the other. Hall & Magrath (2007) went on to show that more coordinated duets are more threatening to territorial male birds and that duet coordination by both males and females correlates positively with the duration of the pair bond.

In the present report, we attempt to determine the control of phrase timing in the black-bellied wren by asking how earlier duet phrases affect the timing of later duet phrases. The null hypothesis, that timing is random with respect to all previous phrases in the duet, predicts that the timing of early phrases in a duet will have no influence on the timing of later phrases. If timing is controlled by an internal tempo, we expect the focal individual's own prior phrases to influence the timing of later phrases. But if birds adjust their timing to coordinate with the phrases of their mate, phrase timing should be influenced by the timing of the mate's prior song. More specifically, if the focal bird simply waits to sing for a more-or-less fixed amount of time after the beginning of the mate's prior phrase, we expect that the beginning of the mate's prior phrase will influence phrase timing. If, however, the focal bird anticipates the end of the mate's prior phrase (or waits until it actually hears the end), we expect that phrase timing will be influenced by the end of the mate's prior phrase. Turning to function, the hypothesis that temporal coordination benefits both pairmates predicts that both sexes will adjust their timing to coordinate their phrases with the phrases of the pairmate (Wiley & Wiley 1977; Hall & Magrath 2007) and that pairs will quickly terminate duets (i.e. produce short duets) unless coordination is high.

METHODS

The study population, duet recordings and experimental protocol used for this study have been described previously (Logue 2007a). Below, we summarize the key information pertaining to data collection. Readers seeking further methodological details are referred to the prior report.

Pairs of black-bellied wrens defend all-purpose territories throughout the year. Individuals of both sexes sing repertoires of sex-specific song types. Sex differences in song are pronounced, making it easy to distinguish male song from female song (Logue et al. 2007). Solo songs are

identical to duet 'phrases'. Both sexes initiate song, and both sexes answer their mate's song to form a duet. After the first answer, the pairmates may allow the duet to end, or they may prolong the duet by continuing to alternate phrases (among natural duets in this study, mean \pm SD = 4.4 ± 2.3 phrases/duet). We recorded birds and conducted experiments near the village of Gamboa, Republic of Panama ($9^{\circ}07'N$, $79^{\circ}41'W$). All but one of the birds used in this study were marked with unique combinations of coloured leg bands.

Field recordings of 12 mated pairs were made during the period 10 June–17 August 2004. Of the duets used in our analyses, 69% were prompted with song playback. Recording equipment consisted of an aluminium parabolic reflector equipped with a Sennheiser microphone (ME62) and a Sony Minidisc recorder (MZ-N1). Recordings were loaded into a Compaq Presario 1693 (ESS Solo sound card) via the microphone input and digitized at 44.1 kHz using the program Syrinx (John Burt, <http://www.syrinxpc.com>). Duets were culled from these recordings and visualized as sonagrams (Hanning window, window size = 512 points) in Syrinx. One of us identified four male-phrase-to-female-phrase (M–F) transitions from each of the 12 focal pairs. These transitions represent pairs of song types that are linked by the females' duet codes; we refer to them as 'coded phrase pairs' throughout this manuscript. We attempted to analyse all recorded duets containing these coded phrase pairs (mean \pm SD = 4.2 ± 3.2 duets/coded phrase pair), but poor recording quality precluded analysis in several cases. Both birds were within 20 m of each other and the microphone during recording, limiting 'speed-of-sound' error to ± 0.058 s (assuming speed of sound = 344 m/s).

