

Eavesdropping and communication networks revealed through playback and an acoustic location system

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Our understanding of animal communication is expanding from a dyadic framework of one signaler and one receiver to a broader communication network model, yet empirical studies of communication networks are scarce. To investigate whether territorial males eavesdrop on interactions occurring outside of their territory boundaries and to quantify the neighborhood-level effects of song contests, we simulated diurnal dyadic countersinging exchanges in the undefended spaces between established territories of black-capped chickadees (*Poecile atricapillus*). In each of 10 neighborhoods, we used stereo playback to simulate interactions between 2 unknown rivals. We simulated 2 types of song contests that differed only in the relative timing and patterning of the songs of the contestants; aggressive treatments contained frequency matching and song overlapping, whereas submissive treatments contained neither matching nor overlapping. We used a 16-microphone acoustic location system to record males in the neighborhood surrounding the playback apparatus. Territorial chickadees responded more intensely to the aggressive treatments than the submissive treatments. Neighborhood song output (number of songs produced by all individuals in the recording area) was twice as high after aggressive playback than after submissive playback. Males with territories bordering the playback apparatus had higher song output than males who were more than one territory removed from the playback apparatus. We did not find an influence of male dominance rank on playback responses. Our results reveal that territorial male chickadees eavesdrop on and respond to interactions occurring outside of their territory boundaries. *Key words*: acoustic location system, black-capped chickadee, countersinging, eavesdropping, overlapping, song matching. [*Behav Ecol* 19:824–829 (2008)]

Animal communication mediates many important social behaviors including mate attraction and resource defense, yet the wider social environment in which communication occurs has only been studied in detail recently (McGregor and Peake 2000). Conventional studies of communication have tested hypotheses using simple dyadic models involving one signaler and one receiver, but recent research emphasizes communication networks involving many signalers and receivers (McGregor 2005). Indeed, there has been a recent surge of interest in the study of the use of public information by animals (reviewed by Bonnie and Earley 2007). A communication network is a group of several individuals within signaling and receiving range of one another, and there is potential for a communication network to exist whenever animal signals travel further than the average spacing between individuals (McGregor 2005).

Early studies of communication networks in chorusing insects (e.g., Otte 1974) and frogs (e.g., Ryan et al. 1981) have prompted investigation of networks in other taxa and signaling modalities. Avian vocal communication, however, has been difficult to study at a network level because of the logistic challenge of recording and monitoring several individuals simultaneously during long-range interactions. Songbirds commonly hold adjacent territories forming neighborhoods, and several males sing within signaling range of one another (Naguib 2005). Recent experimental studies have provided

evidence for several communication network-based behaviors, including eavesdropping, wherein an individual gains relative information about 2 individuals involved in a signaling interaction (e.g., Naguib and Todt 1997; Peake et al. 2001; Mennill and Ratcliffe 2004a), and audience effects, wherein an individual modifies its behavior during a contest based on the presence of bystanders (e.g., Tachon et al. 1999; Matos and McGregor 2002). However, due to the long-range, dynamic nature of songbird vocal interactions and the lack of suitable technology, the study of communication networks in songbirds has been limited thus far to cases of 3-party communication networks and has not been extended to the broader networks theorized to exist in free-living territorial animals.

An acoustic location system (ALS) is a promising new tool for studying communication networks, providing the opportunity to examine the wider social context of interactions and the potential selective effects of eavesdroppers on animal communication systems. An ALS consists of an array of simultaneously recording microphones connected to a multichannel recording device capable of triangulating the position of multiple individuals based on delays in sound arrival time to the microphones. An ALS offers unique advantages for studying networks of songbirds because it is a passive system which allows simultaneous monitoring of multiple individuals while providing accurate location and movement information for these individuals (McGregor et al. 1997; Mennill et al. 2006; Fitzsimmons et al. 2008). An ALS thereby facilitates the recording of networks of songbirds and allows us to evaluate how the singing behavior of territorial males is influenced by the songs of surrounding individuals.

