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Countersinging interactions in black-capped chickadee neighbourhoods: Graded aggressive signals and communication networks

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COUNTERSINGING INTERACTIONS IN

BLACK-CAPPED CHICKADEE NEIGHBOURHOODS:

GRADED AGGRESSIVE SIGNALS AND COMMUNICATION NETWORKS

by

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Abstract

Songbirds frequently engage in countersinging interactions, wherein they vary the type and timing of songs to convey information about their status and intent. I studied frequency matching, overlapping, and movement behaviour during 100 naturally-occurring song contests among male black-capped chickadees (*Poecile atricapillus*) using a 16-microphone Acoustic Location System. Matching was associated with song overlapping and approach, and my results support the idea that chickadees use graded signals of aggression during countersinging interactions. I used stereo playback to simulate two types of song contests that differed in song patterning and timing. I recorded all males surrounding the playback apparatus, which was positioned in undefended space between territorial males. Males responded more intensely to the aggressive treatments than the submissive treatments. My results reveal that male chickadees eavesdrop on and respond to contests occurring outside of their territory boundaries, and provide important empirical support for the communication network model.

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Co-authorship Statement

I am the principal author for all research herein. Both of the data chapters in this thesis (chapters 2 and 3) are co-authored with my supervisor, Daniel Mennill, and our collaborators at Queen's University, Jennifer Foote, and Laurene Ratcliffe. Chapter 2 has been submitted to Animal Behaviour, and chapter 3 will be submitted to Behavioral Ecology. My co-authors on these chapters supported my research, shared in the research design, and provided helpful feedback on the writing of the manuscripts.

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This project required an enormous amount of dedication and persistence in the field. I thank my hard-working field assistants for helping me haul cable and chase chickadees: Roger Bull, Denise Gabriel, Ryan Jamieson, Sarah Lippold, Ann McKeller, Dominique Potvin, and Kathryn Winger. I thank Raleigh Robertson, Frank Phelan, Floyd Connor, Marg Phelan, and Rod Green, the superb staff at the Queen's University Biological Station, for fostering an enjoyable and productive research environment. I sincerely thank my partner in chickadees, Jenn Foote, for her friendship, support, and dedication to our collaborative project. I cherish our evenings of knitting after long days in the field together.

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Chapter 1

General Introduction

Introduction

      An understanding of communication is central to many questions about social

behaviour, including how animals defend territories and attract mates. Conventional

studies of communication have tested hypotheses using simple dyadic models involving

one signaler and receiver, but recent research suggests that animal communication may

be best understood as a network of interacting individuals (McGregor 2005). We now

recognize that it is important to study communication networks involving many signalers

and receivers, because multiple receivers may perceive each signal simultaneously and

signalers may direct their signals towards multiple receivers (McGregor 2005). However,

empirical studies of communication networks are scarce, and we know remarkably little

about naturally-occurring signaling interactions in free-living animals. Among

conspicuous communication behaviour, bird song has proven to be an outstanding model

with which to study the classical questions raised in animal signaling behaviour (Todt &

Naguib 2000). My research investigates how animals exchange information within a

communication network using an Acoustic Location System (ALS) to record

neighbourhoods of interacting songbirds.

Intra- and inter-sexual communication: Evidence for the dual function of song

      Songs are complex acoustic signals produced primarily by males and primarily

during the breeding season (Searcy & Andersson 1986). Bird song is widely regarded as

a model for the study of animal behaviour (reviewed in Todt & Naguib 2000). In the last

40 years, researchers have conclusively shown that bird song is used to communicate

with both rivals and potential mates (reviewed in Collins 2004), and therefore directly

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influences mating success via male contests or female choice. In a classic study, Peek (1972) muted male red-winged blackbirds (*Agelaius phoeniceus*) and revealed that song was central to territory defense; the muted males were ineffective at defending their territories against rival males and lost all or part of their territories. To complement muting experiments, bird song researchers have also conducted speaker occupation studies. Krebs et al. (1978) removed male great tits (*Parus major*) from their territories and replaced them with speakers broadcasting great tit songs. The songs, independent of male presence, successfully deterred other males from moving into the unoccupied areas, and these territories remained unoccupied longer than control territories where no songs were broadcast. These studies highlight the importance of song in male-male interactions and resource defense; muted males were unable to defend territories against rivals, whereas speakers broadcasting songs did so effectively.

In addition to repelling rivals, bird song plays an important role in attracting mates. An experimental manipulation of nest boxes in pied and collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*) revealed that song was attractive to females independent of the presence of males (Eriksson & Wallin 1986). The researchers placed loudspeakers beside nest boxes containing traps, and caught far more females visiting the nest boxes at which the speakers broadcast conspecific song than at silent control boxes. In the laboratory, playback of conspecific song, but not heterospecific song, elicits a copulation solicitation posture in females of many bird species, such as the brown-headed cowbird *(Molothrus ater;* King & West 1977). Examining song rate throughout the breeding season provides strong, albeit indirect, support for the attractant function of song. In many songbird species, male song rate is high before attracting a mate, sharply

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decreases upon pairing, and if the female is removed, males increase song rate to pre-pairing levels (e.g. white-throated sparrows, *Zonotrichia albicollis*; Wasserman 1977). Thus, natural observations combined with carefully-designed experiments have clearly demonstrated that bird song is a dual function signal, integral to both territory defense and mate attraction.

