# Calling in an acoustically competitive environment: duetting male long-tailed manakins avoid overlapping neighbours but not playback-simulated rivals

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Animals that live in communication range of multiple conspecific receivers have the potential to interfere with their neighbours' signals, or to avoid interference by signalling at different times. We used both an observational and experimental approach to study signal timing in lekking tropical birds. We recorded duetting pairs of male long-tailed manakins, *Chiroxiphia linearis*, during periods when two neighbouring pairs were calling concurrently, and during playback of a simulated pair of nearby rival males. We used three complementary analytical techniques to evaluate whether birds varied the timing of their duet calls relative to nearby animals: circular statistics, resampling analysis and duty cycle models. Our analyses reveal that long-tailed manakins produce duets with nonrandom timing with respect to the calls of their rivals. During natural bouts of concurrent calling, all three analytical techniques revealed that manakins time their duets to avoid overlap. In response to playback, males showed more variable strategies. Males overlapped duets more during playback than they did under natural conditions and, in some cases, they overlapped playback duets at higher levels than would be expected based on chance. Our study shows that males alter the timing of their calls in response to the vocalizations of others around them, and it uncovers similarities in the acoustic signalling behaviour of lekking birds relative to the better-studied signalling behaviour of territorial birds. We also show that different null models of signal timing yield different insights into animal signalling behaviour.

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When animals live within communication range of multiple receivers, social factors can have a strong influence on signalling behaviour. Most animals produce long-range communication signals, especially in mating and territory defence contexts (Bradbury & Vehrencamp 2011). These signals can transmit long distances, often beyond the average spacing between individuals, thus creating many opportunities for interference (McGregor 2005). One form of interference is the temporal overlapping of signals. While overlapping can occur as a result of chance alone (Searcy & Beecher 2009), many animals vary the timing of signal production either to increase or decrease interference with other signallers (Schwartz 1987; Greenfield 1994a; Gerhardt & Huber 2002; Naguib & Mennill 2010). The strategies animals use to modify interference can vary with species (Schwartz 1987), population (Höbel & Gerhardt 2007), signal modality (Carlson & Copeland 1985; Johnston et al. 1997) and context (Greenfield 1994b; Schwartz et al. 2002), and can have important fitness

consequences for the individuals involved (Greenfield 1994a; Mennill et al. 2002; Miyazaki & Waas 2002; Amy et al. 2008; Garcia-Fernandez et al. 2010).

There are at least six main reasons why animals might overlap each other's signals (reviewed in Greenfield 1994b; Todt & Naguib 2000; Naguib & Mennill 2010). (1) Overlapping may be an agonistic signal that is an important part of countersignalling exchanges (e.g. for songbirds, overlap appears to be associated with threat and contest escalation; reviewed in Naguib & Mennill 2010; but see Searcy & Beecher 2009, 2011 for an alternate perspective). (2) Overlapping may occur when animals are tightly spaced and must either produce overlapping signals or else decrease their signal output (e.g. in a chorus of toads or a cluster of fireflies; Brush & Narins 1989; Greenfield 1994b). (3) Overlapping signals may make it more difficult for predators to detect a single individual, so that producing an overlapping signal is less risky (e.g. some hylid frogs are more susceptible to predation by bats when they produce alternating calls; Tuttle & Ryan 1982). (4) Females may respond to males' mating signals with signals of their own, and female responses may be easier to detect in the silent intervals between synchronized, overlapping signals (e.g. male and female fireflies exchanging bioluminescent flashes; Buck & Case 1986). (5) Females may assess males on their ability to synchronize signals with other

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nearby males, selecting for overlapping calls (e.g. grey treefrog females prefer the leading males in simulated overlapping contests; Marshall & Gerhardt 2010). (6) Alternatively, overlap may occur by chance if individuals produce signals without reference to the timing of signals of other nearby animals (Moore et al. 1989; Searcy & Beecher 2009, 2011).

There are at least four main reasons why animals might avoid overlap by producing signals in the silent intervals between the signals of nearby animals. (1) Alternating may communicate decreased threat or a de-escalation of aggressive contests (reviewed in Naguib & Mennill 2010). (2) Alternating may allow individuals to broadcast their signal with minimal interference by animals around them (Narins 1992; Schwartz 1993; Greenfield 1994b). (3) For some signals, such as acoustic signals, animals may not be able to produce a signal and detect the signals of others simultaneously; mutual listening may therefore favour signal alternation (Schwartz & Rand 1991). (4) Females may be attracted to signals produced at a higher duty cycle (i.e. proportion of time spent signalling) and since groups that alternate their signals will have higher duty cycle than groups that overlap, selection may favour alternation (Greenfield 1994b).

The acoustic signals of birds have been well studied from the perspective of signal timing. More than 30 observational and experimental studies have documented overlapping behaviour in many species of birds (reviewed in Naguib & Mennill 2010). While the signal function of overlapping is contentious (Searcy & Beecher 2009, 2011), the fact that overlapping is associated with specific behaviours suggests that participants may adjust their responses based on the outcome of overlapping exchanges and use these exchanges to inform their subsequent behaviour (Naguib & Mennill 2010). Overlapping appears to have wide-ranging effects on the behaviour of wild birds, and understanding whether or not it is a directed signal is an important area for research.

In this study we explore call timing in male long-tailed manakins, *Chiroxiphia linearis*. We ask whether males actively avoid signalling at the same time as other males, or whether they interfere with each other's vocalizations by overlapping them. To address this question we used both an observational approach and a playback experiment. We used stereo digital recorders to monitor the timing of signals during naturally occurring bouts of calling by neighbouring manakins. We then conducted a playback study where we used playback to simulate rivals near established birds' display areas. During both the natural bouts of calling and playback-simulated bouts of calling, we determined whether males varied the timing of their calls with reference to others, and compared the level of overlap to levels expected by chance. No single null model for predicting chance levels of overlap has been established (Popp 1989; Searcy & Beecher 2009, 2011; Naguib & Mennill 2010); therefore we analysed the natural and experimental recordings using three complementary approaches to determine whether calls were spaced nonrandomly, and whether overlapping differed from levels expected based on chance.

## METHODS

### Study Site and Study Species

We conducted this study in Sector Santa Rosa within the Guanacaste Conservation Area in northwestern Costa Rica (10°53′N, 85°46′W). This conservation area houses the world's largest remaining stand of Neotropical dry forest and has been designated as a World Heritage Site by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Sector Santa Rosa is home to a large population of individually marked long-tailed manakins that have been studied in detail since 2003 (Doucet

et al. 2007). Since 2003, we have outfitted 675 long-tailed manakins with aluminium leg bands and a unique combination of coloured leg bands to aid in identification, and monitored the display behaviour of males and the mating behaviour of females.