We made playback stimuli of each of the male and female phrase types from the 48 coded phrase pairs. We also made 24 duet stimuli, which were used to stimulate high answering rates during the experiment. Playback trials were conducted during 27 July–4 September 2004. Male song and female song stimuli were presented to the same birds that had generated the recordings used to make stimuli (e.g. we played male song stimuli recorded from male BZ to pair BZ and BI). We presented male song stimuli and female song stimuli in separate trials, with at least 1 week intervening. The male was the focal bird during female song playback trials, and the female was the focal bird during male song playback trials. The playback apparatus consisted of a Minidisc player (Sony MZ-N1), two 5 W loudspeakers (Saul Mineroff Electronics, SME-AFS) lying face up on the ground, 8 m apart, and connecting cables. Peak volume levels were set to 84 dB at 1 m, which is within the natural range shown by this species. We played stimuli approximately every 15 s. During the 'luring phase' that began each trial, duet stimuli were presented from the speaker that was furthest from the nonfocal bird. Duet stimuli were recorded from nonfocal birds and were played at least 6 km away from the origin of the recordings, so it is unlikely that subjects recognized the singers. The luring phase ended when both birds were within 40 m of the speakers and had sung at least two duets.

The 'testing phase' began immediately after the luring phase. During the testing phase we played 24 randomly

ordered blocks of stimuli: eight blocks of the duets that had been used during the luring phase and 16 blocks of either male song or female song stimuli. Each of the four solo-song stimuli in the trial was presented in two blocks of two and two blocks of three, resulting in a total of 40 male or female stimulus presentations per trial. This randomized block presentation is more realistic than a fully randomized presentation, because black-bellied wrens of both sexes usually sing one phrase type several times before switching (Logue 2004). The lack of independence within blocks was addressed in the analyses by only including the first answered stimulus from each block in the data set. Duet stimuli were presented through the speaker furthest from the nonfocal bird, and test stimuli were presented from the speaker nearest to the nonfocal bird. This two-speaker design was intended to simulate an intruding pair (duet playbacks) and a singing mate (solo-song playbacks). The focal bird often answered the song stimuli, generating 'hybrid duets' composed of an initiating song played from a loudspeaker and an answer sung by a live bird. We obtained hybrid duets from nine female trials and 12 male trials. Of the 16 possible responses (one for each stimulus block), males contributed a mean \pm SD of 9.8 ± 4.09 responses to the data set and females contributed 7.2 ± 4.44 responses.

Sonagrams of duet recordings were made in Syrinx (Hanning window, window size = 512 points) and the time at the beginning of each phrase (including the playback stimulus) was measured with the onscreen cursors (temporal resolution = 2 ms). One observer determined the order and timing of phrases in the natural duet recordings, and another measured timing in the hybrid duets. It was not possible to measure the end of phrases precisely because of high levels of reverberation. Instead, one observer measured the duration of the highest-quality recording of each phrase type within individual, which was used to extrapolate the time at the end of each song. Song duration is highly repeatable within phrase type (Logue et al. 2007).

We began by identifying all of the segments in our natural duet recordings in which a male phrase was first followed by a female phrase and then by another male phrase (M–F–M segments) and all of those in which a female phrase was first followed by a male phrase and then by another female phrase (F–M–F segments). Some segments were complete duets, and others were parts of longer duets. The male and female phrase types occupying the first two positions in each segment were a coded phrase pair. The time at the beginning of the first song in each segment was defined as $t = 0$. We determined the times at (1) the end of the first phrase, (2) the beginning of the second phrase, (3) the end of the second phrase, and (4) the beginning of the third phrase (Fig. 1). Some long duets contained more than one nonoverlapping segment of a particular type (M–F–M or F–M–F). In these cases, we determined values (1)–(4) for each segment and averaged them within the duet. We collected measures (1) and (2) from the first hybrid duet recordings from each stimulus block.

We tested for influences on phrase timing while controlling for variance attributable to individuals by

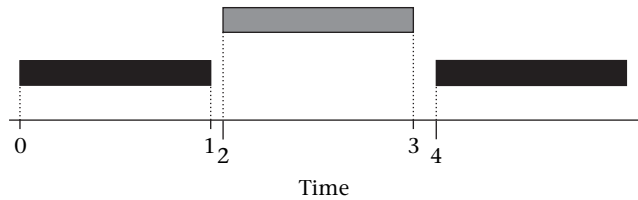


Figure 1. Duet timing measurements applied to a three-phase sequence from a natural black-bellied wren duet. Phrases of one pairmate are represented by black bars, and the phrase of the other pairmate is represented by the grey bar. We measured the times at which (1) the first song ended, (2) the second song began, (3) the second song ended and (4) the third song began.