Songbird interactions

Interactions are among the most common contexts in which animals produce signals, and provide clear evidence that individuals use their signals to communicate with one another. During interactions, participants usually take the role of both a signaler and a receiver, and respond to each others' signals in very specific ways (Todt & Naguib 2000). In songbirds, signaling interactions occur commonly when two males exchange songs with one another. Countersinging interactions in songbirds are used by territorial males to repel rival males and to advertise to choosy females. Interacting males can alter their singing strategies in two ways: by altering the type of song they produce and/or by adjusting the timing of their songs. The way in which males choose to vary their signals during an interaction may provide information on their social status (Todt & Naguib 2000), or their quality, motivation level, and aggressive intentions (Vehrencamp 2001). Recent research reveals that interactions are important not just to the individuals involved, but also to nearby individuals who listen in and gather relative information about the contestants (e.g. Naguib & Todt 1997; Peake et al. 2001; Mennill & Ratcliffe 2004a).

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Communication networks

Songbirds, like many animals, often settle in groups of territories forming a neighbourhood. Within these neighbourhoods, male songbirds routinely interact with several neighbours. Song is a conspicuous, long-distance signal; songs often travel further than the average spacing between individuals, and in such cases, the potential for a communication network exists (McGregor 2005). Quite simply, a communication network is a group of several animals within signaling and receiving range of one another and it is likely the most common context in which communication occurs (McGregor 2005). Studying communication from a network perspective provides the opportunity to investigate the wider social context of communication and enables us to identify behaviours that can only occur outside of the traditional signaler-receiver dyad. One such behaviour is social eavesdropping, in which third party receivers attend to and gain relative information from signaling interactions between conspecifics (Peake 2005). In a variety of taxa and signaling modalities, both males and females pay attention to interactions between rival males and use the information they acquire in future fighting and mating decisions. For example, male (Oliveira et al. 1998) and female (Doutrelant & McGregor 2000) Siamese fighting fish (*Betta splendens*) eavesdrop on visual interactions between dueling males; males approach and interact with losers sooner than with winners, whereas females approach and spend more time displaying to winners. The idea of communication networks is not especially new, particularly among researchers studying chorusing behaviour in insects (e.g. Otte 1974) and frogs (e.g. Ryan et al. 1981). However, songbird communication has been difficult to study at a network level due to

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the logistic challenge of recording and monitoring several individuals simultaneously during long-range interactions.

The Acoustic Location System: A new tool for studying communication networks

An Acoustic Location System (ALS) is an array of simultaneously-recording microphones connected to a central recording device which enables behaviourists to record, monitor, and locate animals based on the sounds they produce (McGregor et al. 1997; Mennill et al. 2006). Studies of marine organisms, particularly large marine mammals (e.g. Clark & Clapham 2004), have employed ALS technology to monitor behaviour, but researchers of terrestrial animals have only just begun to test and use ALS technology in behavioural studies. In terrestrial systems, the use of an ALS to locate vocalizing animals relies on the relatively slow speed of sound in air; we are able to locate animals based on the sounds they produce because of the difference in the timing of when their signals reach different microphones (McGregor et al. 1997). Using a 4-microphone ALS, McGregor et al (1997) found that they could successfully locate bird songs to within tens of centimeters in temperate woodland and meadow habitats, and therefore they could use an ALS to track birds as they changed song perches. In a lush tropical forest, Mennill et al. (2006) used an 8-microphone ALS and, on average, were able to locate bird songs to within 3 meters. In both cases, location error was influenced by vegetation type, topography, the location of the sound source relative to the centre of the array, and the accuracy of the microphone GPS coordinates. Only recently have technical innovations allowed behaviourists to apply ALS recording technology to study free-living animals, and studies that employ ALS recordings are scarce.

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An ALS offers several advantages for monitoring animals. First, an ALS is a passive system, so it does not disrupt the natural behaviour of the animals. Second, an ALS enables behaviourists to locate and track the movement behaviour of vocalizing animals. Third, an ALS is capable of recording several individuals simultaneously, allowing behaviourists to study the wider social context of communication from a network perspective. For my thesis research, I used a 16-microphone ALS to record entire neighbourhoods of singing black-capped chickadees (*Poecile atricapillus*). No other published research to date has used an ALS of this size to record free-living animals.

Study species: The black-capped chickadee, *Poecile atricapillus* (Passeriformes, Paridae)

Black-capped chickadees are small (10-14 grams), resident songbirds found throughout much of Canada and the northern two-thirds of the United States (Smith 1991). Although their taxonomy has recently undergone minor revision, a recent molecular phylogeny confirms that chickadees belong to the order Passeriformes (the songbirds) and family Paridae (Gill et al. 2005). In the fall and winter, chickadees eat seeds and berries; in the spring, their diet shifts to mostly animal matter, and they forage primarily on spiders and caterpillars (Smith 1991). Most chickadees form pair bonds in the fall, although a few form pair bonds during winter and at the beginning of spring due to winter mortality (Smith 1991). Pairs spend the winter together in small flocks of 4-12 birds. The winter flocks are structured by stable, linear dominance hierarchies (Smith 1991), and male dominance in the winter is related to his quality and singing behaviour in

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the spring (Otter et al. 1997). High-quality males have preferential access to food, which allows us to observe the dominance relationships by watching flocks of colour-banded birds interact at feeding stations (Ratcliffe et al. 2007). Chickadees reproduce in the early spring (the last week of April and the first two weeks of May in my eastern Ontario study population), with both male and female parents contributing to excavating nest cavities and feeding the young, while the female is solely responsible for lining the nest and incubating the eggs (Smith 1991). Young chickadees spend two weeks as nestlings, and then spend the rest of the summer in a family group with their siblings and parents. Young male chickadees learn to sing in their first year of life; they begin to babble and practice singing during the late summer and over the winter, and produce crystallized adult songs by the end of their first year of life (Smith 1991).

