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The Song Overlap Null model Generator (SONG): a new tool for distinguishing between random and non-random song overlap

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ABSTRACT

Song overlapping, a behaviour in which an individual begins singing before its counterpart has completed its song, has been the subject of recent debate. Although many studies have suggested that song overlapping functions as a signal, the majority of these studies fail to address the possibility that overlapping is a chance occurrence. Part of the difficulty in determining whether overlap is intentional or accidental lies in the lack of compelling null models for estimating chance levels of song overlap. We have developed the Song Overlap Null model Generator (SONG), a software package for R. SONG uses resampling randomization to predict the expected amount of overlap due to chance, and is applicable to any system in which individuals engage in signalling interactions. To evaluate the effectiveness of SONG, we examined the overlapping behaviour of three avian species: black-capped chickadees (*Poecile atricapillus*), rufous-and-white wrens (*Thryophilus rufalbus*) and long-tailed manakins (*Chiroxiphia linearis*). Our analyses revealed that black-capped chickadees avoided overlapping the songs of playback-simulated intruders, duetting wrens overlapped the songs of their mates and manakins avoided overlapping the duets of their neighbours. We believe that SONG will prove to be a valuable tool for understanding signal timing in songbirds as well as other taxa.

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Introduction

Communication is essential for social behaviours such as mate attraction and resource defence. Many taxa use long-range acoustic signals to accomplish these goals, including mammals (e.g. Behr & von Helversen 2004; Charlton et al. 2007), birds (Catchpole & Slater 2008), amphibians (Gerhardt & Huber 2002), fish (Ladich 1997) and insects (Cade 1985). Through the use of these signals, individuals can communicate their quality (e.g. Forsman & Hagman 2006), condition (e.g. Wagner & Hoback 1999) and motivation (e.g. Searcy et al. 2006) to potential mates and territorial rivals.

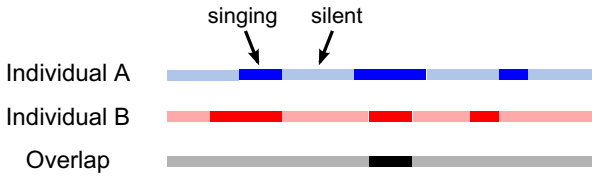
Individuals often use signals interactively, adjusting the structure or timing of their signals in response to those of nearby conspecifics (Todt & Naguib 2000). During such interactions, individuals may produce signals synchronously, overlapping each other's signals. Overlapping is especially common in chorusing taxa (e.g. insects, anurans and songbirds), in which individuals display simultaneously to attract mates (Greenfield 1994a; Todt & Naguib 2000). There are various processes by which overlap can occur. It can occur by chance when competition for acoustic space is high, or when individuals signal without reference to each other. In many species of insects and anurans, females have a strong preference for leading signals (i.e. signals occurring first in a sequence; e.g. Snedden & Greenfield 1998; Höbel & Gerhardt 2007), creating competition among males to begin signalling before nearby conspecifics. In insects, overlapping can emerge as a by-product of this competition (Greenfield & Roizen 1993).

Overlapping can also arise out of intentional processes. This is likely the case for duetting, which involves the coordination of two individuals' signals, usually the male and female of a mated pair. Overlapping is a defining feature of polyphonal duets, which have been observed in many taxa including primates (Haimoff 1986), anurans (Tobias et al. 1998) and birds (Hall 2009). During aggressive interactions between rivals, overlapping can function as a signal. Male grey tree frogs (*Hyla versicolor*) adjust their signal timing to overlap the calls of rival males during close-range interactions, signalling their intent to escalate the contest (Reichert & Gerhardt 2013).

Many studies have suggested that overlapping functions as an aggressive signal in songbirds (reviewed in Naguib and Mennill 2010). The majority of these studies, however, have neglected to address the possibility that song overlapping is a chance occurrence. In the studies that have explicitly tested this idea, overlapping occurred at or below chance levels (Wasserman 1977; Gochfeld 1978; Fitzsimmons et al. 2008; Foote et al. 2008; Maynard et al. 2012; Yang et al. 2014). As a result, whether song overlapping is truly a signal remains controversial (Searcy & Beecher 2009, 2011; Naguib & Mennill 2010).

