Overlapping signals in banded wrens: long-term effects of prior experience on males and females

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We tested the signal value of song overlapping in banded wrens (Thryothorus pleurostictus), using interactive playback to either overlap or alternate with their songs. Males shortened song duration and decreased variability in song length when their songs were overlapped by playback, suggesting that they were attempting to avoid being overlapped and perhaps being less aggressive. A novel finding was an effect of long-term prior experience: song lengths remained relatively short in alternating trials that followed two or more days after overlapping trials. Approach responses to the two treatments did not differ overall, but there was a parallel effect of prior experience: males tended to stay further from the speaker during alternating treatments if they had previously been overlapped by playback. Some females paired to the male subjects sang in response to playback and were also influenced by prior experience, singing more during alternating trials that had not been preceded by an overlapping trial. Male overlappers may signal dominance over a rival to other male or female receivers in a communication network, but it is currently unclear whether overlapping indicates motivation to escalate an aggressive interaction or whether this singing strategy is related to male quality. Banded wrens are long lived and maintain year-round territories, so modifying responses to rivals based on prior experience is likely to be important for success. Key words: communication networks, interactive signals, female song, male quality, song overlap. [Behav Ecol 17:260–269 (2006)]

Overlapping signals are a feature of many communication systems and may mask or enhance one another, depending on factors like signal modality and the importance of individual distinctiveness. In many insects and anurans, signal synchrony or alternation is a consequence of males attempting to produce the leading signals preferred by females (Gerhardt and Huber, 2002; Greenfield et al., 1997). In some systems, the temporal overlap of signals may benefit interactants. For example, groups of lionesses (Panthera leo) increase the effectiveness of their aggressive display by roaring in chorus (McComb et al., 1994), and synchronous vibrational signaling by aggregations of treehopper (Umbonia crassicornis) nymphs elicits maternal antipredator behavior that individual vibrational signals do not (Cocroft, 1996, 1999). However, interactions involving signal overlap are often competitive. The spatial overlap of chemical signals that occurs when rodents overlap one another appears to be competitive (reviewed in Johnston, 2003). Likewise, the temporal overlap of auditory signals in interacting territorial songbirds is agonistic (Todt and Naguib, 2000).

Song overlapping is a relatively infrequently used strategy in many avian systems, but the contexts in which it occurs and the response it elicits from both receivers and eavesdroppers suggest that it is a directed aggressive signal (Tables 1–3). Birds generally avoid singing when conspecifics are singing (Gochfeld, 1978; Wasserman, 1977), but increased numbers of neighbors can increase the chance of overlapping, and some individuals may be more likely to overlap neighbor songs than others (Hultsch and Todt, 1982; Popp, 1989). Furthermore, song playback simulating intrusion can elicit overlapping (Balsby and Dabelsteen, 2001; Brindley, 1991; Langemann et al., 2000; Naguib, 1999). Responses of birds to being overlapped vary. Some respond aggressively with increased song rates when their songs are experimentally overlapped (Dabelsteen et al., 1997; Naguib, 1999). Many increase variability in the timing of their songs, and some reduce approach and song duration (Dabelsteen et al., 1996; Mennill and Ratcliffe, 2004b; Osiejuk et al., 2004). There is evidence that prior experience of being overlapped influences responses (Naguib, 1999).

Individual males may differ in their preferred singing patterns, but few studies have investigated male characteristics associated with these differences. Males may vary consistently in how they respond to simulated intrusion (Nowicki et al., 2002), and a few studies have shown that such individual differences are related to male characteristics such as age or dominance rank (Hyman et al., 2004; Mennill and Ratcliffe, 2004a,b). Though studies focusing on song overlapping have found individual differences in the use of overlapping (Hultsch and Todt, 1982) and in responsiveness to being overlapped (Naguib, 1999), characteristics of these males were not compared, and further work is needed to determine whether song overlapping is related to male quality.

We used an interactive playback experiment to test the communication function of overlapping songs in banded wrens. Socially monogamous pairs are territorial and do not migrate. Males are considerably more vocal than females and have repertoires of around 20 song types, many of which are shared among neighbors (Molles and Vehrencamp, 1999). Matching song types of rivals in vocal interactions is an aggressive signal eliciting rapid approach (Molles and Vehrencamp, 2001). Males also sometimes overlap the songs of rivals during countersinging interactions, but overlapping is correlated with song rate, suggesting that some overlapping may be accidental (Burt and Vehrencamp, 2005). To determine whether song overlapping has signal value in banded wrens, we tested whether males responded differently to a simulated “intruder” that responded to their songs with alternating or overlapping songs. We also monitored the response of females during playback. We replicated the paired experimental design of Naguib (1999), presenting both treatments to each
subject in either “escalating” or “de-escalating” sequences and testing for effects of prior experience. However, we increased the time between presentation of alternating and overlapping playbacks from just a few minutes to several days to determine whether such effects might persist over the longer term.