generating both reduced and complete general linear models (GLMs) for each research hypothesis. The reduced model included all variables (including 'individual') except for the independent variable of interest. The complete model included all variables. The difference in r^2 between the reduced and complete model (r_{effect}^2) was used to generate an F ratio:

$$F(k_2 - k_1, N - k_2 - 1) = r_{\text{effect}}^2 / (1 - r_{\text{complete}}^2) \times (N - k_2 - 1) / (k_2 - k_1),$$

where N represents the number of observations, k_1 is the treatment degrees of freedom for the reduced model and k_2 is the degrees of freedom in the complete model (after Vokey 2003). We used the F value to test the hypothesis that the new variable explained a significant amount of variance in the dependent variable beyond that explained by all other variables. The value r_{effect}^2 , which we report in the test results, represents the proportion of variance in the dependent variable attributable to the variable of interest beyond the variation accounted for by all other variables and any covariation between those variables and the variable of interest.

We applied a 'forward looking' model selection procedure to data from the natural duet segments to determine whether the time that the focal individual's second phrase began (4) was influenced by the following three covariates: the time the focal individual's first phrase ended (1), the time the mate's phrase began (2), and/or the time the mate's phrase ended (3). Separate models were generated to test the influences on phrase timing in males (using data from M–F–M segments) and females (F–M–F data). The model selection procedure began by adding each covariate (1–3) separately to a model containing the factor individual. The covariate with the greatest r_{effect}^2 was added to the model and tested for significance, as described in the preceding paragraph. If this covariate was significant, the remaining two covariates were added separately to the model containing individual and the first covariate. Again, the one that generated the greatest r_{effect}^2 was added and tested for significance. If both of the first two covariates were significant, the third was added and tested for significance. Once the final model was established, we determined each covariate's r_{effect}^2 in the final model. That value represents its effect above and beyond all other included independent variables and any covariation with those variables. General linear models

were also used to determine whether the end of the stimulus (1) influences the beginning of the response (2) in the hybrid duets.

We used the M–F–M segments to determine whether the duration of the first male phrase affected the duration of the female's answer. We avoided pseudoreplication by using only one exemplar of each coded phrase pair. We treat the relationship between male and female phrase duration as causal because the female chooses her phrase type based on the male's phrase type (Logue 2006, 2007a).

We used upper-bound regression (Podols 1997) to test the hypothesis that duet coordination limits duet duration. Using only those duets in which sexes strictly alternated phrases, we determined the mean absolute deviation from perfect coordination (no gaps, no overlap) over the first two answers. For example, if the female phrase in an M–F–M duet overlapped the first male phrase by 0.1 s and the second male song began 0.3 s after the end of the female song, the mean absolute deviation would be $(0.1 + 0.3)/2 = 0.2$. We only used the first two answers because using all answers would generate bias if coordination changed over the course of a long duet. We plotted the mean absolute deviation against the total number of songs in the duet. We then divided the X axis (mean absolute deviation) into 10 evenly sized bins and identified the points representing the maximum number of phrases in each bin. When two or more duets were tied for the maximum number of phrases in a bin, their mean absolute deviations were averaged. Finally, we used a linear regression to compare mean absolute deviation and number of phrases among these points. Note that this analysis used data pooled over pairs of birds, so statistical inferences apply to the population of duets rather than to the population of birds.

We tested whether variability in response time differs between the sexes, while accounting for variation attributable to phrase type. We first measured the mean delay between adjacent male and female duet phrases (from point 1 to point 2) for coded phrase pairs in each natural duet. Next, we determined the standard deviation for each coded phrase pair, within individuals. Finally, we calculated the mean standard deviations for each individual and ran an unpaired t test to compare male deviations versus female deviations (paired comparison would have been inappropriate because some pairs did not contribute to both data sets). All statistical tests were conducted in SPSS 15.0 (2006). P values ≤ 0.05 were considered statistically significant. Distributions are summarized as means \pm SD.