How do we calculate chance levels of overlap? One established technique is the duty cycle method, which states that during an interaction between individuals A and B, the probability that A's song will overlap B's song is equal to the proportion of time that B spends singing (Ficken et al. 1974). This method has a critical limitation: by collapsing singing behaviour down into a simple probability, variation in song duration and timing become confounded. For example, as long as the ratio of song to silence remains the same, a rigidly periodic performance, a highly variable performance and a single long song could all result in the same duty cycle. Therefore, according to this method, each of these performances would result in the same expected amount of chance overlap, even though the opportunities for overlap could be vastly different in each case.

Unlike the duty cycle method, randomization methods can take into account variation in song duration and timing. A randomization test estimates the expected value of a test statistic by rearranging the observed data many times, calculating the statistic for each rearrangement to generate a null distribution (Manly 2006). Randomization tests have proven useful for studying patterns in signalling behaviour (e.g. call type matching: Janik 2000; Miller et al. 2004; mimicry: Payne et al. 2000), and recently, researchers have begun using resampling randomization to study song overlapping in birds (e.g. Maynard et al. 2012; Yang et al. 2014).

Observed interaction:**Calculate the expected amount of chance overlap for Individual B:**

Step 1: Break the performance of Individual B into songs and intervals.



Step 2: Reassemble the performance.

a) SampleGaps method

Randomly sample interval durations, then reassemble by randomizing the order of the songs and intervals.

**b) KeepGaps method**

Preserve the observed interval durations, then reassemble by randomizing the order of the songs and intervals.

**c) KeepSongOrder method**

Preserve the observed interval durations, then reassemble by randomizing the order of the intervals.



Step 3: Calculate the amount of overlap in the randomized interaction.

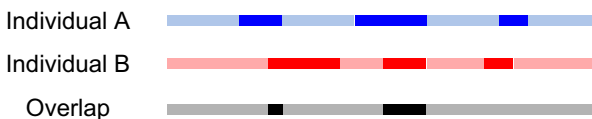


Figure 1. A schematic depicting the randomization process used by the SONG package.

Notes: To calculate the expected amount of chance overlap for Individual B relative to Individual A, the performance of Individual B is broken down into its components, reassembled in a random configuration, and compared to Individual A's observed performance. This process is repeated a user-defined number of times to generate a null distribution.

To make techniques like those described above more widely available for use, we have developed the Song Overlap Null model Generator (SONG). SONG is a software package for the statistical language R (R Development Core Team 2013) that is freely available for download from the SONG GitHub repository (<https://github.com/ChristinaMasco/song>). Given an interaction, SONG uses resampling randomization to predict the amount of chance

overlap, while giving users the option to preserve the natural variation song duration and timing. The input for the SONG package is a tab-delimited text file containing the start time, end time and singer identity for each song during an interaction. These data can be acquired using sound annotation software packages such as Syrinx-PC (J. Burt, Seattle, WA, USA) or Raven (Cornell Laboratory of Ornithology, Ithaca, NY USA). SONG can accommodate files containing any number of individuals, and will calculate the amount of overlap for each possible pairwise interaction. Because the input is a simple list of start and end times, the SONG package can be used to investigate signal timing during any type of interaction.

Given an observed interaction between two individuals, A and B, the SONG package builds randomized performances for A and B independently, which are then assembled into randomized interactions (i.e. A vs. B-randomized and vice versa). The program then calculates the amount of overlap in each of these randomized interactions, generating a distribution that represents the amount of overlap expected due to chance. A comparison of the observed amount of overlap to this null distribution produces a *P*-value, calculated as the probability that a randomized interaction will result in an amount of overlap greater than observed. In other words, if individuals overlap each other's songs more often than expected by chance, the *P*-value will be close to zero; if individuals overlap each other's songs less often than expected by chance, the *P*-value will be close to one.

