

Signal Jamming Mediates Sexual Conflict in a Duetting Bird

Joseph A. Tobias^{1,*} and Nathalie Seddon¹

¹Edward Grey Institute
Department of Zoology
University of Oxford
South Parks Road
Oxford OX1 3PS
UK

Summary

Signal evolution in social animals has produced a wide variety of communal displays, many of them remarkable feats of complex coordination [1–4]. The two main explanations for this temporal precision are: (1) it evolves as a cooperative signal of coalition quality [5] or (2) it minimizes signal jamming (i.e., interference of one signal by another) [6]. However, support for the first hypothesis is inconclusive, and the role of jamming in communal signaling strategies remains unknown. Here, we use playback experiments to examine how social context influences the structure of duets in a pair-living antbird (*Hypocnemis peruviana*). The results show that, although resident pairs produced coordinated duets when responding to rival pairs, conflicts of interest caused duet coordination to break down. Specifically, females responded to unpaired sexual rivals by jamming the signals of their own mates, who in turn compensated by adjusting their signals to avoid interference. In demonstrating this interaction, we provide the first evidence that signal jamming occurs between mates and that strategies for reducing jamming can result in increased signal complexity. These findings highlight the importance of jamming avoidance in determining the structure of duets and suggest that conflict between signalers, rather than cooperation alone, may drive the evolution of sophisticated communal displays in social animals.

Results and Discussion

Coalitions of individuals produce joint displays in a wide range of social animals, from crustaceans to primates [1–4]. Understanding these displays has proven to be a major challenge, because they are often highly complex or variable in structure and they appear to serve multiple context-dependent functions [6–9]. The prevailing view holds that they mediate cooperative resource defense by signaling the relative competitive ability of coalitions, in terms of strength [5], stability [10], commitment [11], or numerical advantage [12, 13]. However, a growing number of studies find evidence that they also mediate conflicts of interest between coalition members [14–22]. Overall, a consensus is emerging that many communal displays have resisted interpretation precisely because they are multipurpose, with a role in both social cooperation and intersexual conflict [7, 16, 17, 19, 22]. The implications of this dual function are not known, but one unexplored possibility is that an interaction between contrasting roles may be the

key to understanding the evolution of complex, temporally coordinated signals in social animals.

Two hypotheses have been forwarded to explain the structure of communal displays: one founded on cooperation, another on conflict. According to the former, temporal coordination between group members arises as an honest signal of coalition quality [10]. This idea is supported by the finding that tightly coordinated duets are more likely to be produced by established pairs and are perceived as more threatening than uncoordinated duets [5]. An alternative possibility is that temporal coordination is an epiphenomenon caused by jamming (i.e., masking) avoidance, whereby individuals adjust their signals to minimize overlap [6]. Jamming avoidance has not been reported within coalition signaling systems, but it is thought to produce nonoverlapping signals in a variety of animals, including insects, amphibians, birds, and mammals [23–27]. A difficulty posed by these two hypotheses is that they tend to generate similar predictions. For example, precisely coordinated duets may elicit stronger responses because coordination either reflects coalition quality [5] or simply reduces masking of signal content [6]. Previous studies fail to discriminate between these possibilities and are, therefore, inconclusive [6].

An additional challenge for explanations of signal structure is the fact that many communal displays are not only temporally coordinated but highly complex [1, 3, 4]. It seems plausible that this complexity is not promoted by cooperation but is, instead, more deeply rooted in sexual selection or sexual conflict, wherein optimal signaling strategies differ between the sexes. Here, again, the role of jamming avoidance may be prominent. In duetting birds, for example, conflict reveals itself in manipulative strategies, by which one individual interferes with the signal of a mate or rival by overlapping it [19, 21]. Signal jamming by one sex theoretically favors strategies for jamming avoidance in the opposite sex, perhaps leading to an increase in overall duet complexity. In this study, we ask: (1) whether signaling decisions made by coalition members vary in relation to social context; (2) whether conflict between coalition members leads to jamming avoidance; and (3) whether jamming avoidance promotes signal coordination and/or complexity.