RESULTS

The forward-looking model selection procedure indicated that, in both M–F–M and F–M–F segments, the timing of the first two phrases explained significant amounts of variation in the timing of the third phrase, allowing us to reject the null hypothesis that phrase timing is random with respect to prior events in the duet. The final model for the M–F–M segments (GLM, predictor variables individual, (2) and (1): $r^2 = 0.82$, $F_{13,105} = 31.89$, $P < 0.001$)

showed that the timing of the final male phrase (4) was most strongly influenced by the beginning of the female phrase ((2): $r^2_{\text{effect}} = 0.06$, $F_{1,92} = 29.8$, $P < 0.001$), less strongly affected by the end of the male's previous phrase ((1): $r^2_{\text{effect}} = 0.03$, $F_{1,92} = 14.2$, $P < 0.001$) and not significantly affected by the end of the mate's previous phrase ((3), not included in final model). In the final model for the F–M–F segments (GLM, predictor variables individual, (3), and (1): $r^2 = 0.67$, $F_{13,63} = 7.7$, $P < 0.001$), the strongest unique influence on the time of the second female phrase (4) was the end of the male phrase ((3): $r^2_{\text{effect}} = 0.10$, $F_{1,50} = 14.4$, $P = 0.0004$), followed by the end of the first female phrase ((1): $r^2_{\text{effect}} = 0.05$, $F_{1,50} = 6.7$, $P = 0.012$). The beginning of the male phrase ((2), which was not included in final model) did not have a significant independent effect. All significant effects in both models were in the positive direction.

Analysis of the hybrid duet data failed to detect any significant influence of the time that the female stimulus ended on the time of the male answer (GLM, effect of adding (1): $r^2_{\text{effect}} = 0.011$, $F_{1,105} = 1.47$, $P = 0.23$; Fig. 2a). The female's timing, however, was influenced by the time that the male stimulus ended (GLM, effect of adding (1): $r^2_{\text{effect}} = 0.159$, $F_{1,68} = 28.30$, $P < 0.001$; Fig. 2b).

Returning to the natural duet data, male phrase duration exerted a marginally significant negative effect on

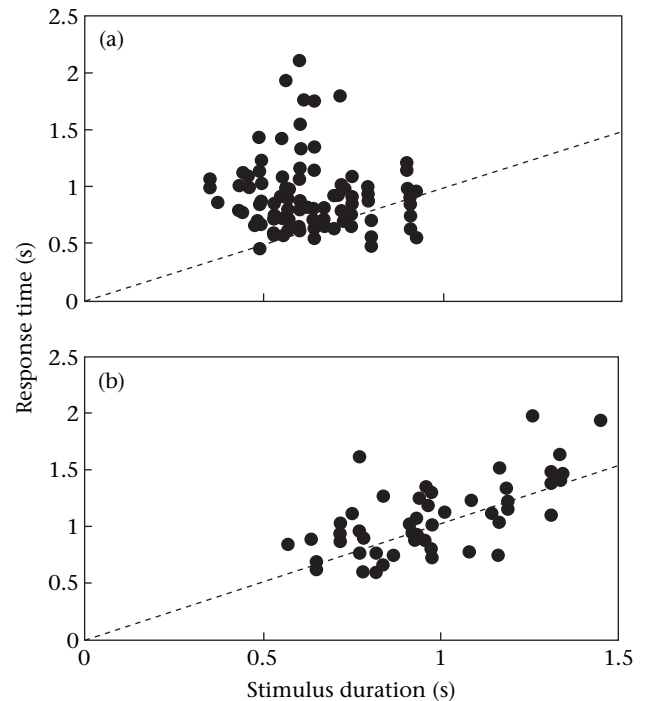


Figure 2. Relation between the duration of a song stimulus (X axes) and the time that it took the mate of the recorded bird to answer the stimulus (Y axes). (a) Male black-bellied wrens answering female songs. (b) Female black-bellied wrens answering male songs. The dashes mark the line $Y = X$. Response times were measured from the beginning of the stimulus: a dot below the dashed line indicates an answer that overlapped the stimulus; a dot on the line indicates an answer that immediately followed a stimulus; a dot above the line marks an answer that began some time after the end of the stimulus. See the text for statistics.