METHODS

We conducted playback experiments from 16 May to 26 June 2003 in Santa Rosa National Park in the Guanacaste Conservation Area, Costa Rica. For details on the habitat and study population, see Molles and Vehrencamp (1999). Subjects were 20 individually color-banded males resident on territories in the study area. Breeding stage of subjects varied and was not always known, so the experiment was designed to minimize variance due to breeding stage by testing the treatment effect within subjects in trials separated by just a few days.

Experimental design

We used a paired design, exposing each subject to the same playback songs in two interactive trials, an overlapping treatment, and an alternating treatment. Trials on the same male were conducted 2–5 days apart, and successive males received treatments in the opposite sequence so that half the subjects received alternating and the other half overlapping treatments first. We employed a two-speaker design to standardize the state and location of subjects at the start of the experiment. We used a lure speaker to attract the subject to the area and stimulate singing and then played experimental stimuli. We used a lure speaker to attract the subject to the area and sing a song. If the subject did not respond within 5 min, we played the lure a second time and abandoned the trial for that day if the subject again failed to respond. Seven males that did not respond were tested again later, and all except one responded and were included in the final analysis. When the bird sang its second song after the end of the lure, we started the experiment by broadcasting a song from the experimental speaker so that the song started immediately after the start of the subject’s song (overlapping treatment) or after the end of the subject’s song (alternating treatment). We played songs in response to each of the subject’s songs, ending playback after 10 songs had been broadcast. We continued to monitor the subject for 3 min after the last playback song.

Playback stimuli

We selected high-quality recordings of several different song types from focal recordings of dawn and early morning song bouts of 13 males to use as playback stimuli. Using songs from 13 males in playback to 20 subjects raises the issue of pseudoreplication. However, this low level of replication was used to reduce the influence of source males on treatment sequence: songs from the seven source males that were played to two subjects were balanced with respect to treatment sequence, so one subject received the alternating treatment first and the other received the overlapping treatment first. Each subject

<table>
<thead>
<tr>
<th>Species</th>
<th>Context</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>European robin</td>
<td>Avoid overlapping conspecific song</td>
<td>(Dabelsteen et al., 1997)</td>
</tr>
<tr>
<td>Nightingale</td>
<td>Avoid overlapping conspecific song</td>
<td>(Dabelsteen et al., 1996)</td>
</tr>
<tr>
<td>Great tit</td>
<td>More with increasing number of neighbors</td>
<td>(Osiejuk et al., 2004)</td>
</tr>
<tr>
<td>Yellowhammer</td>
<td>Some males overlap, others follow; overlap songs of simulated intruders</td>
<td>(Naguib, 1999)</td>
</tr>
<tr>
<td>Corn bunting</td>
<td>Overlap songs of simulated intruders</td>
<td>(Balsby and Dabelsteen, 2001)</td>
</tr>
<tr>
<td>Black-capped chickadee</td>
<td>Overlap intruder unless overlapped</td>
<td>(Langemann et al., 2000)</td>
</tr>
<tr>
<td>Poecile atricapillus</td>
<td>Strangers &gt; neighbors; playback in territory &gt; outside</td>
<td>(Brindley, 1991)</td>
</tr>
</tbody>
</table>
heard several songs from one nonneighboring source male (two to five territories away). We used one song type to create the 45-s lure containing four repeats of that song and two different song types for experimental playback, switching between types halfway through. Exactly the same lure and experimental playback songs were used for the two trials on each subject. We used the cursor-delimited filter in the program Syrinx-PC to filter out noise and amplified all recorded songs to the same peak amplitude.

The interactive playback method results in differences between paired trials caused by variation in bird and experimenter behavior that may include factors other than the one of interest. We chose to standardize the amount of playback between trials by playing the same song types the same number of times. Because playback songs were broadcast in response to subject songs, the duration of playback period depended on the rate at which the subject sang. Thus, the experimental period comprised a playback period of variable duration (mean = 4.5 min, range 1–19.5 min) and a 3-min postplayback period. There was no difference in the duration of the playback period in alternating and overlapping trials (Wilcoxon signed-rank Z = −0.5, n = 20, p = .6). In two trials, males moved away from the speakers during the playback period and may have countersung with neighbors in the distance. Because this happened late in the playback period (after the eighth and ninth playback songs, respectively), we included these experiments but scored song rate and song-type diversity as missing values. In one of these trials, one of the playback songs overlapped a female song by mistake. In six trials, males sang one or two songs during the playback period that were not responded to with playback songs. In one trial only nine playback songs were broadcast and in another 11 songs were broadcast.