SONG contains two methods for measuring the amount of overlap: (1) the duration of overlap in seconds and (2) the number of overlapping songs. A song is considered overlapping if it begins while another song is in progress. For calculating the expected amount of chance overlap, SONG contains three null models (SampleGaps, KeepGaps and KeepSongOrder) that differ in the constraints they impose on the randomization procedure. Users can select whichever model creates randomized performances that most closely resemble the natural signalling behaviour of their study system. (1) The SampleGaps randomization method preserves only the observed song durations, rearranging the order of the songs and placing them at random intervals to create randomized performances (Figure 1(a)). This method is most appropriate for systems in which signal timing is highly variable or unconstrained. (2) The KeepGaps randomization method preserves the observed song and inter-song interval durations, rearranging the order of the songs and intervals (Figure 1(b)). This procedure ensures that the observed variation in signal timing is preserved in each of the randomized performances. The KeepGaps method could be particularly useful for systems in which signal timing is periodic or highly constrained. (3) The KeepSongOrder randomization method preserves the observed song order in addition to the song and interval durations, rearranging only the interval order to create randomized performances (Figure 1(c)). This method was designed specifically with dawn and dusk choruses in mind. During these prolonged performances, individuals of some species 'drift', shortening their songs and lengthening their pauses over time (e.g. Lambrechts & Dhondt 1988). In these cases, it may be important to preserve the relationship between song duration and time over the course of the interaction. Recognizing that users may wish to develop randomization methods that have not been included in the package, we built SONG to easily accommodate user-written methods as well.

In addition to the resampling randomization technique described above, we have included in the SONG package the traditional duty cycle method (Ficken et al. 1974). According to this method, the expected number of overlapping songs, *E*, during an interaction between two animals, A and B, is calculated as: $E = N_A \cdot D_B + N_B \cdot D_A$. In this equation,

N_A and N_B represent the number of songs produced by A and B, respectively, while D_A and D_B represent each individual's duty cycles, or the proportion of time spent signalling. We have also included a modified version of the duty cycle method (Maynard et al. 2012) that calculates the expected duration of overlap as $E = T \cdot (D_A \cdot D_B)$. In this equation, D_A and D_B represent each individual's duty cycles and T represents the total duration of the exchange.

To evaluate the effectiveness of the SONG package, we examined overlapping in three avian species: black-capped chickadees (*Poecile atricapillus*), rufous-and-white wrens (*Thryophilus rufalbus*) and long-tailed manakins (*Chiroxiphia linearis*). Each of these species exhibits song overlapping in a different context, allowing us to investigate signal timing during different types of interactions. In this study, we asked whether overlapping occurred above chance levels during (1) responses by black-capped chickadees to playback-simulated territorial intruders; (2) duet interactions between male and female rufous-and-white wrens; and (3) interactions between long-tailed manakins and their neighbours on adjacent leks.

Methods

For each of the three species, we assembled a data-set consisting of 10 pairwise interactions. Using the SampleGaps, KeepGaps and KeepSongOrder methods, we calculated the expected duration of chance overlap for each of these interactions. Each analysis consisted of 1000 randomizations. We then compared the observed overlap to these expectations to obtain P -values for each interaction. Individuals were considered to be overlapping if $P \leq 0.025$, and avoiding overlap if $P \geq 0.975$. To provide a basis for comparison, we also analysed these data-sets using the traditional duty cycle method. This method compares the observed and expected number of overlapping songs by means of a chi-squared test. Individuals were considered to be overlapping if they overlapped their counterparts more often than expected with $P \leq 0.05$. Similarly, individuals were considered to be avoiding overlap if they overlapped their counterparts less often than expected with $P \leq 0.05$.

Data-set 1: Black-capped chickadees

Male black-capped chickadees engage in vocal interactions at territory boundaries during the breeding season (Mennill & Otter 2007). Song overlapping occurs during these interactions (Fitzsimmons et al. 2008; Figure 2(a)) and has been suggested to function as an aggressive signal (Mennill et al. 2002; Mennill & Ratcliffe 2004), although this idea has been controversial (Searcy & Beecher 2009; Naguib & Mennill 2010). The data that we analysed here came from a playback study by Baker et al. (2012) designed to evaluate whether song overlap and other behaviours during countersinging interactions predict whether a chickadee will attack a rival. Baker et al. (2012) presented territorial male black-capped chickadees with a taxidermic mount of a male conspecific while playing chickadee songs on a fixed loop, recording the songs produced by the territorial male in response to the simulated intrusion. Baker et al. (2012) focused on a comparison of the vocal behaviour of males that subsequently attacked the model and those that did not. Here, we analysed the overlapping behaviour of the subjects with respect to the playback stimuli for both attackers and non-attackers. Our data-set consisted of interactions between 10 different males and the playback stimuli, five of which culminated in an attack of the model.