Long-tailed manakins are suboscine songbirds with a lek-based mating system, where males form obligate male–male partnerships and attract females using a combination of coordinated male–male vocal duets and visual displays (McDonald 1989a; Trainer & McDonald 1995). In many other animals, vocal duets are produced by the male and female of a mated pair (reviewed in Hall 2004; Douglas & Mennill 2010). Long-tailed manakins and some of their congeners are unusual in that their highly coordinated duets are performed by pairs of unrelated males (McDonald & Potts 1994; Prum 1994; DuVal 2007). Long-tailed manakin duets consist of nearly identical phrases produced by the two males, onomatopoeically similar to the word 'toledo', where each phrase is approximately 0.6 s in length and the two males' contributions are synchronized within 0.1 s of one another (Fig. 1a). Males repeat duets every 2.5–4.0 s for extended bouts of calling, and may produce as many as 1000 duets/h (Trainer & McDonald 1995). Male–male pairs call from fixed display areas that remain consistent over many consecutive years (Foster 1977; McDonald 2010). Pairs of males from adjacent display areas tend to be visually isolated from one another by distances of approximately 75 m, but can be as close as 25 m (Trainer & McDonald 1993; D. F. Maynard, K. A. Ward, S. M. Doucet, D. J. Mennill, personal observations). Their vocal signals transmit upwards of 100 m (D. F. Maynard & D. J. Mennill, personal observations), and as a result, neighbouring pairs are routinely in acoustic contact. Consequently, pairs of long-tailed manakins attract females in an acoustically competitive environment. This sets the stage for acoustic interference to influence the signalling behaviour of neighbouring pairs of males.

We located manakin display areas by listening for pairs of males performing vocal duets and then locating the low horizontal branches (display perches) where males perform elaborate dances for prospecting females (McDonald 1989a). We captured birds using mist nets placed near display areas and outfitted birds with coloured leg bands. Not all birds in the study population were banded, yet observations of the colour-banded males demonstrate that the same birds routinely call from the same display areas. Based on this observation, as well as the background information on long-tailed manakin behaviour collected over two decades of field study by D. McDonald (see McDonald 2010), we are confident that the male–male pairs observed at each display area were unique.

### Natural Bouts of Concurrent Calling

We recorded natural instances of concurrent calling between neighbouring pairs of males between 14 April and 24 May 2010. We used a stereo-recording apparatus positioned between two adjacent display areas. We deployed recorders between 0500 and 0700 hours in the morning and allowed them to run continuously, usually finishing between 1200 and 1400 hours. Given that sound propagates slowly through air, we could exploit time-of-arrival differences between the two microphones to assign calls to the pairs of males on either side of the recording apparatus. Our recording system consisted of two omnidirectional microphones (Sennheiser ME62/K6) connected to a solid-state digital recorder (Marantz PMD670; 22050 KHz, 16 bits, WAVE format, stereo recording). We placed one of the microphones near a pair's display area, approximately 10 m from the primary display perch, and the other microphone 15 m away in the direction of the nearest neighbouring display area. We attached both microphones to trees and suspended them approximately 2 m above the ground. This
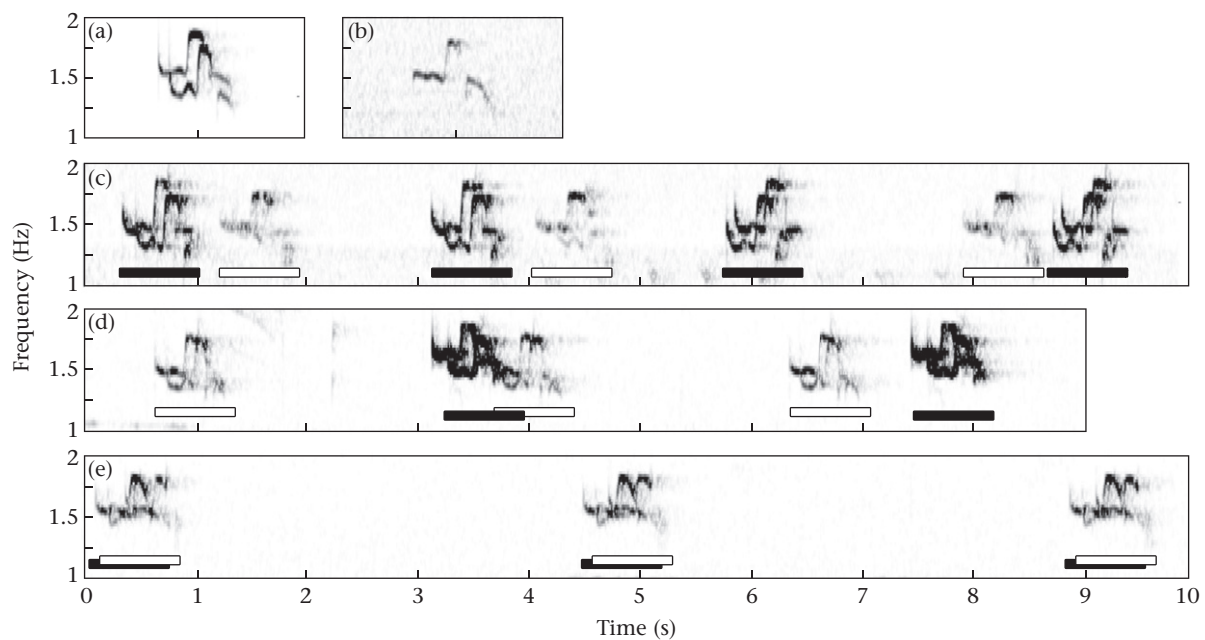
**Figure 1.** Sound spectrograms depicting the toledo calls of male long-tailed manakins, *Chiroxiphia linearis*. (a) A typical duet, composed of tonal calls of a pair of males produced in near perfect synchrony. (b) A solo call, produced by a lone male. Solo calls are uncommon, but occurred in 15% of playback trials. (c) Spectrogram of two pairs of manakins at adjacent display areas. The vocalizations from one pair of males are underscored in black bars and the other in white bars. In this bout of naturally occurring concurrent calling, the two males produced duets in the silent intervals between each other's calls. (d) Spectrogram showing playback stimuli (black bars) and the responses of a pair of manakins (white bars). In this bout of calling, the playback subjects overlapped one call from the playback. (e) Spectrogram showing playback stimuli (black bars) and the solo calls of a lone manakin that overlapped the playback stimuli (white bars). These recordings were collected with the omnidirectional microphones described in the Methods, resulting in low signal-to-noise ratios.

recording system is an extension of the system described in Hill et al. (2006), except that we collected recordings in stereo, rather than monaural.

At each recording location, we remained in the area immediately following set-up of the recording apparatus. For approximately 1 h we made notes on the locations of calling males, allowing us to ground-truth that the stereo recording apparatus could provide reliable information on which pair of birds was calling. We found 100% agreement between our observations in the field (i.e. which pair of males produced which vocalization) and the direction that we determined based on differences in arrival times in the stereo recordings. Consequently, we are confident that this apparatus allowed us to reliably assign duets to the correct pair of males during bouts of concurrent calling.