The black-capped chickadee (*Poecile atricapillus*) provides an excellent study organism for investigating communication at

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a network level. Chickadees spend the winter in flocks structured by stable, linear dominance hierarchies, and winter dominance status serves as a proxy for individual quality (Ratcliffe et al. 2007). Early in spring, winter flocks break up and males establish all-purpose breeding territories. Males defend their territories against former flockmates and males from nearby flocks, forming neighborhoods of breeding pairs that contain high-quality (high ranking) and low-quality (low ranking) males. Males engage in countersinging contests with their neighbors to repel rivals and also to attract social and/or extrapair mates (Mennill and Otter 2007). Singing performance is an honest advertisement of male quality (Otter et al. 1997) and is used by females to assess their partners and neighboring males (Mennill et al. 2002). A network model has the potential to enhance our understanding of chickadee communication, as each neighborhood contains several males and females within signaling range of one another.

Interactions are rarely studied beyond a dyadic context, although the dynamics within a dyadic context are increasingly well understood (Todt and Naguib 2000). During black-capped chickadee countersinging interactions, males adjust the frequency and timing of their songs with respect to their opponent (Fitzsimmons et al. 2008). Males sing a single song type, a tonal 2-note “fee bee,” and are capable of frequency-matching opponents by transposing their song across a continuous frequency range of approximately 860 Hz (Mennill and Otter 2007). Interactive playback experiments (Mennill and Ratcliffe 2004b) and observational studies (Fitzsimmons et al. 2008) reveal that frequency matching and song overlapping occur commonly during countersinging interactions and appear to be signals of aggressive intentions. Both male and female chickadees eavesdrop on male–male countersinging interactions to gain relative information about contestants to direct future antagonistic and reproductive decisions (Mennill et al. 2002, 2003; Mennill and Ratcliffe 2004a). Similar results have been found in other songbird species including nightingales (*Luscinia megarhynchos*; Naguib and Todt 1997) and great tits (*Parus major*; Peake et al. 2001). It is becoming increasingly clear that countersinging interactions may influence other individuals in a communication network.

To evaluate neighborhood-level communication network effects of song contests, we simulated dyadic countersinging exchanges in the undefended spaces between established territories of male black-capped chickadees. We used a 16-microphone ALS to test whether males in the surrounding neighborhood would respond to these simulated interactions. In each of 10 neighborhoods, we used stereo playback to broadcast 2 types of simulated song contests. The contests differed only in the intensity of aggressive signaling between the simulated rivals. One playback treatment (aggressive) simulated a high-intensity exchange between 2 unknown rivals, involving frequency matching and overlapping. The other playback treatment (submissive) simulated a low-intensity exchange between 2 unknown rivals, involving no matching or overlapping. Under the communication network model, we predicted that males in the neighborhood surrounding the simulated interactions would respond by altering their song output or song patterns. Under a dyadic model, in contrast, we predicted that males would not alter their singing behavior in response to the simulated countersinging exchanges. We used the ALS to quantify how far reaching the responses to the simulated interactions may be, evaluating whether the simulated contests influenced only males in territories adjacent to playback sites or males more distant from playback sites as well.

Previous playback experiments revealed that male black-capped chickadees eavesdrop on interactions occurring within their territory boundaries (Mennill and Ratcliffe 2004a). We expanded the scope of the investigation of eavesdropping to

test if males also eavesdrop on interactions occurring outside of their territory boundaries. Our experimental design allowed us to evaluate male eavesdropping because the 2 treatments contained no absolute differences in song output, and only relative differences in the frequency and time characteristics of the songs broadcast through the 2 loudspeakers. If males eavesdrop on countersinging interactions outside their territory boundaries, we predicted that males would respond differently to the 2 types of simulated interactions.

MATERIALS AND METHODS

Field methods

We conducted a 2-treatment playback experiment in each of 10 black-capped chickadee neighborhoods at the Queen's University Biological Station near Kingston, Ontario, Canada (44°34'N, 76°19'W). Playbacks were conducted in 2005 and 2006 between 30 April and 15 May, and 810 and 0945 h. At this time of year, females are fertile and male–male countersinging interactions are common (Mennill and Otter 2007). We banded adult chickadees in the winter of each year with aluminum Canadian Wildlife Services bands as well as unique combinations of colored leg bands ($N = 149$ individuals in 2005 and 236 individuals in 2006). We determined the winter dominance ranks of males by observing pairwise interactions at feeding stations ($N = 2811$ interactions in 2005 and 8423 interactions in 2006). A bird was scored as dominant if it supplanted or chased an opponent, resisted a supplanting attack by an opponent, elicited a submissive posture in an opponent, or fed while an opponent waited to approach a feeder (for details, see Ratcliffe et al. 2007). We classified “high-ranking males” as the top-ranking male in flocks with 2 or 3 males or the top 2 males in flocks with 4 or 5 males. We classified “low-ranking males” as the bottom-ranking male in flocks with 2 or 3 males or the bottom 2 males in flocks with 4 or 5 males. We classified “mid-ranking males” only in flocks with 3 or 5 males.