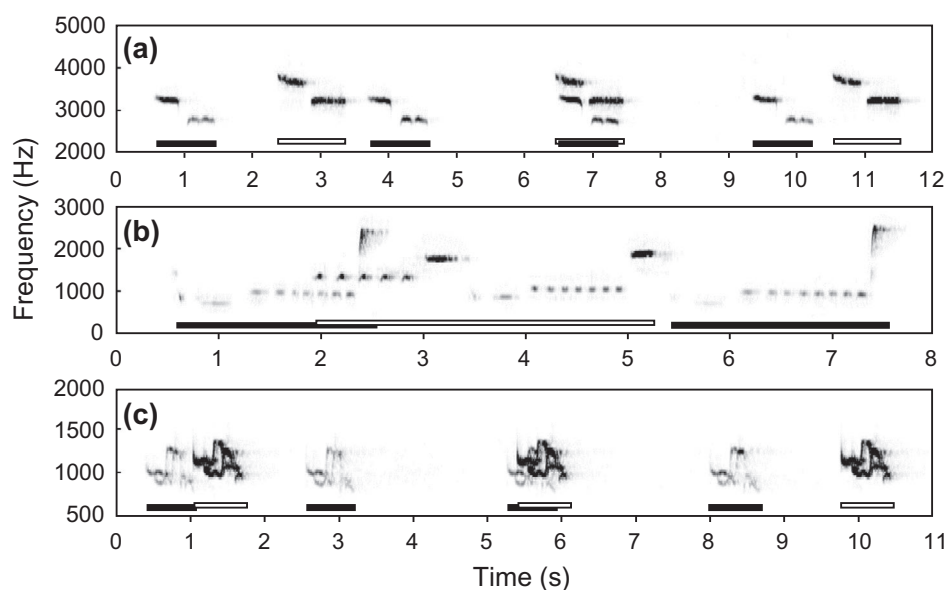


Figure 2. Sound spectrograms showing examples of overlapping in three species.

Notes: (a) An interaction between two male black-capped chickadees, including one instance of overlap. The vocalizations of one male are underscored by black boxes, and the other male by white boxes. (b) A duet produced by a breeding pair of rufous-and-white wrens, in which the song from the female (underscored by a white box) overlaps one of the songs from the male (underscored by black boxes). (c) An interaction between two duetting male–male pairs of long-tailed manakins at adjacent lek sites, showing two instances of overlap. The vocalizations of one pair of males are underscored by black boxes and the other pair of males by white boxes.

Data-set 2: Rufous-and-white wrens

Breeding pairs of rufous-and-white wrens combine their songs to produce vocal duets, resulting in variable degrees of overlap between male and female song (Mennill & Vehrencamp 2005; Figure 2(b)). The data that we analysed here came from 8-channel microphone array recordings of rufous-and-white wrens, designed to passively sample the natural duetting behaviour of breeding partners as they move around their large territories (Mennill et al. 2006; Mennill & Vehrencamp 2008). Our data-set consisted of interactions between 10 different females and their mates.

Data-set 3: Long-tailed manakins

Long-tailed manakins are a Neotropical species in which males perform highly synchronized male–male duets that are so well coordinated that the songs appear to originate from one individual (Trainer & MacDonald 1995). Maynard et al. (2012) noted that pairs of males appeared to vary the timing of their male–male duets with respect to the timing of the duets of the males in adjacent leks (Figure 2(c)). The data that we analysed here came from stereo recordings obtained from two microphones positioned near adjacent leks (Maynard et al. 2012). Our data-set consisted of interactions between 10 male–male pairs and their neighbouring male–male pairs.