We confirmed that the two treatments did in fact differ in the factor of interest by quantifying the extent of overlapping. The proportion of all subject songs during the playback period that were overlapped was significantly higher during overlapping (median = 0.9, range 0.6–1.0) than alternating treatments (median = 0, range 0–0.2; Wilcoxon signed-rank Z = −3.8, p < .001, n = 18). For those subject songs responded to with playback, the time from the end of the subject song to the start of the playback song differed significantly between treatments (paired t = 15.6, p < .001, df = 19). In alternating treatments, playback songs started about 1 s after the end of the subject songs (1.05 ± 0.07 s), while in overlapping treatments, playback started about 1 s before the end of the subject songs (−1.27 ± 0.16 s). This translated into a significant difference in the proportion of the length of subject songs that was overlapped during alternating (median = 0.0, range 0–0.12) and overlapping trials (median = 0.47, range 0.26–0.68; Wilcoxon signed-rank Z = −3.9, p < .001, n = 20).

### Response to playback

We used the playback trial logging feature in Syrinx-PC to record the times all sound files were played and to create an audio record of the entire trial, recording vocal responses of the subjects using a Sennheiser ME67 directional microphone connected to the laptop computer. We extracted the following measures of male vocal response from the audio record: (1) song length—mean length of subject songs responded to with playback; (2) song length coefficient of variation (CV)—CV of song lengths, 100 × SD/M; (3) intersong interval CV—CV of intervals between the starts of consecutive subject songs responded to with playback; (4) song rate—songs per minute over the entire experimental period; and (5) diversity—song types/songs over the entire experimental period. In addition, we observed approach to the experimental speaker and extracted the following measures: (1) closest approach and (2) prop. time close—proportion of time spent within 15 m of the experimental speaker over the entire experimental period, including the postplayback period. We also noted whether males overlapped playback songs. We recorded female songs and computed female song rate for the experimental period.

### Analysis

Log transformation normalized vocal measures of response, and square root transformation normalized closest approach data. The proportion of time spent close to the speaker was bimodal, and no transformation normalized it. Associations between different types of response were explored using Pearson correlations or Spearman correlations (Table 4). We used a principal components analysis of the three correlated vocal

### Table 3

<table>
<thead>
<tr>
<th>Species</th>
<th>Approach</th>
<th>Amount of song</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nightingale</td>
<td>&gt;time near overlapper</td>
<td>&gt;, &gt;time singing</td>
<td>(Naguib and Todt, 1997)</td>
</tr>
<tr>
<td>Great tit</td>
<td></td>
<td>&gt;</td>
<td>(Peake et al., 2001)</td>
</tr>
<tr>
<td>Black-capped chickadee</td>
<td>Approach overlap</td>
<td></td>
<td>(Mennill and Ratcliffe, 2004a)</td>
</tr>
</tbody>
</table>

### Table 4

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Length CV</th>
<th>Closest approach</th>
<th>Prop. time close</th>
<th>Song rate</th>
<th>Diversity</th>
<th>Intersong interval CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Song length CV</td>
<td>0.05</td>
<td>−0.06</td>
<td>0.01</td>
<td>−0.81***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Closest approach</td>
<td></td>
<td>−0.06</td>
<td>0.13</td>
<td>−0.81***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prop. time close</td>
<td>−0.09</td>
<td>−0.02</td>
<td>0.07</td>
<td>−0.03</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Song rate</td>
<td>−0.01</td>
<td>0.21</td>
<td>0.00</td>
<td>0.12</td>
<td>−0.54***</td>
<td>0.35*</td>
<td></td>
</tr>
<tr>
<td>Diversity</td>
<td>0.07</td>
<td>0.21</td>
<td>0.00</td>
<td>0.12</td>
<td>−0.54***</td>
<td>0.35*</td>
<td></td>
</tr>
<tr>
<td>Intersong interval CV</td>
<td>−0.07</td>
<td>0.22</td>
<td>−0.26</td>
<td>0.18</td>
<td>−0.63***</td>
<td>0.35*</td>
<td></td>
</tr>
<tr>
<td>Female song rate</td>
<td>−0.09</td>
<td>0.47**</td>
<td>−0.25</td>
<td>0.16</td>
<td>−0.09</td>
<td>0.05</td>
<td>0.11</td>
</tr>
</tbody>
</table>

* p < .05, ** p < .01, *** p < .001.
responses to generate a combined score (PC1) for each male. This vocal response PC1 was normally distributed, had an eigenvalue of 1.99, and explained 66% of the variance. Component weightings were as follows: song rate $= -0.89$, diversity $= 0.75$, intersong interval CV $= 0.80$. The two correlated approach variables were analyzed separately to take advantage of parametric methods for analyzing closest approach.