We addressed these questions by using acoustic analyses and playback experiments in a free-ranging population of Peruvian warbling-antbirds *Hypocnemis peruviana*. This species provides an ideal system for assessing the relative roles of cooperation and conflict in shaping signal structure. Previous work [19] has shown that pairs of warbling-antbirds use duets to defend shared permanent territories. In addition, male solos are known to function in mate attraction, and the number of unmasked notes that a male is able to produce is under female control [19]. Finally, in comparison with the complex group signals found in many social animals [1, 4, 17, 28], the structure of antbird duets is relatively straightforward to quantify and interpret (Figure 1).

Duet Structure

The songs of warbling-antbirds are multinote, sex-specific signals [19, 29]. They are usually produced as duets, typically as an evenly spaced series of couplets, each consisting of

*Correspondence: joseph.tobias@zoo.ox.ac.uk

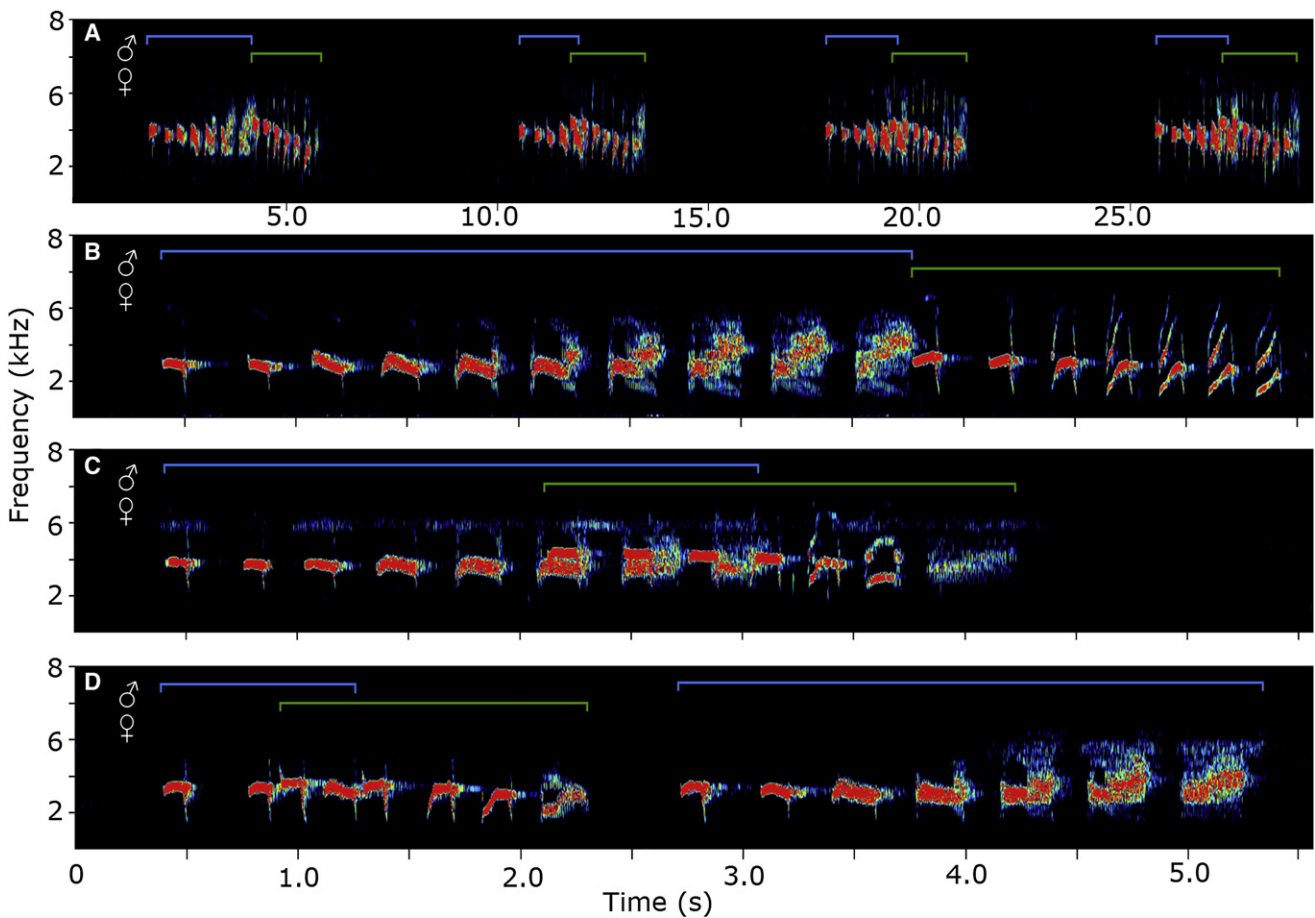


Figure 1. Variation in Structure and Coordination of Natural Duets

(A) Coordinated duet consisting of a series of four couplets, with low overlap of male and female songs, and long “duet intervals.”

(B) Precisely coordinated couplet, with no jamming of male notes by female song.

(C) Poorly coordinated couplet, with three male notes jammed.

(D) Example of jamming avoidance by a male who abandons his song after interruption by the female and interjects a full song after a brief “duet interval.”

Sound files for all spectrograms in Figure 1 are available in [Supplemental Data](#).

a male song followed by a female song (see [Figure 1A](#)). With minor adjustments in timing, females can either coordinate precisely with their partner’s signal ([Figure 1B](#)) or jam the signal ([Figure 1C](#)). Signal jamming may result in males abandoning their initial song prematurely, after which they often interject another song to form a triplet ([Figure 1D](#)). Occasionally, females jam the second male song to form a quadruplet. In both these cases, the regular pattern of couplets in a duet is disrupted by a shortened male song and a much reduced interval between the end of the female song and the beginning of the next male song (the “duet interval”). These permutations of duet structure suggest that temporal coordination is reflected by variance in song overlap, whereas duet complexity is reflected by variance in duet interval ([Figure 1](#)). Hence, we use these measures as indices of duet structure.