Table 1. The singing behaviour of male black-capped chickadees in response to simulated territorial intrusions.

Male	SampleGaps method		KeepGaps method		KeepSongOrder method		Duty cycle method	
	Pattern	P-value	Pattern	P-value	Pattern	P-value	Pattern	P-value
1	Avoid	>0.999	Avoid	>0.999	Avoid	0.999	Avoid	<0.001
2	Avoid	0.993	Avoid	0.981	N.S.	0.973	Avoid	0.005
3	Avoid	>0.999	Avoid	0.995	Avoid	0.993	Avoid	<0.001
4	Avoid	>0.999	Avoid	>0.999	Avoid	0.998	Avoid	<0.001
5	Avoid	0.988	N.S.	0.954	N.S.	0.964	Avoid	0.005
6	Avoid	0.984	N.S.	0.974	Avoid	0.977	N.S.	0.182
7	Avoid	0.999	Avoid	0.999	Avoid	0.999	Avoid	<0.001
8	Avoid	>0.999	Avoid	>0.999	Avoid	0.999	Avoid	<0.001
9	N.S.	0.967	N.S.	0.947	N.S.	0.930	Avoid	0.014
10	N.S.	0.506	N.S.	0.504	N.S.	0.521	N.S.	0.903

Notes: For each interaction, the male's behaviour is categorized as overlapping, avoiding overlap or exhibiting no significant pattern (N.S.). The cases in which the various methods produced conflicting results are highlighted.

Table 2. The singing behaviour of rufous-and-white wrens during duet interactions.

Pair	SampleGaps method		KeepGaps method		KeepSongOrder method		Duty cycle method	
	Pattern	P-value	Pattern	P-value	Pattern	P-value	Pattern	P-value
(a) Male behaviour with respect to their mates								
1	Overlap	<0.001	Overlap	0.001	Overlap	<0.001	Overlap	<0.001
2	N.S.	0.768	N.S.	0.730	N.S.	0.745	N.S.	0.745
3	Overlap	0.011	Overlap	0.018	N.S.	0.026	Overlap	0.009
4	N.S.	0.251	N.S.	0.301	N.S.	0.310	Overlap	0.034
5	N.S.	0.293	N.S.	0.291	N.S.	0.295	N.S.	0.482
6	N.S.	0.409	N.S.	0.405	N.S.	0.385	N.S.	0.591
7	N.S.	0.174	N.S.	0.194	N.S.	0.177	N.S.	0.196
8	N.S.	0.392	N.S.	0.444	N.S.	0.402	Overlap	0.021
9	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	N.S.	0.369
10	N.S.	0.045	N.S.	0.079	N.S.	0.073	Overlap	0.028
(b) Female behaviour with respect to their mates								
1	N.S.	0.770	N.S.	0.871	N.S.	0.894	Overlap	0.024
2	N.S.	0.026	N.S.	0.052	N.S.	0.049	Overlap	0.001
3	N.S.	0.167	N.S.	0.463	N.S.	0.434	N.S.	0.088
4	Overlap	0.019	N.S.	0.042	N.S.	0.047	Overlap	<0.001
5	Overlap	<0.001	Overlap	0.003	Overlap	0.005	Overlap	<0.001
6	N.S.	0.489	N.S.	0.765	N.S.	0.811	N.S.	0.669
7	N.S.	0.029	N.S.	0.032	Overlap	0.011	Overlap	0.029
8	N.S.	0.456	N.S.	0.558	N.S.	0.619	N.S.	0.639
9	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	N.S.	0.281
10	Overlap	<0.001	Overlap	<0.001	Overlap	<0.001	Overlap	<0.001

Notes: For each interaction, the behaviours of the male (a) and female (b) are categorized as overlapping, avoiding overlap or exhibiting no significant pattern (N.S.). The cases in which the methods produced conflicting results are highlighted.