For normally distributed measures of response, we used repeated measures general linear models to test treatment (alternate, overlap) as a within-subject effect and sequence (alternate first, overlap first) as a between-subject effect, and we also tested the interaction between them to assess the effect of prior experience. For proportion of time spent close, we tested for a treatment effect using Wilcoxon signed-rank tests to compare alternating and overlapping trials within males. To assess the effect of prior experience on proportion of time spent close, we analyzed overlapping and alternating trials separately, using Mann-Whitney tests to compare males that received the overlapping treatment first with those that received it second, and likewise for alternating treatments. Female song rate was also not normalized by transformation and was analyzed with the same method.

We examined the structure of male songs sung during the playback period to determine the mechanism underlying observed variation in song length. Songs consist of a series of phrases with a terminal trill, and different song types vary in length depending on the number and type of phrases they contain, as well as the number of elements within phrases (Figure 1). Song length might vary because males select song types from their repertoire that are "short" (Figure 1a,b) or "long" (Figure 1c,d), because they interrupt a song (omit the terminal trill, Figure 1e), or combine two songs to form a compound song (Figure 1f). The most striking difference in length was between alternating and overlapping trials of males that received the alternating treatment first (see Results and Figure 2a), so we compared songs of these 10 subjects. We counted the number of songs responded to with playback that were interrupted, compound, and short in overlapping and alternating trials. To categorize song types as short, we measured the length of exemplars of each song type in the subject’s repertoire using recordings of dawn and early morning song, calculated the mean song length for each song type, and then designated the shortest third of the repertoire as short song types. We used a logistic regression to determine the contribution of short types, interrupted songs, and compound songs to the difference in song length between alternating and overlapping trials.

Following Naguib (1999), we tested for individual differences in male response by conducting separate one-way ANOVAs for each subject, with subject song length as the response variable and treatment as the explanatory variable. We tested for a relationship between male quality and their responsiveness to overlapping by comparing male weight (season adjusted), nesting success (probability of fledging at least one chick), their minimum age (number of years they were known to have been resident on the territory), and whether or not they survived until the following year.

We used SPSS 12.0 for Windows for computation. Means are presented with standard errors. Data presented graphically are shown untransformed for ease of interpretation.

**RESULTS**

**Overall response to playback**

Banded wrens approached the speaker and sang in response to playback (Table 4). Males that approached the speaker closest also spent a greater proportion of time within 15 m of the speaker. Males that sang at high rates also sang with lower song-type diversity and less variable song intervals. However, approach and vocal responses were uncorrelated. Males sang with more variable song lengths when their females sang at high rates, but all other measures of male response were not correlated with female song rate (Table 4). Individual males showed consistency between the two trials in their closest approach (Pearson correlation $= 0.45$, $n = 20$, $p = .05$) but not in vocal behavior (all $p > .3$).

Males sometimes responded to simulated intrusion by overlapping playback songs (15% of 40 trials). Though males only
overlapped playback in six trials, there was a trend for less close approach in these trials than in those where males did not overlap playback (closest approach in trials with overlapping = 16.2 ± 3.1 m, with no overlapping = 9.9 ± 1.2 m; t = −1.95, df = 38, p = .06).

Female banded wrens seldom sing and can be cryptic at times (personal observation; Molles and Vehrencamp, 1999). However, females were clearly present in at least 24 trials and sang during the experimental period in 21 trials (52.5%) with low song rates overall (median = 0.30 songs/min, range 0–3.5).

**Table 5**

<table>
<thead>
<tr>
<th></th>
<th>Treatment (F1,18)</th>
<th>Sequence (F1,18)</th>
<th>Treatment × Sequence (F1,18)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Song length</td>
<td>8.7***</td>
<td>0.2</td>
<td>5.6**</td>
</tr>
<tr>
<td>Song length CV</td>
<td>5.2**</td>
<td>4.4**</td>
<td>0.04</td>
</tr>
<tr>
<td>Closest approach</td>
<td>0.4</td>
<td>2.9*</td>
<td>1.6</td>
</tr>
<tr>
<td>Vocal response PC1</td>
<td>0.3</td>
<td>1.5</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*p * .1 ≤ p < .05, **p ≤ .05, ***p ≤ .01.