The extent to which females influence male behavior can be inferred from the temporal patterning of duets. Under natural conditions, couplets consisted of 6.5 ± 0.3 (mean \pm SE) male notes and 6.9 ± 0.2 female notes, with the female song jamming 2.8 ± 0.3 notes of the male song. The time taken for females to respond to their mates’ songs (the “response time”) varied from 1.2 to 2.8 s, with a mean of 1.8 ± 0.1 s. As response time declined, the number of male notes jammed by female

song increased (general linear mixed model [GLMM]: $F_{1, 94.3} = 1272$, $p < 0.0001$), and the total number of male notes contributed to each couplet decreased ($F_{1, 93.2} = 236.96$, $p < 0.0001$). Thus, short response times were significantly associated with greater jamming of male notes ([Figure 2A](#); [Table S1](#), available online). Males, in turn, adjusted their behavior in response to jamming: the more extensive the interference, the more quickly they abandoned their initial song ([Figure 2B](#)) and commenced the next song ([Figure 2C](#)). As a result, jamming significantly reduced duet intervals ($F_{1, 47.2} = 10.61$, $p = 0.002$; [Table S2](#)). We established that this effect was caused by female behavior, rather than by any other factor shortening male songs, because duet intervals were not related to the number of notes produced in the preceding song when males were singing solo ($F_{1, 45.8} = 2.85$, $p = 0.511$).

On one hand, these findings demonstrate that temporal coordination within antbird duets is controlled largely by females, because they can jam their mate’s signal by responding quickly. On the other, they suggest that males react to jamming with a counterstrategy of jamming avoidance. This evasive tactic is consistent with the ideas that overlapping noise always reduces the information content of acoustic signals [30] and that competition between signalers, therefore,