Our ALS consisted of an array of 16 omnidirectional microphones connected to a central computer by 2200 m of microphone cable. The microphones were housed in rain guards made of PVC tubing mounted on top of 3-m wooden poles. Microphone poles were elevated off the ground and attached to trees with bungee cords. Input from all microphones was digitized using a multichannel data acquisition card (National Instruments DAQ-6260) and stored as 16-channel digital sound files using Chickadee V1.9 recording software (J. Burt, Seattle, WA). This design was an extension of the 8-microphone system used by Mennill et al. (2006). Each 16-channel microphone array recorded an area of approximately 160 000 m² and encompassed the territories of 7–10 male chickadees. Recorded neighborhoods consisted of birds familiar with one another from the previous winter, from either the same winter flock or the adjacent winter flocks.

In April of each year, as winter flocks began to break up and breeding pairs began to defend territories, we visited each pair every 2–4 days. We mapped breeding territories according to the method of Bibby et al. (1992), recording the movements and territorial interactions of each pair on a detailed map by using landscape features and grid flags as landmarks. We considered a pair's territory to be the maximum extent of space exclusively occupied by the pair after the period of winter flock breakup but before the female's fertile period.

Playback design

Our playback apparatus consisted of 2 loudspeakers (Sony SRS-77G) mounted on 1.8-m poles and separated from each

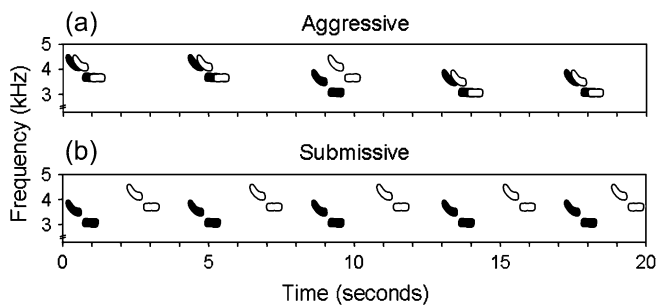


Figure 1

Stylized sound spectrograms of playback stimuli that simulated countersinging interactions between 2 male black-capped chickadees, one shown in black and the other shown in white. (a) In aggressive treatments, the songs of one simulated male overlapped the songs of the other, and the simulated males were frequency matched within 50 Hz. Halfway through the contest, the males switched from being frequency matched at a high frequency to a low frequency. (b) In submissive treatments, the simulated males alternated song timing and sang at distinctly different frequencies. The 10 songs from the middle of each type of treatment are depicted; each treatment contained 30 songs in total, 15 from each simulated male.

other by 24 m. We positioned the 2 loudspeakers in undefended spaces between the established territories of resident males in order to simulate a countersinging interaction between birds attempting to insert themselves in an undefended space.

As part of a larger study of avian communication networks, we recorded each neighborhood of chickadees for 2 or 3 days and then moved the ALS into a different neighborhood. Playback sessions were conducted on the final day of recording in each neighborhood so that playback sessions were never run on successive days. We recorded each neighborhood for a control period prior to broadcasting the 2 playback treatments. Each neighborhood received one treatment where we broadcast a highly “aggressive” interaction between 2 simulated rivals and another treatment where we attempted to broadcast a more “submissive” interaction between 2 simulated rivals (Figure 1). Song overlapping and frequency matching are directed signals of aggression in naturally occurring chickadee song contests (Mennill and Otter 2007; Fitzsimmons et al. 2008). In our aggressive treatments, the songs of one simulated male consistently overlapped the songs of the other and the simulated males were frequency matched within 50 Hz. In the submissive treatments, by contrast, the songs of the 2 simulated males were broadcast at different frequencies (frequency difference: 496 ± 4 Hz) and their songs did not overlap in time.