Male black-capped chickadees sing a single song type: a tonal, two-note *fee bee* (Fig. 1.1). All males sing the same song type and all males are capable of adjusting the frequency of their songs across a continuous frequency range of 860 Hz (Horn et al. 1992). The complexities of this seemingly simple song system have been revealed through a series of observational and experimental studies over the past 20 years. Chickadees sing individually-distinctive songs; variation in the fine structure of the songs provides information about the singer's identity (Christie et al. 2004) and birds can discriminate between the songs of eight or more males (Phillmore et al. 2002). Neighbouring territorial males engage in intense countersinging interactions in the early spring, particularly during territorial establishment and egg-laying (Shackleton & Ratcliffe 1994). Playback experiments have revealed that variation in the timing and type of songs given during a contest elicit different responses from territorial males. For

example, Otter et al. (2002) engaged territorial males with interactive playback, and found that males who were overlapped and frequency matched responded by approaching the singer more closely than did males who were not overlapped or matched, indicating that chickadees perceive these signaling strategies as threatening. A recent interactive playback experiment by Mennill and Ratcliffe (2004b), designed to explore the distinct signal functions of overlapping and frequency matching in chickadees, revealed that overlapping primarily influences males' singing rhythm whereas matching influences males' movement behaviour. Playback experiments have demonstrated that both male and female chickadees eavesdrop on male-male countersinging interactions and gain relative information about opponents to direct future antagonistic and reproductive decisions (Mennill et al. 2002; Mennill et al. 2003; Mennill & Ratcliffe 2004a). Thus, countersinging interactions in chickadees are important to other males and females in the area surrounding the interaction as well as to the rival males engaged in the contests.

Countersinging interactions in black-capped chickadee communication networks

We have learned much about chickadee communication through playback studies. However, natural countersinging interactions have not been well-studied, in chickadees or other songbirds. My thesis focuses on male-male countersinging interactions in black-capped chickadees. I begin by describing naturally-occurring chickadee countersinging interactions in chapter 2. I present detailed analysis of singing and movement behaviour during 100 naturally-occurring song contests, and compare the results to previous playback studies. In chapter 3, I use playback to evaluate how communication networks respond to perturbation, and I simultaneously investigate whether territorial male

chickadees eavesdrop on countersinging interactions occurring outside of their territory

boundaries. I use stereo playback to simulate song contests between unknown rivals and

an Acoustic Location System to record the singing activity of all males in the surrounding

neighbourhood (a cluster of breeding territories with several males defending adjacent

territories against one another). Both data chapters in this thesis (chapters 2 and 3) were

written as papers for submission to journals and are presented here in publication format.

Chapter 2 is submitted for publication in Animal Behaviour. Chapter 3 will be submitted

for publication in Behavioral Ecology.

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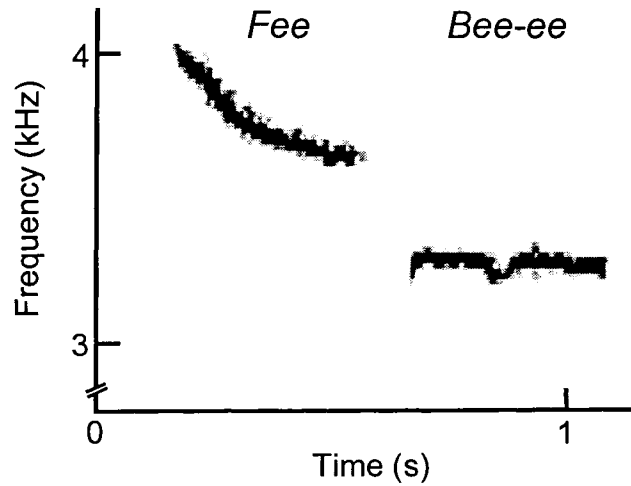
Figure 1.1. A spectrogram of a black-capped chickadee song. Black-capped chickadees

sing a single song type, a tonal, two-note *fee bee*. All males sing this song and all are

capable of transposing their songs up and down a continuous frequency range of 860 Hz.

Chapter 2

Frequency matching, overlapping and movement behaviour

during diurnal countersinging interactions of

black-capped chickadees

Introduction

Communication plays a fundamental role in how animals attract mates and defend territories (Searcy & Andersson 1986). In many animals, females are choosy about their reproductive decisions and males compete with one another for mates. Countersinging interactions in songbirds are used by territorial males for both of these purposes: to advertise to choosy females and to repel competing males (Todt & Naguib 2000). Dueling males can alter their vocal responses in two dimensions, by altering the type of signal they produce (pattern-specific responses) and by adjusting the timing of song production (time-specific responses). Both pattern- and time-specific responses are thought to play a role in communicating graded levels of aggression toward opponents (e.g. Todt & Naguib 2000; Vehrencamp 2001; Mennill & Ratcliffe 2004b).

One well-studied pattern-specific response is signal matching, which occurs when an individual responds with the same type of signal as the preceding signal from his opponent (e.g. Stoddard et al. 1992). Song matching in birds is thought to be a directed signal of aggression and is associated with escalated encounters in species with song repertoires (e.g. Vehrencamp 2001) as well as species that vary the patterns of their songs in other ways (e.g. Morton & Young 1986; Mennill and Ratcliffe 2004b). Evidence from interactive playback studies suggests that increased matching is perceived as an increased threat by males (Vehrencamp 2001; Mennill & Ratcliffe 2004b). Song overlapping, a time-specific response that occurs when a singer starts a song before the end of his opponent's song, has similarly been argued to be an aggressive signal (Todt & Naguib 2000). Overlapping masks part of an opponent's signal, impairs mutual listening, and, like song matching, is associated with escalated contests in several species (Dabelsteen et

al. 1997; Mennill & Ratcliffe 2004b; Poesel & Dabelsteen 2005; Naguib & Kipper 2006). Interacting individuals may use these dynamic signaling strategies to communicate quality, motivation, and intention during countersinging exchanges. Few studies have examined the interplay between pattern- and time-specific responses, and the relative signal function of matching and overlapping. Further, most studies involve song playback to engage animals in simulated contests, and consequently we know very little about variation in pattern- and time-specific responses during natural countersinging interactions. In this study, we investigate frequency matching and song overlapping during naturally-occurring diurnal song contests of black-capped chickadees (*Poecile atricapillus*) using an Acoustic Location System to track the singing and movement behaviour of males.