female phrase duration (GLM, effect of adding male phrase duration: $t_{\text{effect}}^2 = 0.034$, $F_{1,35} = 3.39$, $P = 0.074$). The upper-bound regression supported the hypothesis that deviations from coordination limit the duration of a duet (linear regression: $r^2 = 0.50$, $F_{1,8} = 8.13$, $P = 0.021$; Fig. 3). We averaged 'delay to answer' within coded phrase pair, then within individual, and found that, on average, males answered 0.048 ± 0.12 s before the end of the previous female phrase and females answered 0.071 ± 0.11 s before the end of the previous male phrase (t test for sex difference: $t_{20} = 0.46$, $P = 0.65$). Female response times were more variable than male response times within coded phrase pairs (female SD = 0.14 ± 0.076 ; male SD = 0.07 ± 0.045 ; t test: $t_{20} = 2.61$, $P = 0.017$).

DISCUSSION

Black-bellied wrens of both sexes timed their duet phrases with respect to both the timing of their own prior phrase and the timing of their mate's prior phrase. Male timing was primarily influenced by the time of the beginning of the previous female phrase and secondarily influenced by the male's own internal tempo. Females were primarily influenced by the end of the previous male phrase and secondarily influenced by their own internal tempo. On average, birds of both sexes answered their mates very near (<0.08 s) to the end of the mate's phrase, suggesting that optimal coordination in this species is characterized by little or no overlap or gap between phrases.

In addition to adhering to internal tempos, both sexes of black-bellied wren adjusted the timing of their phrases 'on the spot' to coordinate with their mate's prior phrase. Mutual influences on duet phrase timing have also been described in robin chats, *Cossypha heuglini* (reviewed in Todt et al. 1981). The present findings that both sexes adjusted their timing in ways that improved coordination and that, on average, both sexes answered less than 0.08 s before the end of their mate's phrase suggest that adjustments serve to minimize gaps and overlap between adjacent phrases. Interestingly, however, males and females adjusted their timing in different ways. The timing

of male answers relative to playback stimuli and natural female phrases was influenced by the beginning of the female phrase, but the end of the female phrase did not exert a significant independent influence on male phrase timing (Fig. 2a). Thus, for example, if the female begins a phrase relatively late, the male will delay his answer, but he does not seem to anticipate how long the female's phrase will last. In contrast, data from both playback and natural duets indicated that female timing is strongly influenced by the end of the prior male phrase. Functionally, females anticipate when males will end their phrases.

We have identified three factors that may have influenced the evolution of the observed sex difference in phrase timing. The first factor is the dimorphism underlying phrase type coordination in this species (Logue 2006, 2007a). Female black-bellied wrens adhere strictly to a duet code, almost always answering each male phrase type with a particular phrase of their own, whereas males adhere only very loosely to a duet code. We hypothesize that because females know the male's phrases (they are able to answer each one according to code), they are able to anticipate the end of the phrase and begin their phrases at that time. Males, however, may not know when the female phrase will end, so they simply follow a rule to wait some amount of time before answering. Secondly, because male phrase durations are more variable than female phrase durations (Logue et al. 2007), anticipating variation in the length of the mate's phrase improves females' coordination more than it would improve males' coordination. Thirdly, female response times are more variable than male response times for a given phrase pair, so females may need to take variation among phrases into account to achieve satisfactory levels of coordination.