**Male vocal response to overlapping and alternating playbacks**

Male songs were significantly shorter during overlapping than alternating treatments, and this effect was influenced by the sequence in which treatments were presented (Table 5). Post hoc comparisons showed that songs were significantly shorter in overlapping than alternating trials for males that received the alternating treatment first but not for those that received the overlapping treatment first (Figure 2a). There was a trend for songs to be shorter in alternating trials given after overlapping trials than in alternating trials given first, but no difference in song length during overlapping trials associated with order of presentation (Figure 2a). Males singing shorter songs had a smaller proportion of their song lengths overlapped by playback during overlapping trials (Pearson correlation between song length and percentage of overlap = 0.71, p < .001, n = 20). Song length was less variable in overlapping than alternating trials, and it was also less variable among males that received the overlapping treatment first than among those that received the alternating trial first (Table 5, Figure 2b).

The reduction in song length in overlapping trials presented after alternating trials was attributable primarily to males singing more short song types and interrupting more songs during overlapping than alternating trials (short types: 4.8 ± 0.82 in overlap and 2.4 ± 0.87 in alternate, log likelihood \( \chi^2 = 5.9, p = .02 \); interrupted songs: 1.2 ± 0.44 in overlap and 0.4 ± 0.24 in alternate, log likelihood \( \chi^2 = 4.1, p = .04 \)). The number of compound songs males sang did not contribute significantly to the difference between alternating and overlapping trials (1.3 ± 0.51 in overlap and 1.9 ± 0.70 in alternate, log likelihood \( \chi^2 = 0.3, p = .57 \)).

Song rate, song-type diversity, and variability of intersong intervals did not differ significantly between alternating and overlapping treatments. Vocal response (PC1) did not vary with treatment, sequence, or their interaction (Table 5, Figure 3).

Males overlapped playback in two overlapping trials and four alternating trials. Three of the four males that overlapped playback during alternating trials had previously been exposed to overlapping treatments, suggesting that prior experience with being overlapped by playback may have increased the likelihood that males would overlap playback songs, though the sample size was too small for inference.

**Male approach to overlapping and alternating playbacks**

Males exposed to alternating playback first showed a nonsignificant trend to approach the speaker more closely than males exposed to overlapping playback first (sequence effect), but there were no overall differences associated with treatment or the interaction of treatment with sequence (Table 5). Examination of post hoc contrasts showed that during alternating treatments, those males that had previously been overlapped tended not to come as close to the speaker as
males that had not previously been exposed to playback (Figure 4a). Closest approach during overlapping trials was unaffected by the order of presentation (Figure 4a).

The proportion of time males spent close to the speaker was similar in alternating and overlapping trials overall (Figure 4b; Wilcoxon signed-rank $Z = -0.2, n = 19, p = .83$). However, during alternating treatments, those males that had previously been overlapped tended to spend less time close to the speaker than males that had not previously been exposed to playback (Mann-Whitney $U = 22.0, p = .06$). This was not the case in overlapping trials: regardless of whether the overlapping trial was first or second, males spent similar amounts of time close to the speaker (Mann-Whitney $U = 39.0, p = .40$).

**Male characteristics**

Individual males varied in the extent to which they responded differently to the two treatments. Five males sang significantly shorter songs during overlapping than alternating trials (one-way ANOVAs $F_{1,18}$ range $= 9.0–27.2, p < .01$; three of these males had received the alternating treatment first). Three males showed a trend in the same direction ($F_{1,18}$ range $= 3.0–3.4, .05 < p < .10$; one of these males had received the alternating treatment first). The remaining 12 individuals did not vary song length in response to the two treatments assessed ($F_{1,18}$ range $= 0.08–2.7, .12 < p < .79$). We compared several male quality characteristics of these “nonresponders” with males that showed some difference in song length between the two treatments. Males that responded by tending to sing shorter songs when their songs were overlapped did not differ from nonresponding males in weight, their probability of fledging chicks, age, or how likely they were to survive until the following year (Table 6).

Few males overlapped playback, and they did not differ detectably from males that did not overlap playback in weight, age, or how likely they were to survive until the following year (Table 7; nesting success was unknown for two of five overlappers and therefore not presented).