We used Syrinx-PC Sound Analysis Software (J. Burt, Seattle, WA, U.S.A.) to annotate the stereo recordings of natural bouts of concurrent calling between adjacent pairs of males. We restricted our analyses to instances where the two pairs of males were calling in the absence of any other more distant males. It has been suggested that many species only space their calls relative to their nearest/loudest neighbours (Brush & Narins 1989; Schwartz 1993; Greenfield 1994a). For example, Moore et al. (1989) showed that white-lipped frogs, *Leptodactylus albilabris*, adjust the spacing of their calls to alternate with their nearest neighbours. We therefore restricted our analyses to instances where only two pairs of males were calling concurrently. To ensure that our measurements were taken from bouts of concurrent calling, and not one-off calls from either pair of males, we further restricted analyses to instances where both pairs sang at least 10 duets, where successive duets were at most 10 s apart. We recorded at 27 different locations, but had to discard 14 because there was no suitable period where both the neighbouring pairs produced a bout of 10 duets in the absence of other pairs. Bouts of concurrent calling are common in this species.

Our detailed analyses are based on 13 instances of concurrent calling between neighbouring pairs of males. Each dyad was unique, but six of the 26 pairs were involved in two comparisons. We consider each dyad to be the relevant unit of sampling because concurrent calling is a dynamic process where the response of one pair of individuals is not independent from the response of the other pair of individuals; in this sense the relationship of A to B can be considered different from that of A to C. We also analysed a subset of our data where each particular male was only measured once, and the same patterns that we report in the Results held true with respect to statistical significance and the direction of the relationship.

*Playback Experiment*

We conducted playback trials to simulate a pair of duetting males, allowing us to experimentally test how birds space their calls relative to others. We created nine playback stimuli from recordings collected between 0500 and 0700 hours during 28 April–3 May 2008–2010 from males that were unlikely to have previously encountered the males receiving playback (stimulus birds were recorded more than 4 km away from subjects). We collected recordings from pairs of definitive males using a directional microphone (Sennheiser MKH70) and digital recorder (Marantz PMD660; 22050 kHz, 16 bit, WAVE format, mono recording). From recordings at each of nine different display areas, we selected a single duet with high signal-to-noise ratio (assessed visually) where the recordings were collected within 10 m of the calling males. To present the sound with the minimum amount of background noise, we used Audition software (Adobe Systems Inc.) to reduce background noise by selecting the duet with the lasso tool and decreasing the amplitude of the background noise to 1/20th of its original level. We then normalized the sound file to -1 dB. We used these normalized stimuli to create playback stimuli where the

sound was repeated with 2.4 s or 3.5 s of silence between duets (see below), and stored the stimuli as uncompressed sound files (22 050 kHz, 16 bits, WAVE format). We repeated this process to create nine unique duet stimuli that shared identical amplitude characteristics.

A pilot investigation in early 2010 suggested that males change their intercall interval when calling concurrently with other males. To assess whether this affected a pair's tendency to overlap or alternate, we created two versions of each stimulus: a 'slow rate' stimulus consisting of a duet followed by 3.5 s of silence, and a 'fast rate' stimulus, which consisted of a duet followed by 2.4 s of silence. Under natural circumstances when calling in the absence of other males, our recordings showed that long-tailed manakins spaced their calls with intercall intervals of $2.4 \pm 0.1$ s (mean $\pm$ SE; $N = 19$ display areas with a response during the preplayback period; range 1.7–3.4 s). Comparatively, when calling concurrently with playback-simulated males, long-tailed manakins tended to space their calls with intercall intervals of $2.7 \pm 0.1$ s (mean $\pm$ SE; $N = 26$ display areas with a response during the playback period; range 2.0–4.1 s). Therefore, our fast-rate playback was the most similar to the rate we observed under natural conditions in the absence of other concurrently calling males; while our slow-rate playback was more similar to the rate during bouts of concurrent calling, and was within the range of calling rhythm we have observed in wild birds. These two treatments allowed us to test whether males are sensitive to different call timing in their opponents.

The playback device (Apple iPod classic) was operated by an observer who sat 10 m from the loudspeaker (Anchor Audio Mini-Vox PB-25, Torrance, CA, U.S.A.; frequency response: 100–12 000 Hz). The loudspeaker was mounted on a 1.5 m pole and placed within the subjects' display area, 5–10 m from their display perch. The amplitude of the playback stimulus was held constant across all trials at 80 dB (measured at a horizontal distance of 1 m from the upwards-oriented speaker using a RadioShack 33-2050 sound level meter; fast response setting, C-weighting). This matched our perception of the source amplitude of live duetting males in this forest, based on comparison between the loudspeaker and calling males at equal distances. Long-tailed manakins produce their joint duets while perched within 10 cm of one another (Trainer & McDonald 1993). As such, it is unlikely that playback through a single speaker, rather than a stereo apparatus, would alter the responding males' behaviour.

Playback trials were conducted between 0530 and 1030 hours, a time when natural bouts of duetting were common. After setting up the playback apparatus, but before commencing a trial, we recorded the focal males until they had produced a bout of at least 10 duets (i.e. 10 duets produced in repetition with intercall intervals of less than 10 s) or 30 min had elapsed, whichever came first. We then waited until 10 s of silence had elapsed before commencing playback. By waiting 10 s after a duet from a focal pair, we were able to consider any vocalizations they produced to be a new bout. We repeated the playback stimuli until the focal males produced 10 or more duets in the absence of other neighbouring males' duets (mean $\pm$ SE $= 12 \pm 1$ min, $N = 39$ trials where birds responded). Playback continued until the focal males stopped calling and became silent for 10 s. Once playback stopped, we recorded the males' vocalizations for an additional 15 min. Throughout playback trials we made note of approaches and the behaviour of responding males, although the thick vegetation at this tropical site (Mennill & Vehrencamp 2008) made direct visual observation challenging in some cases.

We conducted 52 playback trials at 32 display areas. At each site we assigned one of the nine playback stimuli (random selection without replacement until all nine stimuli had been used). We randomly assigned whether each subject received a 'slow' or 'fast'

playback rate. For 20 of the 32 display areas, we returned to the site on a different day (mean $\pm$ SE $= 4.5 \pm 0.8$ days later) and broadcast the same stimuli at the alternate rate; we ensured that these trials were conducted at the same time of day, within 1 h, to minimize any influence of time of day on calling behaviour. To prevent desensitization we avoided conducting playback at the same site or adjacent sites within the same 48 h period. In 13 of the 52 trials the males did not produce 10 duets in a row, reducing our final sample size to 39 trials at 24 separate display areas.

We recorded all playback sessions using autonomous digital recorders (Wildlife Acoustics' Song Meters 22050 kHz, WAVE format, 16 bit, stereo recording). These recorders were placed 3–10 m away from the playback speaker. The fine structural details of the stimulus and its known timing allowed us to discriminate between playback stimuli and male responses.