In both treatments, we broadcast an equal number of songs at high and low frequencies (15 songs at each of 3620 ± 3.4 Hz and 3124 ± 6.8 Hz, respectively). In submissive treatments, one simulated male sang all his songs at the higher frequency and the other simulated male sang all his songs at the lower frequency. In aggressive treatments, both simulated males sang songs at the higher frequency and then both males switched to the lower frequency halfway through the simulated interaction (one bird shifted from the high frequency to the low frequency after 7 songs and the other after 8 songs, resulting in 15 songs at each frequency). We alternated the presentation order of playback treatments with each subsequent experiment. We began playback after at least 1 min without any chickadee singing activity across the entire neighborhood, which we monitored by assessing a real-time scrolling spectrograph of input from all 16 microphones at the central computer. Each

playback treatment lasted 1 min and was followed by a 10-min period where we monitored the behavior of all males recorded by the ALS. Once 30 min had elapsed after the first treatment was broadcast, we began the second treatment after observing 1 min with no chickadee singing activity across the entire neighborhood (average delay between playback treatments: 54.80 ± 4.11 min).

Playback stimuli were created using an established protocol (Mennill and Ratcliffe 2004a). We used recordings of 6 different chickadees recorded in our study population in 2000 to create songs for 3 different simulated intruders, pairing the “fee” note of 3 songs with the “bee” note of the other 3 songs at population-typical frequency and time differences. Using CoolEdit 2000 (Syntrillium, Phoenix AZ), we subtly modified the 3 recordings so that they were of the same length, amplitude, and frequency. We used CoolEdit to create 2-channel stimuli, putting the contributions of each of the simulated rivals in either the left or the right channel. We created 12 two-channel sound files, which included all combinations of interactions between the 3 simulated males. For the aggressive treatments, we alternated the roles of overlapping/overlapped male so that each simulated male had these roles an equal number of times (i.e., 6 possible combinations of interactions between the 3 simulated intruders). Additionally, each simulated male was represented in the left and right channel an equal number of times, for a total of 12 two-channel sound files. We then randomly selected an aggressive and a submissive playback treatment for each experiment (random choice without replacement until 10 were assigned).

This playback design allowed us to test whether individuals eavesdrop on interactions occurring outside of their territory boundaries. In all playback treatments, we broadcast the same number of songs for each simulated male (15 songs per male) and the same number of songs at high and low frequencies (15 songs at each frequency), and all songs were broadcast at the same amplitude (90 dB Sound Pressure Level, measured at 1 m from the playback speakers using a Realistic 33-2050 sound-level meter). The sole difference between aggressive and submissive treatments was the pattern and timing with which the songs were broadcast from the speakers. In other words, birds would only respond differently to the 2 treatments if they were eavesdropping on the relative information contained in the playback stimuli (i.e., pattern- and time-specific features) because there were no absolute differences in the output of the 2 treatments.

Analysis of playback responses

We examined singing activity in each neighborhood at 3 time points: during the 10 min immediately preceding the first round of playback (control period), during the first round of playback and the 10 min immediately after playback, and during the second round of playback and the 10 min immediately after playback. We used Syrinx-PC (J. Burt, Seattle, WA) to view and annotate 16-channel spectrograms of array recordings. We annotated all chickadee songs in the time periods of interest using the frequency and time cursors in Syrinx-PC. From the resulting annotation files, we analyzed playback responses at 2 levels. At the neighborhood level, we evaluated 1) the number of males singing, per minute, throughout the entire recording area and 2) neighborhood song output, which we define as the total number of songs produced by all individuals in the recording area, expressed per minute. At the individual level, we evaluated the number of songs produced by each individual within the recording area, expressed as songs per minute, and compared this with the male’s territory position and his dominance status. We used a combination of focal recordings, field notes, fine structural characteristics,

and location information to confirm the suspected identities of singing males. We could not identify the singing male for 3 of 118 recorded song bouts; singing data from these 3 males were included in all analyses except for the analysis of rank because the rank information was unknown for these unidentified males. Males were classified by location relative to playback; “adjacent” males had territories bordering the area where we set up the playback apparatus, whereas “distant” males had at least one male’s territory between their territory and the playback area.