Males exposed to the alternating treatment first did not differ significantly from males that received the overlapping treatment first in any of the male quality characteristics assessed (Table 8).

**Female response to overlapping and alternating playbacks**

Females did not sing at different rates overall in trials where playback alternated with versus overlapped their partners (Wilcoxon signed-rank $Z = -1.6, n = 19, p = .12$), but like males, their response was influenced by the sequence in which treatments were presented (Figure 5). Females sang significantly more during alternating trials if their partner had not previously been overlapped (Mann-Whitney $U = 15.5, p < .01$). However, females sang at similar low rates during overlapping trials regardless of whether the overlapping trial was first or second (Mann-Whitney $U = 42.0, p = .84$).
DISCUSSION

Overlapping elicited an aversive response from banded wrens. Males shortened their songs, apparently to avoid being overlapped. This effect was maintained in alternating trials conducted several days after overlapping trials, indicating that males modify their behavior based on prior experience with a rival. Males also tended to stay further from the speaker if they had previously been overlapped. Shorter songs and reduced approach suggest a less aggressive response, indicating that overlapping may be so threatening that it inhibits aggression. Female response showed a similar effect of prior experience, with females singing at lower rates when playback overlapped the songs of their partners and during alternating trials that had been preceded by an overlapping trial. There were individual differences among males in their responsiveness to the treatments, but we found no difference in the quality of “responding” versus “nonresponding” males.

Male banded wrens sang songs that were shorter and had less variable lengths during overlapping trials than during alternating trials. Experimental studies on song overlapping have consistently shown that birds modify the timing of their songs to avoid being overlapped (Table 2). Black-capped chickadees (Poecile atricapillus) also sang shorter songs when overlapped by playback, with a similar trend in corn buntings (Miliaria calandra). In contrast to banded wrens, variability in song length increased in response to overlapping in black-capped chickadees and great tits (Parus major; Table 2). Nightingales (Luscinia megarhynchos) and black-capped chickadees increased the variability of intervals between songs when overlapped (Table 2), but intersong intervals were unaffected by overlapping in banded wrens.

Like nightingales and black-capped chickadees, male banded wrens reduced song length by interrupting more songs in overlapping than alternating trials (Mennill and Ratcliffe, 2004b; Naguib, 1999). In addition, banded wrens selectively used more short song types from their repertoire. Repertoires of song types increase signal diversity, but different song types are sometimes considered functionally equivalent (Krebs, 1976). However, there is increasing evidence that song types (Vehrencamp, 2001) and some structural features (Podos, 1997; Staicer, 1996) may differ functionally. Banded wrens selectively use song types of longer duration and broader bandwidth during intense dawn chorus singing versus later in the morning and when countersinging at the territory edge versus solo singing in the territory center (Trillo and Vehrencamp, 2005). This use of longer songs during more aggressive contexts is consistent with our interpretation of reduced aggression during overlapping treatments in this study.

Despite paired trials being separated by 2–5 days, the responses of male banded wrens were influenced by prior experience with an overlapping intruder. The reduction in song length associated with being overlapped was significantly influenced by the sequence in which treatments were presented. The interaction between treatment and sequence was not significant for any other measure of response (Table 5), but the reversal in the direction of the difference in median responses to the two treatments associated with sequence of presentation evident for song length was also evident for all other measures of response (Figures 2–4). The trend for males that had previously been overlapped to sing shorter songs during alternating playback (Figure 2a) was paralleled by trends for males previously overlapped by playback to sing songs with less variable lengths (Figure 2b), approach the speaker less closely, and spend less time close to the speaker (Figure 4). This was not merely a consequence of general previous experience with playback as responses to overlapping trials did not differ depending on whether they followed an alternating trial or not.

Female banded wrens responded to playback of male song by singing and were also influenced by prior experience of a male intruder overlapping the songs of its partner, reducing the intensity of their response during alternating trials that had been preceded by an overlapping trial several days before. This is the first study to document effects of song overlapping between males on the behavior of females during playback. Other studies on signal overlap have shown that female assessment of relative male quality and subsequent choices about pairing and mating are influenced by the relative timing of signals in vocal interactions between males, with females preferring males that do the overlapping to those that are overlapped (Mennill et al., 2002; Miyazaki and Waas, 2002; Otter et al., 1999). In banded wrens, females may have been inciting competition between males to facilitate assessment of male quality, or they may have been engaging in intersexual territorial defense. Banded wrens do not duet (Molles and Vehrencamp, 1999), but most of their congeners do (Brown