*Data Analysis*

Which null model is most appropriate for determining whether animals space their signals nonrandomly is a controversial topic (see Searcy & Beecher 2009, 2011; Naguib & Mennill 2010). Research on invertebrates and anurans has often involved circular statistics and phase response curves (e.g. Greenfield 1994a, b). Some research on anurans, cetaceans and birds has involved a resampling approach (e.g. Popp 1989; Schwartz et al. 2002; Miller et al. 2004; Fitzsimmons et al. 2008; Schulz et al. 2008), or duty cycle models to estimate chance levels of overlap (Ficken et al. 1974; Searcy & Beecher 2009). Given the diversity of null models for estimating call timing and chance levels of overlap, and the fact that each model can provide different information, we opted to use three complementary approaches to assess whether pairs of male long-tailed manakins space their duets nonrandomly relative to one another, to increase or decrease levels of overlap: (1) circular statistics, (2) resampling analyses and (3) duty cycle calculations. The circular statistics approach allowed us to assess whether males called nonrandomly relative to one another and accounted for the cyclic nature of calling bouts. The resampling approach, in contrast, allowed us to assess whether overlapping is more or less frequent than expected if males are calling without reference to one another while maintaining the same call rate. Finally, the duty cycle approach allowed us to assess whether the total number of overlaps and the amount of call overlap differed from that expected based on the total amount of vocal output from both groups of males.

In our analysis of playback trials, we treated the playback sounds as the reference against which the natural males' response was measured. In naturally occurring bouts of concurrent calling, there is no obvious reference pair of males, because the two pairs of males call back and forth in succession. We arbitrarily chose a reference pair in natural bouts of concurrent calling, assigning the pair of males that produced the final duet within a bout of calling as the reference pair, and collected measurements relative to this pair. We then reanalysed each interaction, treating the other pair of birds as the reference pair. We only report the results of the first of these analyses here, but the reciprocal analysis showed an identical pattern in terms of both directionality and statistical significance at all levels of analysis.

*Null model 1: circular statistics*

To calculate the timing of each duet relative to the reference males we performed circular statistical calculations following the methods outlined in Zar (1999).

$$A = \frac{360(X - R_1)}{R_2 - R_1} \tag{1}$$

where $A$ is the degrees between the onset of the responding males' duet and the last duet from the reference males; $X$ is the time of the onset of the response of interest (in this case the duet of the responding males); $R_1$ is the time of the onset of the reference males' duet preceding the responding males' duet; and $R_2$ is the time of onset of the next duet from the reference males. A value for $A$ of 180° would represent a duet from the responding males that began exactly halfway between two successive duets from the reference pair; a value of 10° would represent a duet from the responding males that began shortly after the onset of a duet from the reference pair; and a value of 350° would represent a duet from the responding males shortly before that of the reference males' next duet.

To calculate the average response for each trial we converted $A$ to $X-Y$ coordinates by taking the sine ($X$ coordinate) and cosine ($Y$ coordinate) of the angle $A$. By taking the average of the $X$ and $Y$ points for each recording we were able to calculate an average response for each pair of males (Zar 1999). We plotted this on a circular graph (see Results, Figs 2–4), where the angle from the origin represented the average timing of the responding males relative to the reference pair's duets (analogous to $A$ described above), and where the distance from the origin ($r$) represented the consistency of call spacing ($r$ varies from 0 to 1; a value of 1 would mean males were invariant in where they spaced their duets relative to the reference males' duets, while a value of 0 would indicate that males were timing calls randomly). We then calculated the 'mean of the means' by taking the average across all of our recordings, giving a mean angle and associated effect size for the population (Zar 1999). We then performed a parametric one-sample second-order analysis of angles to test the null hypothesis of no directionality as one would predict if males were calling randomly (Zar 1999). When the combined trials showed an effect that was significantly different from the null hypothesis of no directionality, we calculated 95% confidence limits for the second-order mean angle where possible (for circular statistics, confidence limit calculations are not possible when the 95% confidence interval exceeds 180°; Zar 1999).

To analyse playback responses using circular statistics, we repeated the method described above using the playback as the reference against which we judged the responding males. Interestingly, in six of the 39 trails where males responded, there was a playback period (>10 playback duets) where a lone male produced solo calls (Fig. 1b), in contrast to the typical response where both males responded with coordinated duets. Our preliminary observations suggested that these 'solo males' timed their calls differently, often overlapping the playback. We therefore chose to analyse solo responses separately from the duet responses. We analysed solo responses using only the circular statistics method of analysis; solo responses were not easily analysed with resampling or duty cycle techniques (see below) because they were produced infrequently and seldom continuously (Planck et al. 1975).

*Null model 2: resampling statistics*

Our resampling approach involved comparing the observed numbers and amount of overlap during bouts of concurrent calling (either naturally occurring, or in response to playback) to the amount of overlap during computer-simulated bouts of calling where the relative timing of calls had been altered by the addition of a fixed random interval. Again, we assigned the males producing the final duet as being the reference pair against which we measured the other pair. Keeping the timing of the calls of the reference pair fixed, we shifted the responding males' duets by a random amount of time, between zero and the average rate of the reference males' duets, in seconds (range 0–4.2 s). We then measured two features: (1) the total amount of time (in seconds) that overlapping of duets occurred in this manufactured bout of calling and (2) the total number of instances that calls overlapped within a single simulated bout. Using a macro (Microsoft Excel, 2007) we repeated this process 5000 times for each recording, varying the random number each time, to calculate a null distribution of the total amount of overlap. We calculated the median of the null distribution for each pair of males and then compared this to the observed value using a Wilcoxon signed-ranks test.

To analyse playback responses using a resampling approach, we followed the same method, assigning the playback duets to be the reference against which we judged the natural males' response. We calculated the number of overlaps as well as the total amount of overlap (i.e. playback overlapping responding males and responding males overlapping playback), and compared these to our null value using two separate Wilcoxon signed-ranks tests, one for slow-rate playback and one for fast-rate playback.

*Null model 3: duty cycle analysis*

We followed a modified version of the duty cycle methods outlined by Ficken et al. (1974) for determining the expected number of overlapping vocalizations (equation 2) and the amount of overlap in seconds (equation 3). We performed the same analyses for natural calling bouts and those simulated through playback. As far as we are aware, no previous study has used a duty cycle approach to calculate the amount of overlap; we elected to include such an analysis to facilitate a direct comparison to the resampling approach.

$$P_0 = N_A D_B + N_B D_A \qquad (2)$$

Here, $P_0$ is the total number of calls that would be expected to be overlapping if males called randomly with no reference to one another; $N_A$ is the total number of calls produced by the first pair of males; $D_B$ is the duty cycle, or proportion of time spent calling, of the second set of males; $N_B$ is the total number of calls produced by the second pair of males; and $D_A$ is the duty cycle of the first set of males. This equation determines the total number of times that A is expected to overlap B, plus the number of times that A is expected to be overlapped by B if A and B are calling with no reference to one another.

$$A_0 = T(D_A \times D_B) \qquad (3)$$

Here, $A_0$ is the total amount of time that the calls should overlap if males call randomly with no reference to one another; $T$ is the total duration of the exchange when both individuals are calling; and $D_A$ and $D_B$ are as described above. We compared the predicted numbers and amount of overlap based on duty cycle to the observed numbers using two Wilcoxon signed-ranks tests.

Given that neighbours were separated by distances of 25–75 m, that the speed of sound is approximately 352 m/s at 35 °C at 70% relative humidity (typical conditions in the mid-morning at our site at this time of year), and that manakin duets are 0.6 s long, the separation between pairs was not enough to cause time lags to influence the interpretation of our results.