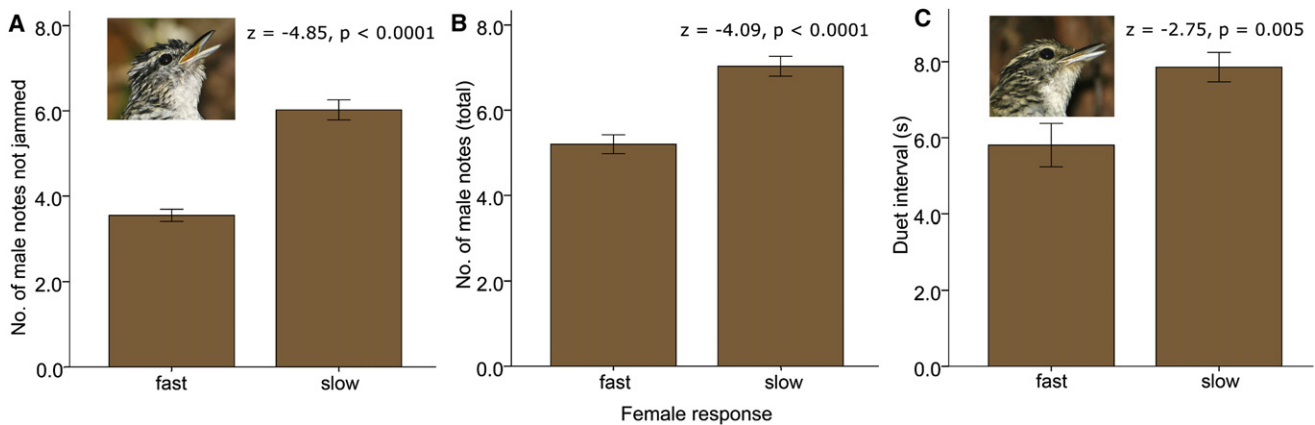


Figure 2. Effect of Signal Jamming on the Structure of Natural Duets

Comparison of the effects of fast (<1.5 s; $n = 12$ pairs) versus slow (>1.5 s; $n = 18$ pairs) female responses on duet structure, including variation in (A) the number of unjammed male notes per couplet, (B) the total number of male notes per couplet, and (C) the interval between the end of the female song and the beginning of the next male song. Fast response times were significantly associated with (A) increased jamming, (B) lower vocal output by the male, and (C) shorter “duet intervals.” Data are presented as mean \pm SE; statistics are from Mann-Whitney U tests; effect sizes for all comparisons are presented in Table S4. Insets show singing male (upper) and female (lower).

occurs over access to “acoustic windows” [31] or “signal space” [32]. The novelty of our finding rests in the demonstration that competition for signal space may operate within coalitions and between sexes. Testing how this competition is related to conflicts of interest and whether those conflicts modify signaling strategies requires an experimental approach.

Examining the Roles of Cooperation and Conflict

We used playback experiments on 17 individually marked pairs to simulate territorial intrusions by rival pairs and solitary females. We assumed that the threat from paired intruders was symmetrical, because both male and female residents stood to lose their shared territory. Conversely, we assumed that the threat from solitary intruders was asymmetrical, because an unpaired female represents a risk to the resident female and an opportunity for the resident male. This view is supported by high rates of divorce in antbirds [33], along with evidence of extrapair copulations and occasional polygamy (Seddon et al., unpublished data). Therefore, we expected the duet treatment to elicit a cooperative response and the female solo treatment to elevate the level of conflict between the sexes. This experimental design allowed us to assess the role of cooperation and conflict in shaping duet structure [16, 18].

We found that resident pairs responded to playback of rival pairs by producing equally coordinated but less complex duets, when compared with behavior recorded under natural conditions (Figure 3). After playback of female solos, however, resident females responded to more of their mates’ songs (Figure 3A) and jammed a greater proportion of notes (Figure 3B) than they did under natural conditions or after playback of duets. Duets given in response to female solos also showed greater variation in both degree of song overlap (Figure 3C) and duet interval (Figure 3D) than those given in response to playback of duets. In other words, pairs produced simpler, more rhythmic, and more precisely coordinated duets when threatened by intruding pairs, but duet coordination broke down and duet complexity increased when females were threatened by solitary rivals. We again found a positive association between jamming and duet interval ($F_{1,440} = 68.7, p < 0.001$), regardless of playback treatment (the interaction term

“jamming \times treatment” had no significant effect: $F_{1,433} = 0.17, p = 0.678$; Table S3).