The black-capped chickadee provides an excellent system for examining pattern- and time-specific variation in singing behaviour. 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 male chickadees establish breeding territories. Males defend their territories against former flockmates and males from nearby flocks, forming neighbourhoods of breeding pairs (Mennill & Otter 2007). Males engage in countersinging contests with their neighbours to defend territories and also to attract social and/or extra-pair mates. Male dominance position in the winter influences singing behaviour during the breeding season: singing performance is an honest advertisement of male dominance status (Otter et al. 1997) and is used by females to assess both their partner and neighbouring males (Mennill et al. 2002). Although male chickadees possess only a single song type, a tonal

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two-note *fee bee*, they are capable of frequency-matching opponents by transposing their song across a continuous frequency range of approximately 860 Hz (Mennill & Otter 2007). Black-capped chickadees provide a unique opportunity to investigate dynamic signaling strategies because dominance rank serves as a proxy for the quality of males who regularly interact in song contests involving frequency matching and overlapping.

An Acoustic Location System (hereafter ALS) consists of an array of simultaneously-recording microphones that triangulate the position of birds based on differences in sound arrival time. An ALS offers unique advantages for studying countersinging exchanges because it is a passive system which allows simultaneous monitoring of multiple individuals while providing accurate locations of these individuals (Mennill et al. 2006).

In this study, we examined male movement behaviour and quantified frequency matching and song overlapping during naturally-occurring chickadee song contests. Previous research allowed us to generate specific predictions about male behaviour during countersinging interactions. The use of songs in interactions may communicates a male's social status (Todt & Naguib 2000), and may also convey information about motivation and aggressive intentions (Vehrencamp 2001). We therefore predicted that a chickadee's social rank in his winter flock would be related to his singing behaviour in the spring, such that dominant males would use more aggressive signaling strategies during song contests. Given that frequency matching is a signal of directed aggression (Mennill & Ratcliffe 2004b), we predicted that males would match the frequency of neighbours of similar or lower rank, but would avoid matching the frequency of males with higher rank. Further, given that overlapping is a signal of aggression (Mennill &

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Ratcliffe 2004a, b), we predicted that males would overlap neighbours of similar or lower rank, but would avoid overlapping males of higher rank. Based on the results of earlier playback studies in chickadees (Otter et al. 2002; Mennill & Ratcliffe 2004b), we predicted that male singing strategies would be associated with male movement behaviour during contests, whereby birds involved in intense contests would interact at close range. Lastly, based on the sequential assessment model (Enquist et al. 1990), we predicted that contests between males of similar dominance rank would involve more exchanges than contests between males of disparate dominance ranks.

Methods

Field methods

We studied black-capped chickadees at the Queen's University Biological Station near Kingston, Ontario, Canada (44° 34' N, 76° 19' W) between January and July of 2005 and 2006. We captured adults in the winter using treadle traps baited with seeds. We banded each individual with an aluminum Canadian Wildlife Services band as well as a unique combination of coloured leg bands (N = 149 birds in 2005, N = 236 birds in 2006). We determined the dominance ranks of birds in winter flocks by observing pairwise interactions at feeding stations (N = 2811 interactions in 2005, N = 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 (see Ratcliffe et al. 2007 for details). We classified "high-ranking males" as the top-ranking male in flocks with two or three males, or the top two males in flocks with four or five males. We

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classified "low-ranking males" as the bottom-ranking male in flocks with two or three males or the bottom two males in flocks with four or five males. We classified "mid-ranking males" only in flocks with three or five males.

During late April and early May of each year, as birds began defending all-purpose territories, we recorded the dawn chorus of all territorial males using directional microphones (Sennheiser MKH-70) and solid-state digital recorders (Marantz PMD660 or PMD670). Fine structural characteristics of black-capped chickadee song are individually distinctive (Christie et al. 2004a) and the focal recordings were used to verify male identity in the passive ALS recordings.

Our ALS consisted of an array of 16 omni-directional 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 multi-channel data acquisition card (National Instruments DAQ-6260) and stored as 16-channel AIF files. 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 m^2, encompassing the territories of 7-10 male chickadees. We used this ALS to record 10 different neighbourhoods of territorial chickadees between 27 April and 15 May 2005 and 2006. At this time of year, females are fertile and male-male song contests are common (Mennill & Otter 2007). Neighbourhoods consisted of birds familiar with one another from the previous winter, either from the same winter flock or adjacent winter flocks. We recorded each neighbourhood continuously between 0425 hours (prior to first

light) and 1130 hours for two or three consecutive days. Chickadees sing in two primary

contexts: an extended bout of song at dawn, and countersinging interactions after dawn

(Mennill & Otter 2007). Here we limit our analysis to post-chorus countersinging

behaviour (after 0600 hours).

Array analysis

We used Syrinx-PC (J. Burt, Seattle, WA) to browse 16-channel spectrograms of

array recordings. Our recordings consisted of periods of silence, periods of solo singing,

and periods of interactive countersinging. We define a contest as occurring when males

sing interactively (i.e. alter their singing and movement behaviour with respect to their

opponent) at a distance less than 200 m apart. This definition matches our field

observations, in which opponents typically begin singing in their own territories, alter

their pattern- and time-specific responses with respect to one another, and often approach

shared territory boundaries for close-range interactions. Ten countersinging contests were

selected from each of the 10 neighbourhoods. We chose countersinging interactions that

were isolated from other singing events by at least one minute before and after each

contest, and that were recorded in three or more microphones to allow triangulation of

singing males. We attempted to analyze 10 contests per neighbourhood, although for two

neighbourhoods it was difficult to find contests to match our criteria, resulting in an

average of 10.0 ± 0.5 contests per neighbourhood (range: 7-13). These contests involved

34 males from 16 flocks in 2005 (17 high-ranking, 5 mid-ranking, 12 low-ranking) and

30 males from 19 flocks in 2006 (14 high-ranking, 10 mid-ranking, 6 low-ranking). We

selected contests arbitrarily with respect to male identity; consequently a few contests

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within years involved the same pair of males. We ensured that no pair of males was represented in more than two contests. We observed the same patterns when only one contest per pair of males was selected arbitrarily; we therefore present analyses of all 100 contests.