### Table 6

<table>
<thead>
<tr>
<th>Male characteristics (means ± SD or probability): males that responded to being overlapped (n = 8) versus nonresponders (n = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Responder</td>
</tr>
<tr>
<td>Weight (grams)</td>
</tr>
<tr>
<td>Nest success</td>
</tr>
<tr>
<td>Minimum age (years)</td>
</tr>
<tr>
<td>Survival</td>
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</tbody>
</table>

### Table 7

<table>
<thead>
<tr>
<th>Male characteristics (means ± SD or probability): males that overlapped playback songs (n = 5) versus males that did not overlap playback (n = 15)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overlapper</td>
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<tr>
<td>Weight (grams)</td>
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<td>Minimum age (years)</td>
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<td>Survival</td>
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</tbody>
</table>
Table 8
Male characteristics (means ± SD or probability): males receiving overlapping treatment first versus alternating treatment first

<table>
<thead>
<tr>
<th></th>
<th>Overlapping first</th>
<th>Alternating first</th>
<th>Test</th>
<th>n (df)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight (grams)</td>
<td>20.2 ± 0.9</td>
<td>20.4 ± 0.9</td>
<td>Mann-Whitney U = 37.5</td>
<td>19 (17)</td>
<td>.57</td>
</tr>
<tr>
<td>Nest success</td>
<td>0.67</td>
<td>0.33</td>
<td>Fisher’s Exact</td>
<td>20 (1)</td>
<td>.61</td>
</tr>
<tr>
<td>Minimum age (years)</td>
<td>3.4 ± 3.8</td>
<td>2.7 ± 2.5</td>
<td>Mann-Whitney U = 40.0</td>
<td>20 (18)</td>
<td>.44</td>
</tr>
<tr>
<td>Survival</td>
<td>0.5</td>
<td>0.8</td>
<td>Fisher’s Exact</td>
<td>20 (1)</td>
<td>.35</td>
</tr>
</tbody>
</table>

and Lemon, 1979; Farabaugh, 1982), and partners defend territories together (Logue and Gammon, 2004). In banded wrens, male and female song rates were not correlated, and their approaches did not appear to be closely coordinated (males also occasionally chased their partners during playback), but further work is needed to determine whether or not males and females coordinate their response to simulated intrusion. This is the first field study to demonstrate an effect of being overlapped maintained over several days in both male and female responses to playback. Further testing is required to determine whether this was a generalized response to all intruders or specific to the individual (or song types or location) associated with the prior interaction. In a study on two captive blackbirds that avoided singing from perches where their song was consistently overlapped, this conditioned aversion diminished only slightly over 4 days without playback (Todt, 1981). A field study on nocturnally singing nightingales where the two trials were presented a few minutes apart also showed an effect of prior experience being overlapped (Naguib, 1999). Male nightingales sang at higher rates during overlapping than alternating trials and at higher rates in alternating trials that followed overlapping trials than in those presented first. The latter may have been a consequence of high arousal during overlapping causing high song rates in the alternating trial following soon after (Naguib, 1999). The reduced song length of banded wrens in alternating trials following overlapping trials was clearly not an immediate effect of being overlapped and is consistent rather with a functional modification of response due to prior experience with a rival (Naguib, 1999). Individual males showed some consistency between trials in the closeness of their approach to playback, and individuals also differed in their responsiveness to the treatments. However, we found no significant differences in the characteristics of males who responded to overlapping by reducing song length. We also found no differences in the characteristics of males that overlapped playback versus those that did not. However, few males overlapped playback in this study, and a larger sample size is necessary to determine whether males that overlap differ in quality from males that do not overlap. A possible alternative explanation for response differences between males receiving different treatment sequences might be that there were some underlying differences in male “quality” in the two groups of males. However, we found no differences in any of the measures tested.