Statistical analyses

We conducted 1-factor analysis of variance (ANOVA) to examine the effect of playback treatment (aggressive and submissive) on the number of males singing within the 10 recorded neighborhoods and on the neighborhood song output. We conducted 3-factor ANOVA to examine the effects of playback treatment (aggressive and submissive), male proximity to playback (adjacent and distant), and male dominance rank (high, mid, and low) on males’ individual song rate. Data on individual song rate were square-root transformed to meet the assumptions of normality necessary for parametric statistical analyses. We performed all statistical analyses in JMP 5.1 (SAS, Cary, NC). Values are given as mean \pm standard error. All tests are 2 tailed.

RESULTS

At the neighborhood level, we found no difference in the number of males singing before playback and after the 2 playback treatments (Figure 2a; ANOVA: $F_{2,27} = 0.94$, $P = 0.40$). However, neighborhood song output after aggressive playback was more than double that after submissive playback (Figure 2b; ANOVA: $F_{2,27} = 3.78$, $P = 0.04$).

At the individual level, we analyzed all 118 bouts of singing recorded in 10 experiments: 40 in control periods, 44 after aggressive playback treatments, and 34 after submissive playback treatments. The song rates of individual males varied significantly with proximity to playback and showed a nonsignificant trend with respect to playback treatment (Figure 3) but showed no relationship with male dominance rank (ANOVA—whole model: $F_{5,103} = 2.67$, $P = 0.02$; proximity to playback: $F_{1,103} = 7.08$, $P = 0.01$; playback treatment: $F_{2,103} = 2.86$, $P = 0.06$; rank: $F_{2,103} = 0.65$, $P = 0.52$). Males showed a tendency to sing more songs after aggressive playback than submissive playback, and males with territories bordering the playback apparatus sang more songs after playback treatments than distant males.

DISCUSSION

Our neighborhood-level recordings support the prediction, under the communication network model, that male black-capped chickadees respond to simulated dyadic interactions in their neighborhood, even when these interactions take place outside their breeding territory. Territorial males responded differently to playback treatments varying only in the relative contribution of the 2 simulated opponents; males responded with higher song output to simulated countersinging interactions that featured frequency matching and song overlapping, and with lower song output to countersinging interactions that featured neither matching nor overlapping. Neighborhood song output was higher after aggressive playback treatments than after submissive treatments. Individual song output after playback was influenced by proximity to playback; males with territories bordering the playback apparatus had higher song output than more distant males in the neighborhood. In using an ALS to record entire neighborhoods