For each contest, we annotated all songs using the frequency and time cursors in Syrinx-PC. For frequency analysis, we used a focal window with 1024 Blackman FFT, and measured song frequency one-quarter of the way into the *bee* note (following Christie et al. 2004b), which was repeatable to 2 Hz. For each song contest, we quantified the occurrence of frequency matching within 50 Hz (a conservative estimate of frequency matching, based on frequency of the *bee* note), and the rate of song overlapping. We used a combination of focal recordings, field notes, fine structural characteristics, and location information to confirm the suspected identities of singing males.

We used software written in MatLab (Mathworks Inc., Natick, MA) to triangulate the positions of singing males during each countersinging exchange, employing the localization process described in Mennill et al. (2006). We calculated the distance between males at the beginning and end of the contest, the average distance between males throughout each contest, and the closest and furthest distances between males for each song contest to the nearest decimeter. For individual males, we calculated the average distance moved between successive songs and the coefficient of variation of distance moved between successive songs.

Statistical analyses

Data on the number and proportion of songs frequency matched, the number and proportion of songs overlapped, the number of exchanges, and the average distance moved between songs were log-transformed to meet the assumptions of normality necessary for parametric statistical analyses. To control for variation in the length of contests, we used the residuals of linear regressions of the number of frequency matches and song overlaps against the number of exchanges during contests (i.e. an "exchange" occurs when one male sings and the opponent responds).

To compare the relative ranks of the contestants, we assigned a rank disparity score to each contest, such that contests involving males of the same rank category would receive a score of 0, contests with males differing by one rank category would receive a score of 1, and contests between males differing by two rank categories would receive a score of 2. For our analyses of singing behaviour, we investigated the differences in behaviour between high- and low-ranking males. In analyzing the distances between singing males, we included males of all rank categories. To calculate the minimum and maximum distances between countersinging birds, we took the average of the 3 smallest and 3 largest distances between the birds, respectively, to control for slight variation in location estimates.

We performed a Pearson's chi-square test to investigate if either frequency matching or overlapping occurred as the first aggressive response in a contest more often than expected by chance. To test the effects of dominance rank on measures of contest intensity (number of exchanges, proportion of songs frequency matched and overlapped, direction of movement, and distance moved between songs), we conducted analyses of

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variance (ANOVA). For our non-normal data, we used Mann-Whitney U tests and Kruskal-Wallis tests to compare rank disparity and minimum, average, and maximum distances between birds, as well as dominance rank and the number of songs during a contest. We performed chi-square tests to investigate if interactions containing matching or overlapping were more likely to occur between former flockmates or non-flockmates. We performed all statistical analyses in JMP 5.1 (SAS Institute, Cary, NC). Descriptive statistics are given as mean ± SE. All tests are two-tailed.

Results

We analyzed 100 naturally-occurring countersinging interactions in 10 neighbourhoods of breeding black-capped chickadees. Song contests occurred between 0602 and 1119 hours. A peak in countersinging interactions was observed in the early morning; 74% of contests occurred between 0602 and 0900 hours. Contests lasted, on average, 142.4 ± 18.0 s, and consisted of 40.66 ± 2.26 songs and 30.7 ± 2.7 back-and-forth vocal exchanges between contestants. On average, countersinging males were separated by a distance of 57.6 ± 3.6 m.

Overlapping exchanges were commonplace. Eighty percent of contests had one or more instance of song overlapping. Exchanges involving frequency matching were less common. Thirty-seven percent of contests included males countersinging with songs that were frequency matched at ≤ 50 Hz. Thirty-five percent of contests included both frequency matching and song overlapping. In 57% of contests with both matching and overlapping, overlapping preceded matching, in 34% matching occurred before overlapping, and in 9% of these contests matching and overlapping occurred

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simultaneously in the same exchange (Chi-square test: $\chi^2{}_2 = 12.40$, $N = 35$, $P = 0.002$). Of the average 30.7 exchanges between contestants, $7.9 \pm 1.6\%$ and $15.9 \pm 1.2\%$ were matches and overlaps, respectively. The number of songs sung during a contest did not vary significantly between males of different rank (Mann-Whitney U test: $U = -1.12$, $N_1 = 106$, $N_2 = 39$, $P = 0.29$), and the number of exchanges did not vary with rank disparity between the contestants (ANOVA: $F_{2,97} = 1.95$, $P = 0.15$).

Of the 80 contests that contained song overlapping, contests that contained frequency matching had more instances of overlapping (Fig. 2.1; ANOVA: $F_{1,78} = 10.56$, $P = 0.002$). The number of frequency matches was not significantly related to the number of song overlaps per contest, although the slope was positive ($R^2 = 0.04$, $P = 0.24$). The proportion of opponent's songs frequency matched did not differ by rank (ANOVA: $F_{1,53} = 0.62$, $P = 0.43$). Similarly, the proportion of opponent's songs overlapped did not differ by rank (ANOVA: $F_{1,99} = 0.66$, $P = 0.42$). Contests in which the birds approached each other featured more matching exchanges than contests in which the birds moved away from each other (Fig. 2.2; ANOVA: $F_{1,34} = 2.43$, $P = 0.13$), although this trend was not significant.