Song overlapping is viewed as a directed agonistic signal (Todt and Naguib, 2000), yet overlapping playback seldom elicits aggressive responses from receivers. Though banded wrens use longer song types in more aggressive contexts (Trillo and Vehrencamp, 2005), they were less likely to use long song types or approach closely if they had previously been overlapped. This contrasts with the rapid approach elicited by song-type matching, another singing strategy used in this species (Molles and Vehrencamp, 2001). Though European robins (Erithacus rubecula) and nightingales sang at higher song rates when their songs were overlapped by playback and robins switched more quickly to an aggressive mode of singing, “twittering”, no studies have found that overlapping playback elicits closer approaches or longer songs from receivers than alternating playback (Table 2). Rather, black-capped chickadees sang shorter songs when overlapped, with a similar trend in corn buntings. Corn buntings also spent less time close to the speaker during overlapping trials, while yellowhammers (Emberiza citrinella) were slower to approach the speaker (Table 2). The slower approach by yellowhammers may have been a proximate effect of overlapping playback limiting the ability of subjects to detect and locate their “rival” (Osiejuk et al., 2004). However, this was clearly not the case in banded wrens, as the tendency to spend less time close to the speaker occurred when playback songs followed subject songs, in alternating trials presented after overlapping trials. The tendency for banded wrens to reduce approach and song length if they had previously been overlapped suggests rather that overlapping is so threatening that it is intimidating and reduces the likelihood of aggressive close approaches and long song types. Intrusions into the territory center are uncommon in our population, and playback simulating an intruder singing well within territory boundaries and overlapping 10 songs in succession would have been extremely threatening.

Figure 5
Female song rate (per minute) during trials when playback alternated with or overlapped the songs of their partner. Responses of females paired with males that received the alternating trial first are presented separately from those that received the overlapping trial first. Asterisks indicate significant differences (**p < .01).
Examining overlapping from the perspective of the signaler, rather than the receiver, may shed light on why overlapping elicits an aversive response. Some signals are aversive because they are given at close range and associated with willingness to escalate an interaction or a high probability of attack. For example, screeching in red squirrels (Tamiasciurus hudsonicus) is closely associated with attack by the signaler and retreat by the receiver (Lair, 1990). Likewise, the A-songs of willow warblers (Phylloscopus trochilus) are associated with overt attack behavior and tend to cause receivers to withdraw (Jarvi et al., 1980). The honesty of such signals is likely to be maintained by vulnerability to retaliation by the receiver (Vehrencamp, 2000). Robins were more likely to overlap songs of strangers than those of neighbors and approached songs of strangers more closely than those of neighbors (though the correlation between overlap and approach was not explicitly tested), and playback from just inside the territory boundary was more likely to be overlapped than playback from further away outside the territory (Brindley, 1991). However, great tits overlapped playback from a distance, and when playback escalated, they approached more closely but overlapped playback less (Langemann et al., 2000). Likewise, the closest approach of banded wrens that overlapped playback tended not to be as close as that of males that did not overlap playback. Further work from the signaler’s perspective to identify behaviors associated with overlapping is necessary to determine whether song overlapping in birds indicates willingness to escalate an interaction.

Individuals also attend to the timing of vocal interactions between others, discriminating between overlapper and overlapped in these interactions. Studies on the response of cavedroppers suggest that signal overlap is aggressive because it indicates dominance over a rival to other potential receivers by masking the signal of a rival, without necessarily indicating willingness to attack. For example, cavedropping males respond more aggressively to leaders of dyadic interactions (Naguib et al., 1999), but if the second signal overlaps the first, then the overlapper elicits a more aggressive response than the overlapped (leading) male (Mennill and Ratcliffe, 2004a; Naguib and Todt, 1997). Female birds may prefer the male that does the overlapping over males who are overlapped (Mennill et al., 2002; Miyazaki and Waas, 2002; Otter et al., 1999). In rodents too, females may devalue males whose scent has been overmarked or may show no preference for them (reviewed in Johnston, 2003). Females prefer leading males in many insects and anurans, and this tends to lead to call alternation among neighboring males when song rates are low and call synchrony when song rates are high (Greenfield, 1994; Greenfield et al., 1997). A notable exception to synchrony as an epiphenomenon among anurans is the running frog (Kassina pusca), where females prefer leaders of overlapping interactions if the percentage overlap is high and followers if it is lower (Grafe, 1999). Males in this species time their signals competitively, overlapping rival males at the low percentage overlap that results in a female preference for followers (Grafe, 1999).

In summary, receivers generally respond to overlappers by temporal modification of their own signals to avoid being overlapped. Being overlapped influences the behavior of male banded wrens and their partners for a number of days following the interaction. Being overlapped may be costly if overlapping indicates dominance to other same- or opposite-sex individuals in the communication network. Though song overlapping in birds is considered an aggressive signal, it rarely elicits overt aggression in response, and further work is needed to determine whether signalers accompany song overlapping with other aggressive behaviors to escalate an interaction. Likewise, further investigation of the individual characteristics of males who overlap other males or who are responsive to being overlapped is necessary to determine the causes and consequences of these individual differences.

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REFERENCES


Trillo PA, Vehrencamp SL, 2005. Song types and their structural features are associated with specific contexts in the banded wren. Anim Behav 70:921–935.