Multiple Contexts, Flexible Strategies

Our results reveal that duet contributions of male and female antbirds varied according to context. When resident pairs faced a symmetric threat, the strategies of both sexes converged toward precise temporal coordination. However, when faced with an asymmetric threat, their strategies diverged; males attempted to signal normally and females jammed their mates’ signals. Divergent strategies presumably reflect conflicting fitness outcomes because, in the presence of an unpaired female, male antbirds theoretically increase fitness through extrapair copulation, polygamy, or switching to higher quality mates, whereas females are more likely to increase fitness by protecting their position in monogamous partnerships.

Conflict between the sexes over signaling decisions is likely to be widespread in coalitions, and indeed, it would appear to be inescapable wherever territorial displays double up as mating signals. In most birds, for example, songs typically function in both resource defense and mate attraction [34]. This dual function may explain the variable signaling strategies revealed by our experiments and reported more broadly in avian duets [18, 19, 21]. Turning this argument around, we expect signals to be less complex and signaling strategies to be less flexible in coalition displays with a single function. This may explain the coordinated snapping of *Synalpheus* shrimps [2], which appears to serve entirely in colony defense, as well as the stereotyped call-and-response duetting of insects, which functions purely in courtship [35]. Similarly, a lack of intersexual conflict between signalers may explain the synchronous signals of *Neoconocephalus* katydid and *Pteroptyx* fireflies [36, 37], which arise from cooperation or competition between displaying males [38].

Duets as Joint Signals Structured by Jamming Avoidance

Jamming is widely considered a potent force shaping animal signals [26, 31, 39], whereas jamming avoidance has been postulated as a fundamental mechanism structuring communal displays [6]. In agreement with these ideas, there is increasing