Interactions between former flockmates were present in 33% of song contests, with the remaining 67% of song contests occurring between non-flockmates. Former flockmates did not have more or fewer aggressive interactions than non-flockmates. In 25 (67.57%) of the 37 contests with instances of frequency matching, contestants were non-flockmates (Chi-square test: $\chi^2{}_1 = 0.009$, $P = 0.93$). Of the 80 contests with instances of overlapping, 51 (63.75%) involved non-flockmates (Chi-square test: $\chi^2{}_1 = 1.91$, $P = 0.15$).

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Contestants moved often during countersinging exchanges (Fig. 2.3). Males moved on average 22.3 ± 1.3 m between songs. In 51 contests, the males approached each other; in 46 contests, the males moved apart; in the remaining three contests, the males did not move relative to each other (estimated distance between birds changed by less than 1.0 m from beginning to end of contest).

The distance moved between songs did not differ by rank (ANOVA: $F_{1,142} = 1.93$, $P = 0.17$). The minimum, maximum, and average distances between birds did not vary with the rank disparity of the contestants (Kruskal-Wallis test: minimum distance: $H_2 = 0.11$, $P = 0.94$; maximum distance: $H_2 = 1.99$, $P = 0.37$; average distance: $H_2 = 2.41$, $P = 0.30$).

Discussion

Our evaluation of naturally-occurring countersinging exchanges between territorial male black-capped chickadees in 10 different neighbourhoods reveals that song contests are commonplace and dynamic exchanges of information, where variation in both pattern and timing of songs are important acoustic signals. Our analysis of 100 countersinging interactions reveals that overlapping is a more common singing strategy than frequency matching, occurring in 80% and 37% of song contests, respectively. On average, 16% of exchanges between opponents were song overlaps, whereas only 8% were frequency matches. Contests in which males were frequency matched contained more instances of song overlapping. In contests with both matching and overlapping, the first aggressive singing strategy was consistently overlapping, followed by matching. There were no rank-related differences in the proportion of opponents' songs frequency

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matched or overlapped, or in the distance moved between songs. Song contests in which the birds moved closer together had more instances of frequency matching than contests in which the birds moved apart. Contrary to our expectation, the number of exchanges between opponents did not vary with their rank asymmetry.

Frequency matching is thought to function in chickadees like song-type matching functions in other species, as a conventional signal of aggression (Vehrencamp 2001). We predicted that males involved in contests containing matching would interact at closer range than males in contests with no matching (Krebs et al. 1981). Indeed, we found that frequency matching was associated with other indicators of contest escalation; levels of song overlapping as well as approach during contests were positively related to frequency matching. In an earlier playback experiment, Otter et al. (2002) found that males that were frequency matched escalated contests more than males that were not matched. Similarly, Mennill & Ratcliffe (2004b) found that chickadees who were frequency matched made more passes over the playback speakers and had closer distances of approach than males who were not matched. Our results support the idea that frequency matching in black-capped chickadees is a directed signal of aggressive intentions, and is associated with escalated encounters.

Higher levels of song overlapping were associated with higher levels of frequency matching, but overlapping itself was not related to subsequent approach in escalated contests. This is in contrast to Mennill & Ratcliffe (2004b), who found that overlapping was related to how closely chickadees approached the playback apparatus. Our results based on natural interactions are more difficult to tease apart than controlled playback studies, because many of our contests involving song overlapping also contained

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frequency matching. Similarly, Otter et al. (2002) found that males who received just overlapping playback treatment often began frequency matching, thereby escalating contests themselves. Overlapping in chickadees appears to serve as a signal of arousal or willingness to escalate a contest, as has been found, for example, in European robins (*Erithacus rubecula*; Dabelsteen et al. 1997) and nightingales (*Luscinia megarhynchos*; Naguib & Kipper 2006). In addition to matching and approach responses, other behaviours might act in concert with overlapping to convey information during song contests. In blue tits (*Parus caeruleus*), intruder location influences the effect of overlapping on territorial males' responses to a challenge (Poesel & Dabelsteen 2005). Thus, since overlapping is a common aggressive singing strategy, often associated with frequency matching, it is difficult to distinguish its distinct functional role in natural chickadee song contests.

Many territorial animals display lower levels of aggression toward familiar neighbours than toward unfamiliar strangers (reviewed in Temeles 1994). Playback experiments at territory boundaries in numerous songbirds have demonstrated that males perceive the songs of established neighbours as less threatening than the songs of strangers (reviewed in Stoddard 1996). We might expect black-capped chickadees to respond differently in countersinging interactions with established neighbours, the focus of the present study, versus strangers, the focus of previous playback experiments. In such experiments, researchers have simulated unknown intruders broadcasting highly aggressive singing strategies (Mennill et al. 2002; Otter et al. 2002; Mennill & Ratcliffe 2004b). Using interactive playback, Mennill & Ratcliffe (2004b) were able to simulate intruder males who frequency matched 100% of focal males' songs and overlapped up to

96.8% of focal males' songs. Broadcasting highly aggressive playback elicited strong approach responses (Otter et al. 2002; Mennill & Ratcliffe 2004b), and incited eavesdropping females to seek extra-pair copulations after hearing their mates dominated by the simulated aggressive males (Mennill et al. 2002). However, our results indicate that when neighbours engage in natural song contests, they use aggressive singing strategies much more sparingly. The highest levels of matching and overlapping we observed in natural contests between neighbours were 75.0% and 55.0%, respectively, and the mean levels were 7.9% and 15.9%, respectively. Thus, our study reveals that previous playback experiments may have been broadcasting aggressive signals at an unnaturally high levels.