Results

More than half of the male black-capped chickadees included in this analysis overlapped the playback stimulus significantly less often than expected by chance (Table 1). When overlapping did occur, the playback stimulus began during the male's song more often than *vice versa* (Wilcoxon signed rank test, $V = 48.5$, $P = 0.04$). Whether a male attacked the taxidermic mount was independent of the duration for which his songs were overlapped by

Table 3. The calling behaviour of male–male pairs of long-tailed manakins during interactions with neighbours.

Interaction	SampleGaps method		KeepGaps method		KeepSongOrder method		Duty cycle method	
	Pattern	P-value	Pattern	P-value	Pattern	P-value	Pattern	P-value
(a) Male–male pair behaviour with respect to their neighbours (e.g. Pair A vs. Pair B)								
1	N.S.	0.600	N.S.	0.656	N.S.	0.644	N.S.	0.492
2	N.S.	0.942	N.S.	0.903	N.S.	0.909	N.S.	0.389
3	Avoid	0.990	Avoid	0.983	Avoid	0.983	N.S.	0.444
4	N.S.	0.884	N.S.	0.878	N.S.	0.870	N.S.	0.225
5	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	N.S.	0.068
6	N.S.	0.887	N.S.	0.902	N.S.	0.888	N.S.	0.303
7	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	Avoid	0.042
8	N.S.	0.953	N.S.	0.947	N.S.	0.957	N.S.	0.206
9	Avoid	0.990	Avoid	0.979	Avoid	0.978	N.S.	0.106
10	N.S.	0.845	N.S.	0.806	N.S.	0.815	N.S.	0.674
(b) The reciprocal interactions (e.g. Pair B vs. Pair A)								
1	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	N.S.	0.079
2	N.S.	0.488	N.S.	0.414	N.S.	0.418	N.S.	0.724
3	Avoid	0.997	Avoid	0.998	Avoid	0.993	Avoid	0.020
4	N.S.	0.627	N.S.	0.629	N.S.	0.605	N.S.	0.517
5	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	Avoid	0.050
6	Avoid	>0.999	Avoid	>0.999	Avoid	>0.999	Avoid	0.047
7	N.S.	0.877	N.S.	0.818	N.S.	0.829	N.S.	0.492
8	Avoid	>0.999	Avoid	0.999	Avoid	0.999	Avoid	0.005
9	N.S.	0.963	N.S.	0.943	N.S.	0.949	N.S.	0.143
10	N.S.	0.666	N.S.	0.572	N.S.	0.57	N.S.	0.507

Notes: For each interaction, the behaviour of the male–male pair is categorized as overlapping, avoiding overlap or exhibiting no significant pattern (N.S.). The cases in which the methods produced conflicting results are highlighted.

the playback stimulus (Wilcoxon rank sum test, $W = 9$, $P = 0.55$). Overlap avoidance was also independent of attack (Fisher's exact test, $P > 0.44$ for all methods).

In about half of the rufous-and-white wren interactions, either one or both of the individuals in the breeding pair sang non-randomly with respect to their mate when randomization methods were used (Table 2). Two males and three females overlapped the songs of their mates more often than expected by chance (all $P < 0.025$). One breeding pair significantly avoided overlapping each other's songs ($P > 0.999$). According to the duty cycle method, half of the individuals (five males and six females) exhibited song overlapping (all $P < 0.05$), and no individuals avoided overlap.

In 7 of the 10 long-tailed manakin interactions, male–male pairs overlapped the duets of their neighbours significantly less often than expected by chance when randomization methods were used (Table 3). Overlap avoidance was reciprocal in two cases, for a total of 9 of the 20 male–male pairs avoiding overlap (all $P > 0.975$). According to the duty cycle method, 5 of the 20 male–male pairs exhibited overlap avoidance (all $P \leq 0.05$).

Discussion

Overlapping is a taxonomically widespread feature of signalling interactions, thought to function as an aggressive signal in songbirds (Naguib & Mennill 2010). In many cases, however, it is unclear whether overlapping is the result of intention or chance, and the lack of a compelling null model has made distinguishing between these two possibilities difficult.

To address this issue, we have developed SONG, a freely available software package for R designed to predict chance levels of song overlap.