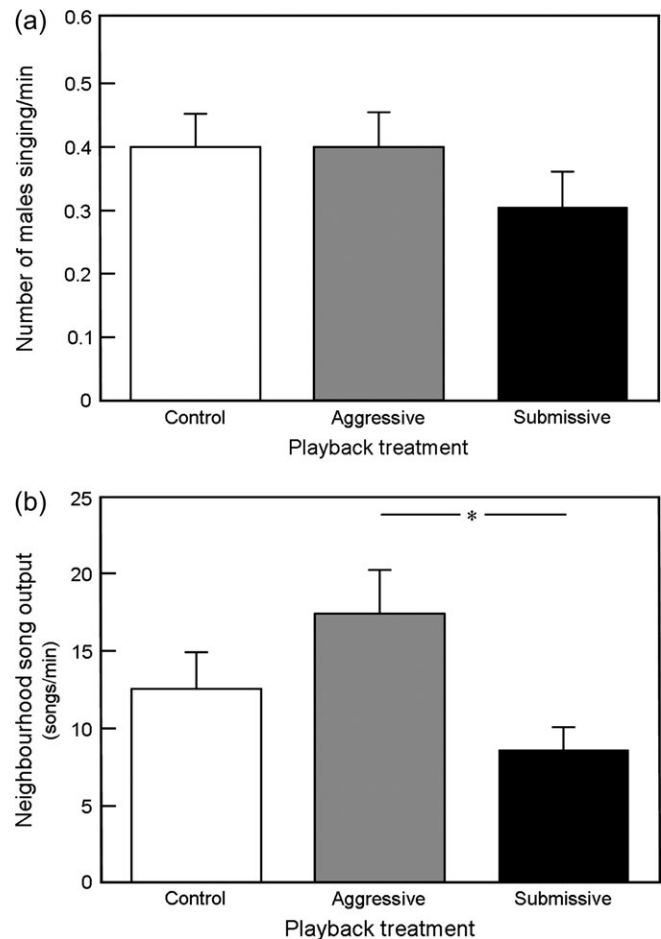


Figure 2

The influence of playback treatment on the number of males singing and neighborhood song output. (a) The mean number of males singing in the neighborhood. (b) The mean neighborhood song output; song output was significantly higher after aggressive playback treatments than after submissive treatments. Asterisk shows significant difference between groups at $P < 0.05$. Error bars show standard errors.

of black-capped chickadee territories, this study is the first to quantify the extent of the effect that dyadic exchanges have on a communication network in free-living animals.

Higher song output, both at the neighborhood and at the individual level, indicates that the simulated males engaged in an aggressive interaction may have been perceived as more threatening to territory holders than males engaged in a submissive interaction. Previous playback studies involving a variety of different songbird species have revealed that territorial males respond more strongly to intruders who overlap (e.g., Naguib and Todt 1997; Mennill and Ratcliffe 2004a) and match (reviewed in Vehrencamp 2001) during countersinging interactions. On hearing an aggressive interaction between 2 strangers outside their territory, male black-capped chickadees may have increased song output to assert their presence and to prevent future direct threats to their own territories. Additionally, males may have increased song output in response to their neighbor’s increasing singing activity. Not surprisingly, males bordering the playback area had higher song output than more distant males in the neighborhood. Males adjacent to the simulated conflict are at a greater risk of facing one of the rivals in a future interaction. Alternatively, more distant males may not have heard the playback and

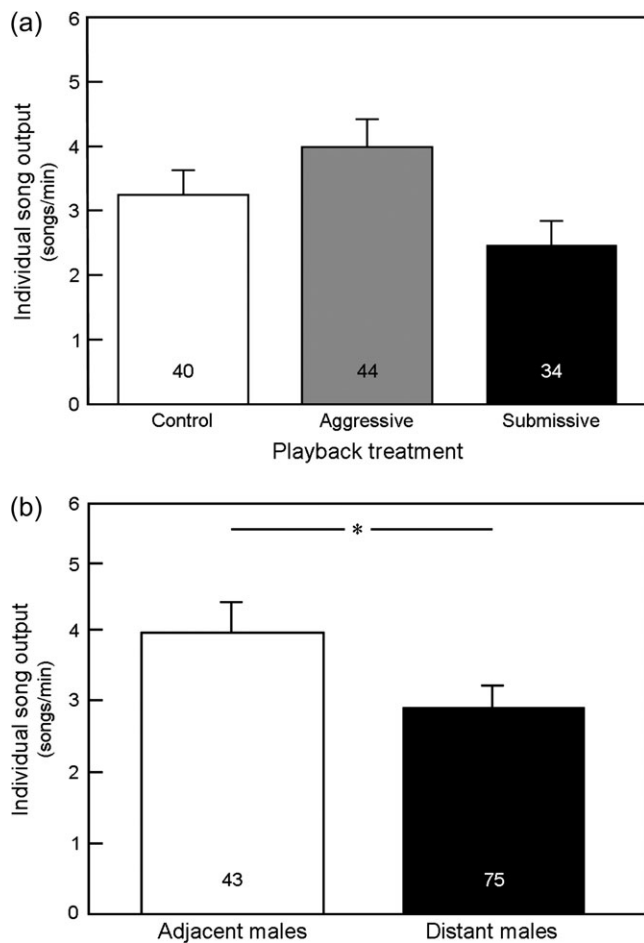


Figure 3

The influence of playback treatment and male proximity to playback on individual song output. Numbers of song bouts are shown at the base of each bar. (a) Individual song output was higher after aggressive playback treatments than after submissive treatments. (b) Song output was higher for males with territories bordering the playback area than for distant males in the neighborhood. Asterisk shows significant difference between groups at $P < 0.05$. Error bars show standard errors.

hence did not alter singing behavior with respect to playback. Indeed, many distant males were farther than 80 m from playback, beyond the distance that chickadee song has been conservatively estimated to travel (Christie et al. 2004).