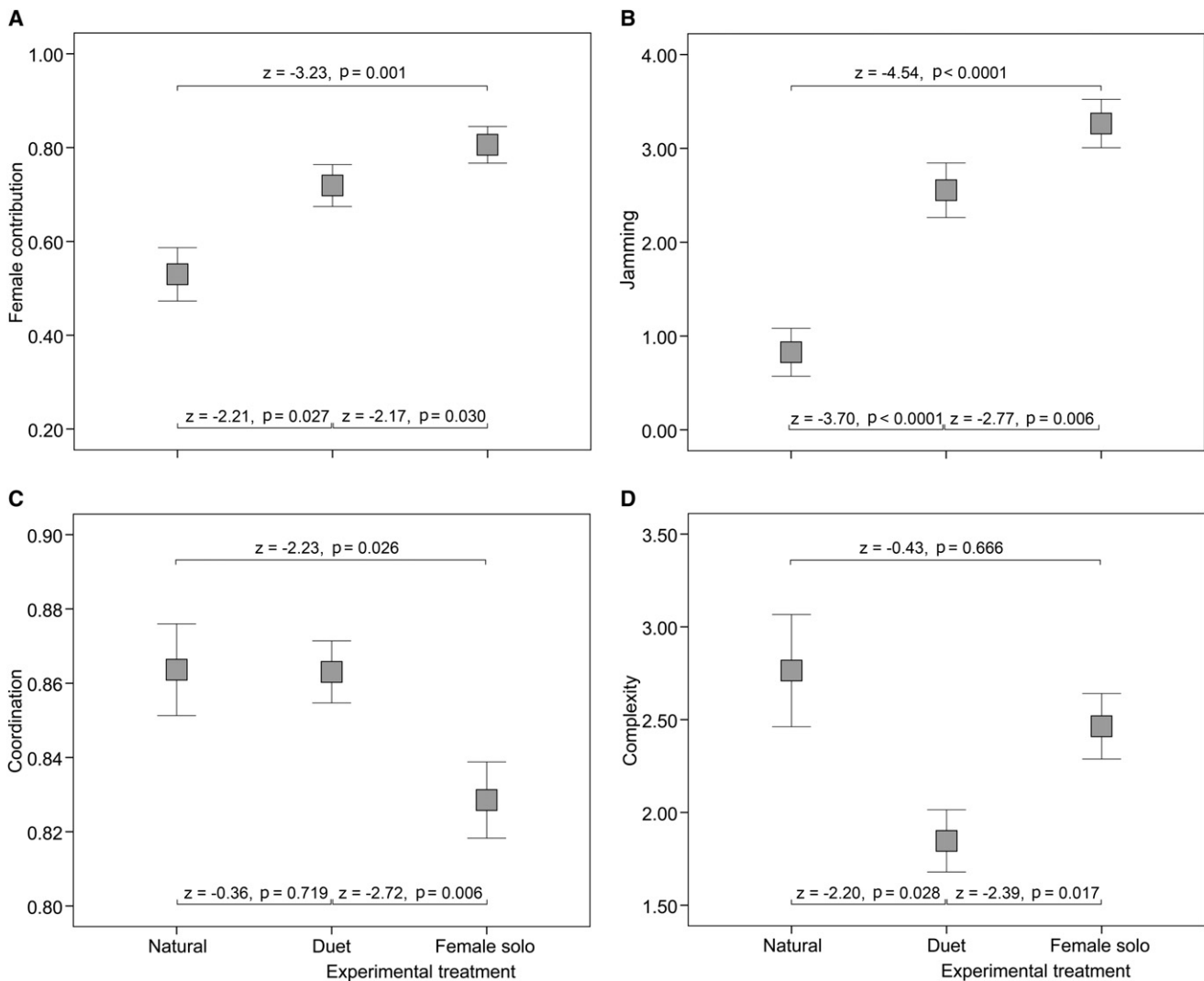


Figure 3. Effect of Context on Duet Coordination and Complexity

Variation in (A) the proportion of male songs replied to by the female, (B) the extent of jamming by the female, (C) duet coordination, and (D) duet complexity in relation to three contexts. Jamming was measured by subtraction of the number of notes that a male was able to sing before interruption by the female from the mean number of notes in a male solo song. Coordination was calculated as the standard deviation in “degree of overlap” (we subtracted this value from 1 so that higher values signified greater duet coordination, thus facilitating interpretation). Complexity was measured by standard deviation in “duet interval.” The results reveal a significant (C) decrease in duet coordination and (D) increase in duet complexity after playback of female solos as compared to playback of duets. Complexity is high under natural conditions (D) because of variable duet intervals when subjects are foraging. Data are presented as mean \pm SE; statistics are from Wilcoxon signed-rank tests of comparisons among duet and solo treatments and Mann-Whitney U tests of comparisons between natural and experimental conditions (n = 20 pairs for natural bouts of duetting; n = 17 pairs for experimental treatments). Effect sizes for all comparisons are presented in Table S5.

evidence that signal overlapping has a manipulative or aggressive function during territorial interactions [39, 40] and that signalers perceive overlapping as costly [30]. However, our finding that male antbirds attempt to evade overlap by abandoning jammed songs and interjecting extra songs provides the first demonstration of jamming avoidance in a communal signal. It confirms that individuals of one sex have the incentive and ability to avoid jamming by the other sex and that this process can lead to increased signal complexity.

The discovery that duetting birds compete over signal space suggests that, even in cooperative contexts, the precise coordination of communal signals may arise as the inevitable outcome of jamming avoidance. This view is supported by the observation that most animal duets are alternating or

antiphonal rather than synchronous [7, 16, 35]. Evidence for the alternative hypothesis that temporal coordination evolves as a signal of coalition quality [5] is further weakened by our finding that duet structure is an ephemeral, context-dependent trait, which is perhaps unlikely to serve as an honest signal of quality. The variation that we detected may also help to explain why coordination is not usually correlated with the duration of partnerships [6, 17, 41], contrary to the predictions of the honest-signaling hypothesis.

Conclusions

Our results show that the duetting behavior of antbirds is influenced by the level of cooperation and conflict operating within

coalitions. They further suggest that conflict can lead to signal jamming, as well as strategies to avoid jamming, thereby increasing complexity in joint displays. We conclude that an interaction between cooperation and conflict mediated via two simple mechanisms—jamming and jamming avoidance—can explain the evolution of sophisticated communal signals. Our findings may therefore shed light on the processes giving rise to spectacular duets and choruses in social apes [3, 4] and birds [1], and they may perhaps even provide a clue to the origins of dance and music as human traits [42, 43].