To evaluate the effectiveness of this new tool, we used SONG to examine overlapping in three avian species: black-capped chickadees, rufous-and-white wrens and long-tailed manakins. When confronted with a simulated intruder, more than half of the black-capped chickadees in this analysis avoided overlapping the playback stimulus. When overlap did occur, the playback stimulus overlapped the bird's song more often than *vice versa*, suggesting that instances of overlap were accidental rather than intentional. In our analysis, a male's overlapping behaviour was independent of whether he eventually attacked the mount; a lack of relationship between overlapping and attack was found in the full data-set as well (Baker et al. 2012; $n = 38$). Overlap avoidance has not been observed during natural countersinging interactions in this species (Fitzsimmons et al. 2008). Further investigation is necessary to determine whether overlapping functions as a signal in natural interactions as suggested by prior studies (Mennill et al. 2002; Mennill & Ratcliffe 2004).

For rufous-and-white wrens, our analyses revealed variation in duetting behaviour. In some cases, the female overlapped the male's songs to form duets; in others, the male overlapped the female's songs. In half of the interactions analysed, either one or both of the individuals in the breeding pair sang non-randomly with respect to their mate. Whether variation in duetting behaviour is individually repeatable, or has any impact on reproductive success in this species is a matter of on-going investigation. Analysis of longer recordings of these birds, along with parallel studies of their reproductive behaviour, will enhance our understanding of vocal duets in rufous-and-white wrens.

For long tailed-manakins, half of the male-male pairs that we analysed significantly avoided overlapping the duets of their neighbours. These results match the pattern found in the full data-set analysed by Maynard et al. (2012). Because these duets primarily function in mate attraction, it is possible that overlap avoidance functions as a strategy to minimize signal masking. Investigating whether males that avoid overlapping their neighbours are more successful in attracting females would help shed light on the function of overlap avoidance in this species.

For each of the species analysed, the duty cycle and randomization methods often produced conflicting results. Because the duty cycle method confounds variation in signal duration and timing, its estimations for chance overlap may be less accurate than the estimations generated by the randomization methods. This effect should be most pronounced in animals that show high variation in signal duration or signal timing. However, without knowing the true value of the amount of chance overlap in an interaction, we cannot be sure which method yields the most accurate prediction. Whether it is possible to rigorously test the accuracy of a song overlap null model is a worthwhile topic for future study.

It is important to note that, even though song overlapping may occur more often than expected during an interaction, this does not necessarily imply that overlapping functions as a signal. To demonstrate signal value, we recommend using SONG as a first step to inform subsequent experimentation. Searcy and Beecher (2009) have provided a useful set of criteria for assessing whether a behaviour functions as an aggressive signal, emphasizing the importance of gathering evidence from both the sender's and receiver's perspectives. Helfer and Osiejuk (2015) have offered alternative explanations for the function of song overlapping, presenting a series of working hypotheses and specific predictions. Together, these works provide a valuable theoretical framework to guide future research on song overlapping.

Similarly, even though overlapping may occur less often than expected during an interaction, subsequent investigation is necessary to determine why individuals avoid overlap. Overlap avoidance may function as a strategy to minimize interference (Wasserman 1977; Egnor et al. 2007), facilitate mutual listening (Schwartz & Rand 1991) or in the case of mate attraction aggregations, maximize the overall duty cycle of the group (Greenfield 1994b). Beyond its utility in detecting overlap avoidance in response to conspecific and heterospecific sound, the SONG package may also prove useful in examining whether urban species exhibit overlap avoidance in response to intermittent anthropogenic noise.

Although the primary focus of this paper has been song overlapping in birds, the SONG package is not avian specific. Signal timing in chorusing insects and anurans has also been an area of extensive study. In these taxa, the mechanisms involved in sound production constrain temporal features of the calls such as pulse rate and call duration, resulting in highly stereotyped performances (Gerhardt & Huber 2002). Methods included in the SONG package can preserve this stereotypy, potentially leading to more accurate estimations of chance overlap than the traditional duty cycle method.

The SONG package can also be used to study signalling interactions outside of the acoustic modality. Because the input is a simple list of start and end times, our package can be used to study the coordination of any temporally patterned behaviour, including visual displays, movements and multimodal signalling interactions.

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