*Behaviour during playback*

To characterize the responses of males to playback, we compared the interval between their calls during preplayback, playback and postplayback periods. We were interested in understanding whether males adjusted their calling rate in response to playback, and whether their calling rate varied with the two rates of playback. As explained above, the preplayback and playback period varied in length depending on the behaviour of the subjects. For this analysis, we focused on the first 10 consecutive duets (where

the time between successive calls did not exceed 10 s) of the pre-playback, playback and postplayback periods. Our response variable was the average intercall interval between the first 10 calls within a bout. We normalized this response variable using a log transformation, but present the raw values in our figures.

Circular statistics were calculated manually (in Microsoft Excel, 2007). All remaining statistical analyses were conducted in JMP v8 (SAS Institute, Cary, NC, U.S.A.). All analyses are two tailed and all values are reported as means ± SE.

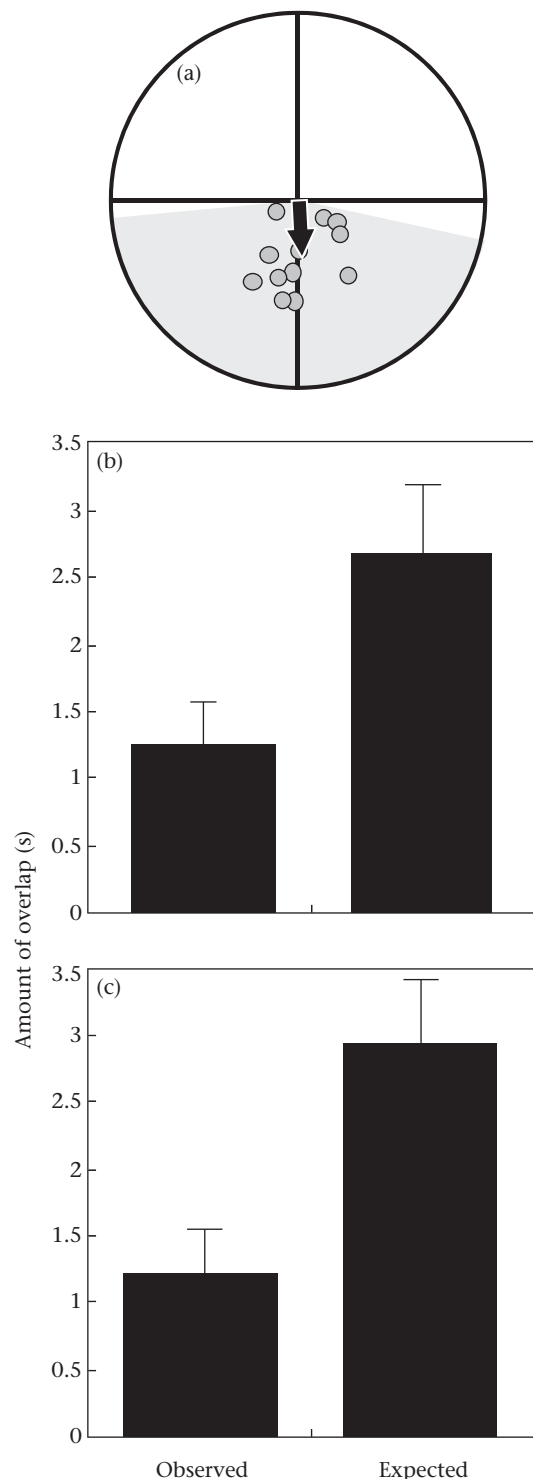## RESULTS

### Natural Bouts of Concurrent Calling

During natural exchanges between neighbouring pairs of duetting males, long-tailed manakins selectively called in the silent interval between their neighbours' duets (e.g. Fig. 1c). We used circular statistics to analyse these exchanges. We found a significant departure from the null model of no directionality (parametric one-sample second-order analysis of angles: $F_{2, 11} = 57.1$, $N = 13$ dyadic exchanges between neighbouring pairs of males, $P < 0.001$; Fig. 2a). The mean phase angle was 176.6° (Fig. 2a) with an $r$ value of 0.28, placing the average timing of calls almost perfectly out of phase with the reference males' duets. In other words, circular statistical analysis demonstrated that neighbouring pairs of long-tailed manakins alternate their calls during natural bouts of concurrent calling.

We used a second null model to evaluate call overlap using a resampling approach. This approach showed that the amount of overlap was significantly less than that expected by chance (Wilcoxon signed-ranks tests: Fig. 2b: $T = 45.5$, $N = 13$, $P < 0.001$), as was the number of overlaps ($T = 33.0$, $N = 13$, $P = 0.001$). Overlapping occurred at about half the level expected if males called at the same rate with no reference to one another. In other words, our resampling analyses supported the conclusion that long-tailed manakins avoid overlapping the duets of neighbouring males.

We used a third null model to evaluate call timing involving duty cycle calculations. This approach also showed that the amount of overlap was significantly less than that expected if males were calling randomly (equation 3; Wilcoxon signed-ranks test: $T = 45.0$, $N = 13$, $P < 0.001$; Fig. 2c) as was the number of overlaps (equation 2; $T = 45.5$, $N = 13$, $P < 0.001$). These analyses also support the conclusion that males overlap the duets of neighbours less than that expected under a null model of random calling.

### Playback Experiment

In contrast to their behaviour during natural bouts of concurrent calling, duetting male long-tailed manakins responded differently during playback of an unfamiliar pair of rivals in close proximity to their display area. Relative to playback duets, males called with substantial variability in timing (e.g. Fig. 1d). Circular statistics revealed that responses to playback of duets at a slow rate departed significantly from the null hypothesis of no directionality ($F_{2, 13} = 6.4$, $N = 15$ pairs receiving slow-rate playback, $P = 0.01$; Fig. 3a). The average phase angle was 171.2°, representing males calling near the middle of the silent interval between playback duets, on average; yet the strength of this relationship was weak ($r = 0.03$) indicating substantial variation in the timing of calls (Zar 1999). Similarly, responses to playback at the fast rate showed a significant departure from the null hypothesis of no directionality ($F_{2, 19} = 11.3$, $N = 21$ pairs receiving fast-rate playback, $P < 0.001$; Fig. 3b). Here, the average phase angle was 282.3°, representing males calling late in the silent interval between playback duets; however, the strength of this relationship was also weak ($r = 0.06$),