Our results corroborate previous findings, which demonstrate that male black-capped chickadees eavesdrop on countersinging interactions between rivals (Mennill and Ratcliffe 2004a), and, importantly, our results provide evidence that male chickadees eavesdrop on interactions that occur outside of their territory boundaries. Because the 2 playback treatments used in our experiment differed only in the singing strategies used by the 2 simulated rivals and not in the absolute number, frequency, or amplitude of songs, resident males could only gain relative information from the simulated interactions. The higher song rate that we observed in response to aggressive treatments, but not submissive treatments, therefore demonstrates that males were eavesdropping on the exchanges between the simulated rivals (*sensu stricto* social eavesdropping; Peake 2005). Using radio tracking to monitor silent movements, Naguib et al. (2004) found that male nightingales eavesdrop on interactions occurring in neighbor's territories and intrude earlier after intense interactions. Peake

et al. (2001) found that territorial male great tits also eavesdrop on countersinging exchanges occurring outside of their territory boundaries. Using stereo playback, they simulated a countersinging interaction between 2 strangers outside of a focal great tit's territory boundary. After the simulated interaction outside of their territory, focal males were directly challenged inside their territory by one of the simulated males. Territorial great tits adjusted their song rate during these challenges based on the relative information they had gathered by eavesdropping on the previous interaction between 2 simulated strangers (Peake et al. 2001). Taken together, these studies of eavesdropping and communication networks demonstrate that birds are attentive to the behavior of conspecific individuals outside of their territory boundaries.

Singing strategies in different social contexts are under different selection pressures; animals may behave very differently when faced with a rival intruding directly into their territory compared with an indirect, but nearby, interaction between 2 strangers. We did not simulate an intrusion or attempt to actively engage a territory holder as in most playback experiments (e.g., Naguib and Todt 1997; Peake et al. 2001; Mennill and Ratcliffe 2004a); rather, we simulated unfamiliar rivals attempting to establish a territory nearby without directly threatening the resident birds' territories. Communication network-level effects may be more subtle than responses to playback directly challenging males within their territories. Individuals may store information for a later time instead of acting on it immediately (e.g., Hall et al. 2006; Schmidt et al. 2007). Future studies should expand the approach we have used here by engaging territorial males directly in a countersinging exchange and evaluating the subsequent behavior of males in nearby territories. Such an interaction may have a broader influence on the communication network because neighbors may be able to gain more information from overhearing a known neighbor interacting with a stranger than they can from 2 strangers interacting with each other.

We did not find an influence of male rank on playback responses, which may be related to our playback design involving indirect challenges to resident males. Mennill and Ratcliffe (2004a) observed rank-related differences in song output when they directly challenged territory holders by simulating rivals intruding into resident birds' territories. Male dominance status may factor into singing behavior when males actively engage rivals within their own territories, but both high- and low-ranking males may behave in a similar fashion when they sing in response to a nearby but indirect threat.

In many territorial songbirds, individuals settle within singing distance of several conspecifics and use vocal signals to interact with one another. Our study adds to the growing body of evidence that dyadic interactions are important not only to the individuals directly involved in these interactions but also to nearby eavesdropping individuals. Only one other study has investigated countersinging exchanges at a network level: the study of Burt and Vehrencamp (2005) of one morning of countersinging interactions in banded wrens (*Thryothorus pleurostictus*). They found a high level of song matching between neighbors during the dawn chorus, indicating that males adjust their singing strategies with respect to their neighbors' songs and that they do, in fact, interact with territorial neighbors at dawn. Our results complement the findings of Burt and Vehrencamp (2005) by showing that interactions among neighbors form the fabric of a communication network.

Our study is the first to quantify the extent of a communication network effect in territorial songbirds. Studying songbird interactions from a communication network perspective provides an opportunity to investigate the wider social context

of communication; using a microphone array is possibly the only way to detect and study songbird communication networks (Burt and Vehrencamp 2005). Our study reveals that dyadic interactions have an immediate effect on adjacent neighbors but may also have a ripple effect and cause more distant neighbors to adjust their singing behavior. Thus, an understanding of dyads is essential for studying information transfer within a communication network. Network-level studies benefit from first considering the dyadic perspective of interactions and then integrating the dyadic perspective into a network perspective.

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