Why is overlapping a more common response than frequency matching? Time-specific variation (i.e. overlapping) appears to be a more dynamic singing strategy than pattern-specific variation (i.e. matching) in black-capped chickadees. Birds may be capable of altering their time-specific responses with each successive song, whereas frequency shifting may be more constrained. For instance, at dawn, male chickadees sing bouts of approximately 41 songs before shifting frequencies by >80 Hz (Horn et al. 1992). Black-capped chickadees may be unable to shift song frequency as often as they can shift song timing, perhaps due to motor or neurological constraints on song production, contributing to an asymmetry in their use of pattern- and time-specific responses during countersinging interactions. Alternatively, overlapping may be more common because it serves as the first aggressive response in graded contest escalation. In contests that involved both frequency matching and overlapping, overlapping was consistently the first aggressive singing strategy used. Our results therefore support the

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idea that chickadees use graded levels of aggression (Otter et al. 2002), beginning with overlapping and escalating to matching if necessary. Graded aggressive displays are widespread in an array of animal taxa and sensory systems (Searcy & Andersson 1986). In vocalizing fish, most sounds are produced in concert with other aggressive behaviours (Ladich 1997). A similar pattern of stereotyped levels of aggression during agonistic interactions is seen in a mormyrid electric fish (*Gnathonemus petersii*; Terleph 2004) as well as a cichlid fish (*Nannacara anomala*; Enquist et al. 1990). African painted reed frogs (*Hyperolius marmoratus*) use a graded system of aggressive calls to escalate contests in a continuous fashion (Grafe 1995). Graded aggressive displays are seen in several bird species; the nonmatching/repertoire matching/type matching system in song sparrows (*Melospiza melodia*) is a well-studied example (e.g. Burt et al. 2001).

We predicted that male rank would be related to singing behaviour, such that high-ranking males would use more aggressive signaling strategies during song contests. However, we found no rank-related differences in the use of frequency matching or overlapping. Mennill & Ratcliffe (2004b) found rank-related differences in behavioural responses to these singing strategies, whereby high-ranking males responded with lower agitation levels and spent more time farther away from playback-simulated opponents. This finding, taken in concert with the present study, provides insight into the complexities of chickadee countersinging strategies. In natural contests between neighbours (present study), both high- and low-ranking males use similar degrees of aggressive vocal signals; playback experiments (Mennill & Ratcliffe 2004b) reveal rank-related differences during interactions with unknown intruders. High-ranking males may suffer considerable loss of paternity as a consequence of aggressive song contests

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(Mennill et al. 2002); an aggressive intruder poses more of a threat to high-ranking males, and the benefits of escalating contests at close range may outweigh the costs.

The sequential assessment model (Enquist et al. 1990) states that assessment of a rival is an important function of signaling contests, and information about opponents is accumulated in a gradual process. The model predicts that contests with a smaller asymmetry in fighting ability should have longer mean duration. That is, highly escalated contests are more likely to occur between well-matched opponents because the difference between the contestants in cost of fighting will be small. Following the sequential assessment model, we predicted that contests between well-matched males would involve more exchanges. We found no relationship between the rank disparity of dueling males and the number of exchanges in chickadee song contests. This result stands in contrast to studies of agonistic interactions in a cichlid fish (Enquist et al. 1990), in which contests between well-matched individuals are lengthier and proceed through a series of escalations, culminating in costly physical fighting. Instead, it appears that chickadees use a graded system of aggressive signals to escalate contests, using overlapping first and matching if a contest escalates further.

Using an Acoustic Location System to passively record naturally-occurring interactions allows us to investigate song contests in a previously undescribed way. To date, all studies of countersinging interactions have used playback, simulating an intruder, to engage territorial males and record their subsequent responses. Our natural, observation-based approach reveals the sophistication of the chickadee communication system, and the complex interplay between pattern- and time-specific responses as directed signals of aggression. Further, an ALS is a promising new tool for the study of

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communication networks, in which several individuals are within signaling range of one another (McGregor & Peake 2000), providing the opportunity to examine the wider social context of interactions and the potential selective effects of eavesdroppers on animal communication systems.

In summary, our results reveal that song contests containing frequency matching are often escalated; they contain more instances of song overlapping, and males approach each other during these matched contests. Our results indicate that black-capped chickadees use graded aggressive signals in countersinging interactions, such that an opponent's song is first overlapped, and may be subsequently frequency matched in escalated interactions. Song matching has been shown to serve as a conventional signal of aggressive intentions in several species (Vehrencamp 2001), and our results support the evidence for this function in chickadees (Shackleton & Ratcliffe 1994; Otter et al. 2002; Mennill & Ratcliffe 2004b; Mennill & Otter 2007). Contrary to the sequential assessment model and findings in other systems (Foster 1981; Enquist et al. 1990; Grafe 1995; Terleph 2004), contests between evenly-matched chickadees are not more escalated or lengthier than contests between males of disparate dominance ranks. Further research into naturally-occurring contests is needed in a variety of systems in order to formulate accurate models and predictions of dynamic signaling behaviours during social interactions.

Acknowledgments

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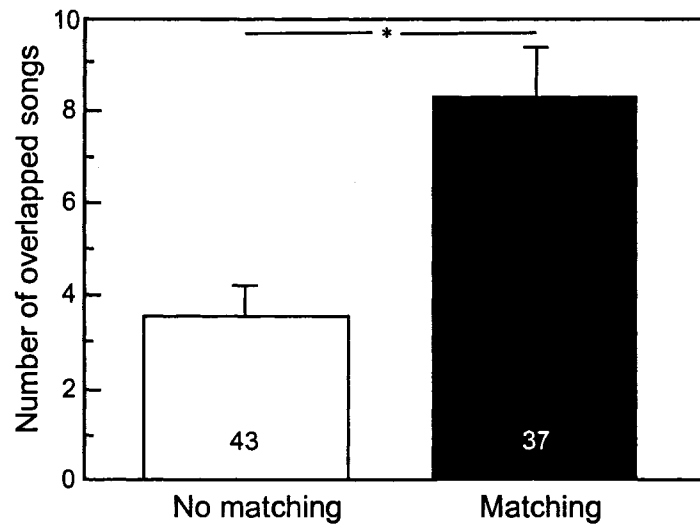
Figure 2.1. Mean number of overlapped songs in song contests with and without

instances of frequency matching. Numbers of contests are shown at the base of each bar.