**Figure 2.** Neighbouring pairs of long-tailed manakins avoided overlap during natural bouts of concurrent calling. (a) Circular statistical analyses revealed that duetting males called in the silent interval between their neighbours' calls (0°, i.e. the top, represents the onset of the duet from the reference males, so that perfectly alternating calls are represented by a phase angle of 180°, i.e. the bottom; grey points show the mean for each trial; the black arrow is the mean for the population where the length of the arrow corresponds to the effect size, $r$; the shaded areas correspond to the 95% confidence interval around the population mean). (b) Analysis involving a resampling approach revealed that adjacent pairs of males overlapped each other's duets less than expected by chance (measured in seconds of overlapped sounds). (c) Analysis involving duty cycle models similarly revealed that adjacent pairs of males overlapped their duets with those of their neighbours less than expected by chance. Values in (b) and (c) are means ± SE.
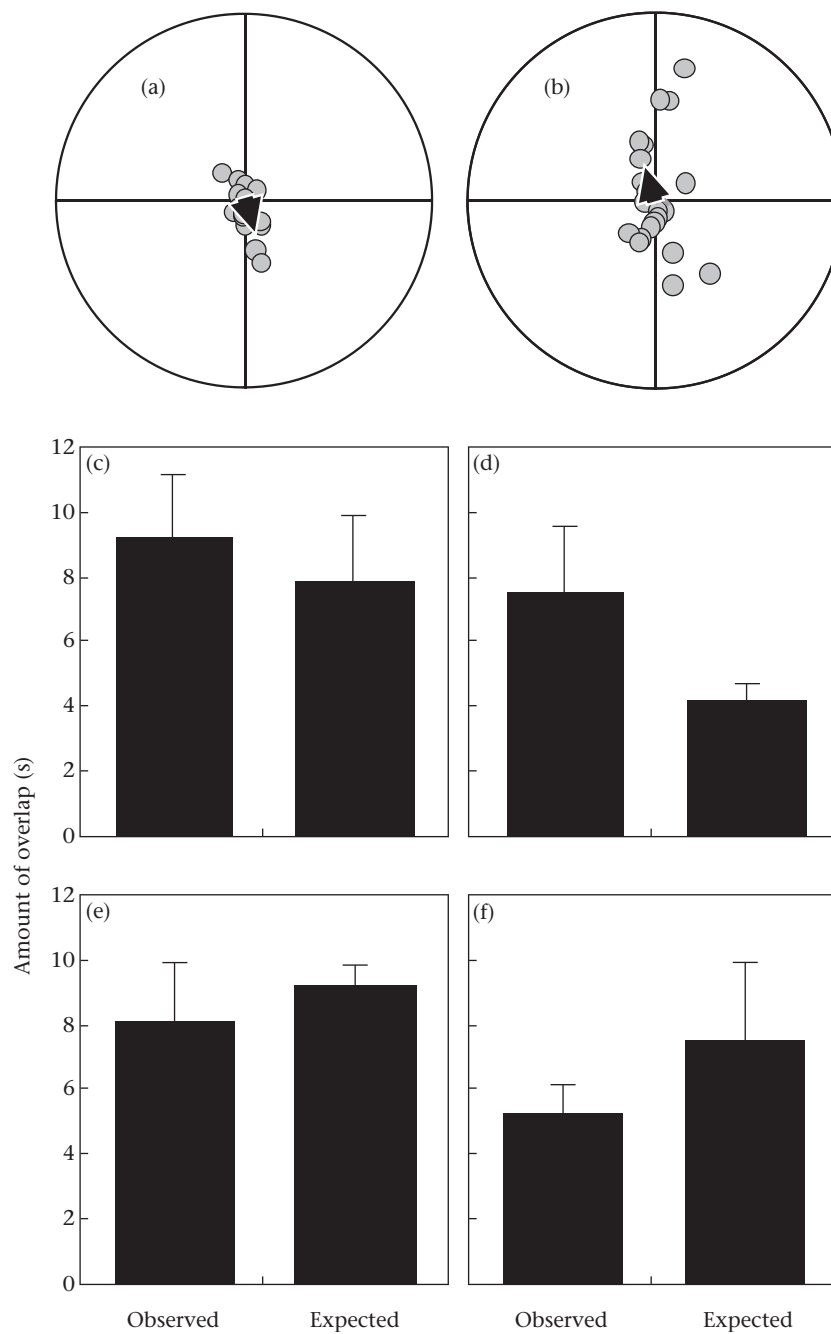
**Figure 3.** In response to playback simulating a rival pair, male long-tailed manakins called with substantial variation, both for playbacks broadcast at a slow-rate with an intercall interval of 3.5 s (a, c, e) and for playbacks broadcast at a fast-rate with an intercall interval of 2.4 s (b, d, f). Circular statistical analyses (see text) revealed no strong directional pattern in the timing of subjects' calls relative to playback duets either at a slow rate (a) or a fast rate (b), as indicated by the short vectors corresponding to the mean phase angles (0°, i.e. the top, represents the onset of the playback duets; grey points show the mean for each trial; black arrows show means for the population where the length of the arrow corresponds to the effect size, *r*). Analysis involving a resampling approach (c, d; see text) revealed that subjects overlapped playback duets to a significantly greater extent than expected by chance for duets broadcast at a slow rate (c), and showed a tendency in the same direction for duets broadcast at a fast rate (d). In contrast, analysis involving duty cycle models revealed no difference between the observed and expected amount of overlapping for duets broadcast at a slow rate (e) or a fast rate (f). Values in (c) through (f) are means ± SE.

indicating substantial variation in the timing of calls (Zar 1999; note that the weak directionality for both slow- and fast-rate playbacks precluded calculation of confidence intervals). Taken together, these results suggest that pairs of males do not call randomly, but they do not space their duets relative to playback according to a consistent pattern as we observed during natural bouts of concurrent calling.

Using a null model based on resampling to calculate chance levels of overlap, we found that male–male pairs of long-tailed

manakins overlapped playback for more total time than would be expected by chance. Pairs overlapped playback up to 50% more compared to the null hypothesis of chance overlapping. This higher-than-chance level of overlap was true for playback duets presented at a slow rate (Fig. 3c) and a fast rate (Fig. 3d), although only the fast rate was significant at the two-tailed level (Wilcoxon signed-ranks tests: slow rate: $T = 39.5$, $N = 18$, $P = 0.09$; fast rate: $T = 64.5$, $N = 21$, $P = 0.02$). Although males also overlapped a larger number of calls as assessed with resampling, this pattern was not

significant (slow rate: $T = 2.5$, $N = 18$, $P = 0.92$; fast rate: $T = 15$, $N = 21$, $P = 0.53$).

Using a null model based on duty cycle to calculate chance levels of overlap, we found that the total amount of call overlap was not significantly different from levels expected by chance (equation 3). This was true for both slow-rate playback ($T = 21.5$, $N = = 18$, $P = 0.37$; Fig. 3e) and the fast-rate playback ($T = 31.5$, $N = 21$, $P = 0.28$; Fig. 3f). The total number of calls that males overlapped (equation 2) was also not significantly different from levels expected by chance. This was true for both slow-rate playback ($T = 30.5$, $N = 18$, $P = 0.20$) and the fast-rate playback ($T = 22.5$, $N = 21$, $P = 0.45$).

In 36 of 39 playback trials, birds responded with vocal duets. However, during six trials there was a period where a single male produced solo 'toledo' calls (e.g. Fig. 1b) in response to the playback (in three slow-rate playback trials, only solos were produced; in three fast-rate trials, both solos and duets were produced). These solo-calling males timed their calls to begin just after the start of the playback duets (e.g. Fig. 1e). The small sample size ($N = 3$ instances in both the slow- and fast-rate playbacks) precluded the use of circular statistics to test for directionality, yet the strength of the effect appeared high ($r = 0.49$ and $0.90$, respectively) and the direction in which males were spacing their calls was consistent ($4.1°$ and $17.2°$, respectively; Fig. 4). Therefore, solo-calling males appeared to space their calls differently from duetting males, actively overlapping playback by calling immediately after the onset of playback duets.