Experimental Procedures

Study Site and Species

We studied 27 color-banded pairs of Peruvian warbling-antbird, a sexually dimorphic passerine bird occurring in lowland rainforests of western Amazonia [29]. In this species, males and females defend shared territories year round and spend much time consorting <10 m apart (Seddon et al., unpublished data). We estimated the position of pair-territory borders by visually tracking birds during focal watches, gathering GPS coordinates of positions where pairs were observed, then drawing minimum convex polygons around these points. Fieldwork was carried out at the Centro de Investigación y Conservación de Río Los Amigos (CICRA; 12°34'S, 70°06'W), Madre de Dios, Peru, from August to December 2006.

Acoustic Analyses

Duets were defined as a bout of singing by paired males and females. Both sexes produced a single distinctive song type, such that male song was easily distinguished from female song [19, 29]. All duets could be broken down into male-initiated phrases, separated by ~5 s pauses (Figure 1A). Each phrase consisted of a solo (one male song), a couplet (male-female), a triplet (male-female-male), or, rarely, a quadruplet (male-female-male-female). We recorded duets in natural (i.e., nonexperimental) conditions and after playback of female song (see below). Duets contained 6.8 ± 0.5 phrases under natural conditions ($n = 20$ pairs; 26 duets in total), and 16.5 ± 0.8 phrases after playback ($n = 17$ pairs; 34 duets in total). This provided a sample of 177 phrases from natural duets and 560 phrases from postplayback duets.

Using broad-band spectrograms generated from duet recordings (see Figure 1), we quantified the incidence of solos and couplets. Triplets and quadruplets were treated as couplets, and no data were collected from the third or fourth songs in the phrase. From each couplet we measured (1) number of male notes, (2) number of female notes, (3) number of notes a male sang before interruption by the female, (4) proportion of male notes overlapped by female notes ("degree of overlap"), (5) interval between the beginning of the male song and the beginning of the female song (the "response time"), and (6) interval between the end of the female song and the beginning of the next male song (the "duet interval").

Because interrupted males often abandon their songs (Figure 1D), "degree of overlap" does not adequately capture the extent to which a female jams her partner's signal. Therefore, to quantify "jamming" within each couplet, we subtracted the number of notes that a male was able to sing before interruption by the female from the mean number of notes in a male solo song—i.e., the number of notes that we assume the male would have produced had the female not interrupted. We calculated duet coordination as the standard deviation in "degree of overlap," and we calculated duet complexity as the standard deviation in "duet interval."

Playback Experiments

To test whether the type of threat to partnerships influences the structure of duets, we presented 17 pairs with two treatments: a female solo and a duet. Each playback cut lasted 1 min and contained four solo or duet repetitions given by a unique individual or pair (for avoidance of pseudoreplication). The duet treatment consisted of a tightly coordinated natural duet with minimal overlap between male and female songs (e.g., Figure 1B). Successive treatments on the same pair were separated by an interval of 2–3 days and were conducted at a similar location (within 20 m) and time of day (within one hour). Songs were played through a loudspeaker placed ~0.5 m above, 15–20 m away from subjects and at least 30 m from territory boundaries. Each treatment lasted 10 min (1 min of playback, followed by 9 min of silence).

Statistical Analyses

Relationships among duet-structure variables 1–6 were examined with the use of normally distributed GLMMs with pair identity included as a random effect (for full models, see Supplemental Data). The effect of playback treatment on duet coordination and complexity was examined with the use of Wilcoxon signed-rank tests. The extent to which natural levels of duet coordination and complexity differed from those given after playback was investigated with the use of Mann-Whitney U tests. GLMMs were undertaken with Genstat 11.01; all other statistical tests were carried out in SPSS 16.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, three tables with the full models for each GLMM analysis, and audio files for all spectrograms shown in Figure 1 and are available with this article online at [http://www.current-biology.com/supplemental/S0960-9822\(09\)00746-5](http://www.current-biology.com/supplemental/S0960-9822(09)00746-5).

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