Upper-bound regression revealed that long duets were always highly coordinated (i.e. characterized by small gaps and areas of overlap). Todt et al. (1981) included a virtually identical distribution of coordination versus duet length obtained from captive robin chats. The hypothesis that highly coordinated duets communicate some aspect(s) of pair quality (Hall & Magrath 2007) predicts that birds should cut off uncoordinated duets to minimize the risk of alerting neighbours that they are a low-quality pair. Our results seem to support this prediction. We wish to point out, however, that our analyses fail to account for the known limiting relationship between duet duration and distance between pairmates (Logue 2007b) and the expected negative limiting relationship between duet coordination and distance. A study measuring distance between pairmates, duet duration and duet coordination would clarify the strength of interactions among these variables and allow for a better assessment of the information that may be communicated by duet structure.

We found that both sexes modified their behaviour to improve duet coordination, suggesting that coordination benefits both pairmates. What is the nature of this benefit? We believe our results are most compatible with the set of functional hypotheses that state that participating in a coordinated duet indicates to potential intruders that the pairmates are close to one another, are attentive to one another and are ready to defend the territory as

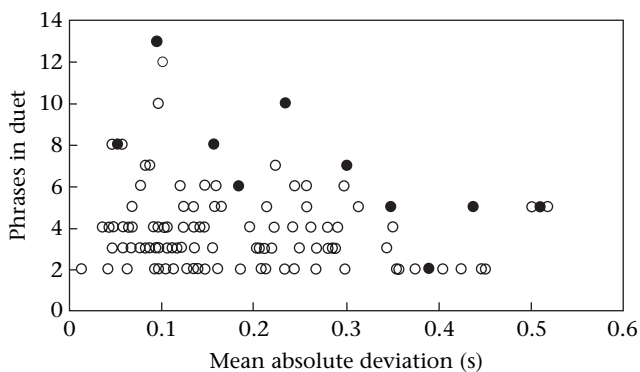


Figure 3. Mean absolute deviation of the first two answers in a black-bellied wren duet (or just the first answer, in the case of two-phrase duets) versus the number of phrases in the duet. ○: individual duets; ●: points used in an upper-bound regression. See the text for statistics.

a team (Hall 2004, 2006; Logue 2005, 2007b; Hall & Magrath 2007). If duets function in these ways, we would expect both sexes to maximize coordination and so minimize the risk of intrusion. In contrast, some 'conflict-based' hypotheses suggest that the initiating pairmate is attempting to manipulate the answerer (Smith 1994), or that the answerer is attempting to block the signal of the initiator (Levin 1996a,b). Two studies on other duetting passerines found that males tend to stop singing when females answer them to form a duet (Sonnenschein & Reyer 1983; Seddon & Tobias 2006). Both studies concluded that females were interrupting males' attempts to solicit extrapair females. This type of conflict-based scenario seems incompatible with our observations that both sexes adjusted their timing in ways that minimized gaps and overlap between adjacent phrases.

Our study revealed a marginally significant negative relationship between the durations of male and female phrase types that are joined by the female's duet code. In other words, females tend to answer long male phrases with short phrases of their own, and vice versa. This finding was surprising because there was no previous indication of a structural relationship between phrases joined by the duet code. If this association is 'real', it may be adaptive because it limits variability in the duration of coded phrase pairs, and so reduces the need to adjust phrase timing to produce a well-coordinated duet. This finding and the finding that females functionally anticipate the duration of male phrases suggest that the duet code may function to improve duet coordination.

Acknowledgments

We thank M. C. Baker, W. A. Searcy and two anonymous referees for commenting on an earlier draft of this manuscript. J. R. Vokey, L. Barrett and J. Burt offered helpful advice on analyses. B. Veber ably assisted in the field. D.M.L. was supported by the Smithsonian Tropical Research Institute, the American Museum of Natural History, the Cooper Ornithological Society, an Abbott grant to E.S. Morton administered via the Smithsonian Office of Fellowships and Grants, and a postdoctoral fellowship based partially on a grant to William Cade from the Natural Sciences and Engineering Research Council of Canada. The Autoridad del Canal de Panamá and the Autoridad Nacional del Ambiente (permit no. SE/A-61-04) granted permission to conduct the fieldwork described in this study.

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