*Behaviour during Playback*

Compared to preplayback call rates, males slowed their rate of calling during playback. A linear mixed effects model of intercall interval before, during and after duets played back at slow and fast rates revealed significant variation, where the intercall interval was significantly shorter before playback than it was during playback, returning to an intermediate level following the end of playback (fixed effect of playback period: $F_{2,77} = 3.1$, $P = 0.05$; Fig. 5); call rate did not vary significantly between slow-rate and fast-rate playback treatments (fixed effect of playback rate: $F_{1,87} = 0.0$, $P = 1.0$).

In 22 of our 52 playbacks, male long-tailed manakins approached the area near the playback speaker, sometimes coming as close as 5 m from the loudspeaker, but usually 10 m or farther. This occurred at 15 of the 32 display areas where we performed playback. Males were observed flicking their wings and producing 'chitter' vocalizations, which are thought to function in agonistic
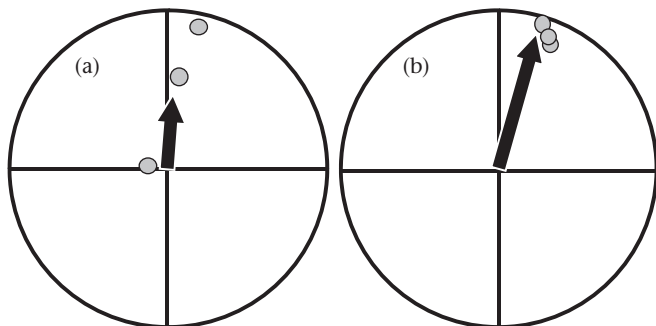
**Figure 4.** In the few cases where male long-tailed manakins produced solo toledo calls in response to playback, circular statistics revealed that the solo callers showed a strong tendency to produce solos immediately after the start of playback ($0°$, i.e. the top, represents the onset of the playback duets; grey points show the mean for each trial; black arrows show means for the population where the length of the arrow corresponds to the effect size, $r$). This pattern was evident for both duets broadcast at a slow rate (a) and duets broadcast at a fast rate (b).
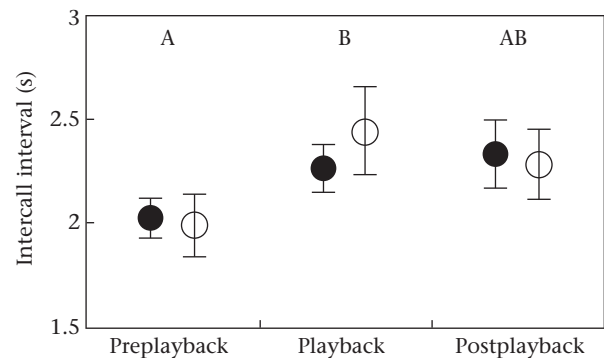
**Figure 5.** Pairs of male long-tailed manakins varied their intercall interval in response to playback. Prior to playback, birds called with the shortest intercall intervals; during playback, males called with significantly longer intercall intervals; after playback had ceased, males called at statistically intermediate levels. Circles represent means and whiskers show SEs. Filled circles represent slow-rate playback responses, and open circles represent fast-rate playback responses. Letters show a post hoc test of honestly significant differences, where categories not connected by the same letter were statistically different.

interactions in this species (Trainer & McDonald 1993). The forest at our study site is very dense (Mennill & Vehrencamp 2008), so it is possible that males may have shown aggressive behaviour during more playback trials, but we were unable to detect them.

**DISCUSSION**

Stereo recordings of naturally occurring bouts of calling between long-tailed manakins revealed that males time their vocalizations to avoid overlapping neighbours. Birds were more likely to produce duets in the middle of the silent interval between their neighbours' duets, and they overlapped their neighbours' duets less frequently and for less total time than would be expected under two different null models. In contrast to natural bouts of calling, males behaved differently when presented with playback simulating a pair of unfamiliar males calling near their display area. Different analytical models yielded different conclusions about overlapping during playback: circular statistics showed that males called nonrandomly but with substantial variation; a resampling approach showed that males overlapped fast-rate playback for more total time than expected by chance, and slow-rate playback showed a trend in the same direction; yet duty cycle models showed that neither number of overlapping calls nor the total amount of time spent overlapping deviated from levels predicted by chance. Overall, our analyses reveal that males avoid overlapping the calls of known neighbours at adjacent display areas, but increase their levels of overlap to that expected based on chance (or higher) when calling with unfamiliar rivals in close proximity to their display area.

*Call Timing during Natural Bouts of Concurrent Calling*

More than 30 studies have examined overlapping during vocal interactions in birds (reviewed in Naguib & Mennill 2010). These studies reveal that animals may alter the degree of overlap depending on context (e.g. Kunc et al. 2007), or they may alter their behaviour after being overlapped (e.g. Todt 1981). Several studies reveal that levels of overlap under natural circumstances are lower than expected based on chance (e.g. Fitzsimmons et al. 2008; Foote et al. 2008), just as we found for natural concurrent bouts of calling in this study. At least one previous study has demonstrated that neighbouring males vary their song rate relative to their neighbours, producing a predictable pattern of alternation (Smith &

Norman 1979). Compared to these previous investigations, our findings most closely resemble those of Brindley (1991), who found that European robins, *Erithacus rebecula*, overlapped playback of familiar neighbours less than playback of unknown territorial intruders. Taken together, these studies support the following conclusions: under natural circumstances with familiar neighbours, birds tend to avoid overlap; during encounters with other rival individuals, birds show more variable call timing and sometimes an increase in their level of overlap.

During natural bouts of concurrent calling, duetting male long-tailed manakins avoid overlapping their neighbours. Similar behaviour has been observed in other species with highly clustered mating aggregations, including anurans and insects (Brush & Narins 1989; Schwartz 1993; Greenfield 1994a, b). Manakins may avoid overlapping neighbours for several reasons. First, if overlapping sounds mask the identity of the callers or obscures the attractive properties of their vocalizations, males may avoid overlap to preserve the fine structural qualities of their duets. Second, if overlapping is an aggressive signal, males may avoid overlapping to minimize aggressive interactions between frequently encountered animals. Third, males may assess the quality of nearby animals by listening to their duets, and may avoid overlapping so that they have the opportunity to hear their neighbours during their intercall intervals. Fourth, by alternating their calls, males can create a higher duty cycle of species-typical vocalizations for the region around their display areas, which might increase female mate attraction to the region; this might be especially important in lekking animals such as long-tailed manakins. Taken together with our playback results, which showed that males did not avoid overlap to the same degree as in the natural interactions, our results do not provide support for the third or fourth explanation. The third explanation was not supported because males did not show the same behaviour during playback trials; males should be particularly attentive to the quality of unfamiliar rivals (Ydenberg et al. 1988). Similarly, the fourth explanation was not supported because males should be expected to enhance the duty cycle of their display area regardless of whether the other duetting males are familiar or unfamiliar. Given that the duet calls of long-tailed manakins are understood to function primarily in mate attraction, and the fine structural details are thought to be associated with mating success (Trainer & McDonald 1995), the first of these four explanations seems most likely; males may maximize their sexual advertisements if they minimize their broadcast of overlapping calls. The overlapping of unknown rivals that we observed during playback may represent an aggressive attempt to interfere with the acoustic information of another pair's calls. Our observation that some males responded to playback-simulated rivals with behaviours associated with physical aggression, including approach to the loudspeaker and agitated behaviours, supports this idea.

*Call Timing in Response to Playback*

Our playback results reveal a different pattern from our natural observations, where male long-tailed manakins called with greater variation during interactions with playback-simulated rivals. These results suggest that lekking birds behave differently when calling with unfamiliar rivals or when rivals are calling in immediate proximity to their display area. This may be analogous to the 'dear enemy' phenomenon known from studies of territorial songbirds, where neighbours' songs are less threatening because their position and behaviour are known (Fisher 1954; Temeles 1994). Conversely, the elevated levels of overlapping during playback might represent an aggressive form of signal interference, as has

been suggested by previous studies of territorial songbirds (Naguib & Todt 1997; Mennill & Ratcliffe 2004; Naguib & Mennill 2010). Another possible explanation for the difference between the responses of males to familiar neighbours versus unfamiliar playback-simulated rivals is that the responding males did not perceive our simulation as a pair of manakins. This explanation is unsatisfactory, particularly since our circular statistics showed that males were calling nonrandomly with respect to playback sounds and males often moved to the area immediately around the speaker when responding.

Another interpretation is that pairs of male long-tailed manakins responded differently to playback duets compared to neighbours' duets because of the location of the acoustic competitors. We presented playback 5–10 m away from the display perch of the subjects, which is closer than the typical distance between neighbours (display areas are typically separated by $\geq 25$ m). Although lekking birds are understood to be nonterritorial, hearing such a nearby pair of rivals may incite different behaviours. Female long-tailed manakins show site fidelity, returning to previously favoured display areas in successive years (McDonald 1989a; McDonald & Potts 1994), and males are thought to build the 'reputation' of their display area through duets and visual displays each year (McDonald 2010). As a result, unknown males performing duets near the focal pair's display area could negatively influence the reputation of the area, or the unfamiliar males could be seen to be taking advantage of a display area's reputation to enhance their own mating opportunities (McDonald 1993). Future work could tease apart these two alternative explanations by presenting playback from familiar and unfamiliar males at different distances from the display perch. If proximity to the subject's display perch is a key factor, this effect should disappear when playback sounds are presented from a distance more akin to normal distances between neighbours (i.e. more than 25 m away).

A final possibility is that birds may have altered their overlapping behaviour during playback because of the nondynamic nature of the loop playback. Calling interactions under natural circumstances are dynamic, and animals may alter their call timing in response to being overlapped (e.g. Greenfield 1994b; Kunc et al. 2007; reviewed in Naguib & Mennill 2010). Had we conducted an interactive playback study, where we actively overlapped or avoided overlapping individuals (e.g. Dabelsteen & McGregor 1996; Mennill & Ratcliffe 2000), we may have elicited different responses. The dynamic nature of overlapping interactions is a worthwhile area for future experimental and descriptive studies.

Although anecdotal, our results on the solo-calling behaviour of playback subjects provide interesting insights into call timing. Like many congeners, long-tailed manakins produce joint male–male displays to attract females (McDonald 1989b; DuVal 2007). However, unlike some congeners, this male–male association is obligatory for long-tailed manakins; males displaying alone have never been observed to copulate with a female (Trainer & McDonald 1993; Prum 1994; DuVal 2007). The overlapping behaviour we observed from solo-calling males may have represented an attempt for the solo male to join an existing pair, effectively turning their duets into 'trios' in an attempt to join the mate attraction activities at the display perch (McDonald 1993; Trainer et al. 2002). Note that the only previous study to quantify the number of solo toledo calls found that 'no bout of more than eight consecutive solo *toledos* was noted during more than 3,000 hours of scheduled observation' (Trainer & McDonald 1993, page 772). In contrast, we found six instances of males producing bouts of solo toledo calls (average = 15.4 solo toledo calls in a row). This occurred over a comparatively small timescale (the total recording time was 27 h). Our findings suggest that solo males respond differently to playback than do pairs of males.

*Null Models for Assessing Overlap*

There is no widely accepted null model for calculating chance levels of overlap for comparison to the measured behaviour of interacting animals (Searcy & Beecher 2009, 2011; Naguib & Mennill 2010). For this reason, we used three different null models in our analyses of call timing: circular statistics, resampling analysis and duty cycle models. We demonstrate that different conclusions arise from different null models. For example, in our investigation of playback responses, our resampling analyses showed that males overlapped playback for longer than would be expected based on chance, whereas our duty cycle analyses revealed that male duets overlapped with the playback at levels that would be expected based on chance (although both approaches revealed higher levels of overlap than under natural conditions). Had we used only a duty cycle model, and only performed a playback experiment, we would conclude that manakins do not deviate from chance levels of overlap. Had we used only a resampling approach, we would conclude that males overlapped significantly more often than expected based on chance. Consequently, the analytical approach used to calculate chance levels of behaviour must be considered carefully.

The three analytical approaches used here provide different insights, and each one has strengths and limitations. Circular statistics provide an excellent descriptive tool, allowing the researcher to assess easily whether there is deviation from randomness. Circular statistics are an effective tool for detecting subtle patterns in cyclical data, and the back-and-forth dynamics of many animal signalling interactions can be understood as cyclical phenomena. The circular statistics approach is limited when call rate or call duration of the reference signal varies substantially. Also, this technique is unable to detect even strong effects at low sample sizes. Comparatively, resampling analysis is an effective tool for preserving even highly variable timing of calls, and for establishing chance levels that incorporate the actual spacing of calling animals. Resampling requires substantial computing power, however, as the bouts of signals must be shuffled several thousand times to create appropriate estimations. Analyses based on duty cycle models are relatively simple to perform, which may be the reason they have received more widespread use (Searcy & Beecher 2009). Duty cycle models provide a similar approach to resampling analysis, and may be especially helpful when analysing natural calling exchanges with variable call rates or very long intercall intervals. Both duty cycle models and resampling analyses must be restricted to a single continuous bout where both parties are calling (Ficken et al. 1974; Planck et al. 1975). We recommend the use of circular statistics to determine whether the spacing of calls between calling individuals is random. Circular statistics provide a compelling tool for visualizing call timing, revealing that males place their calls midway between the onset of their opponent's calls. If circular statistics reveal nonrandom call timing, we recommend resampling as a follow-up analysis to quantify the amount of overlap that occurs, given that this technique appears capable of detecting subtle differences from background variation in call timing.

## Acknowledgments

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