Asterisk shows significant difference between groups at $P < 0.05$. Error bars show
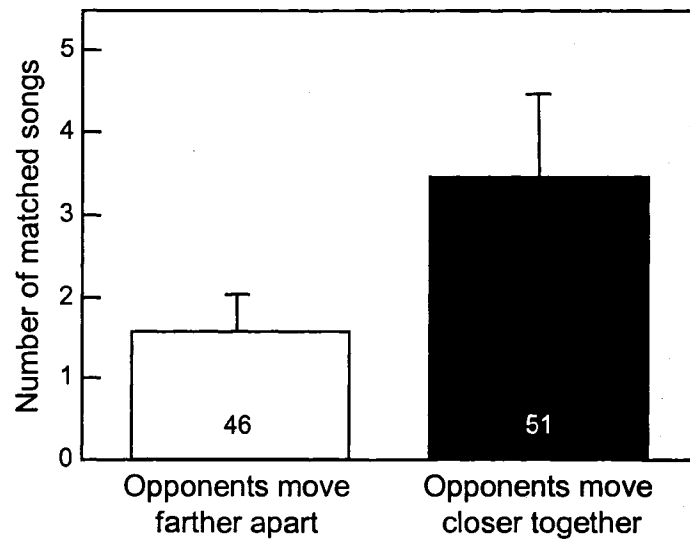
standard errors.

Figure 2.2. Mean number of frequency matched songs during contests in which males either approached each other or retreated. Numbers of contests are shown at the base of each bar. Error bars show standard errors.
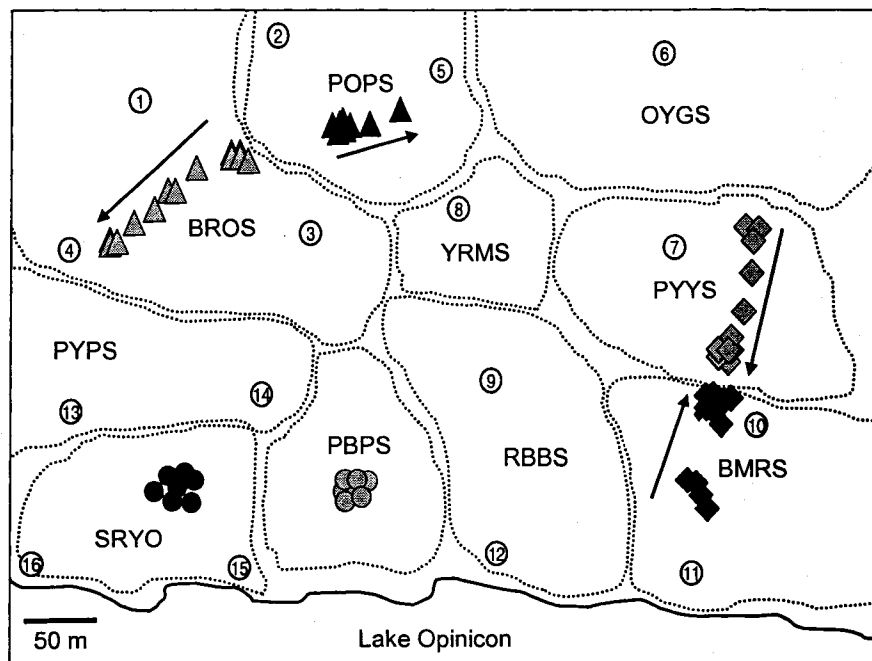
Figure 2.3. Locations of singing males recorded with a 16-microphone Acoustic

Location System (numbers indicate microphone locations). Three examples of

countersinging contests are shown; male identity is indicated by four-letter abbreviations,

and arrows indicate direction of male movement. The contest between a high-ranking

male and mid-ranking male (locations ▲) begins with the contestants at their territory

boundary; the males move apart as the contest progresses. This movement pattern was

observed in 46% of contests. The contest between two high-ranking males (locations ◆)

escalates and the birds approach each other, facing off at their territory boundary.

Contesting males approached each other in 51% of contests. A high-ranking male and a

low-ranking male (locations ●) are engaged in a long-distance contest. There is no

approach or retreat in this contest, which was observed in 3% of naturally-occurring

chickadee contests.

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Chapter 3

Shaking up the neighbourhood: Eavesdropping and communication networks revealed through the use of stereo playback and an Acoustic Location System

Introduction

Animal communication mediates many important social behaviours including

mate attraction and resource defense, yet the wider social environment in which

communication occurs is often overlooked (McGregor & Peake 2000). Conventional

studies of communication have tested hypotheses using simple dyadic models involving

one signaler and one receiver, but a recent paradigm shift emphasizes communication

networks involving many signalers and receivers (McGregor 2005). A communication

network is a group of several animals 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 neighbourhoods, and several males sing within signaling

range of one another (Naguib 2005). Dyadic signaling interactions between territorial

individuals may be important not just to the individuals involved in these interactions, but

also to those around them (Todt & Naguib 2000). Recent experimental studies in

songbirds have provided evidence for several communication network-based behaviours,

including eavesdropping, wherein an individual gains relative information about two

individuals involved in a signaling interaction (e.g. Naguib & Todt 1997; Peake et al.

2001; Mennill & Ratcliffe 2004a), and audience effects, wherein an individual modifies

its behaviour during a contest based on the presence of bystanders (e.g. Tachon et al. 1999; Matos & 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 to date to cases of three-party communication networks and has not been extended to the broader networks theorized to exist in free-living territorial animals.

An Acoustic Location System (hereafter 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 multi-channel 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; Reed et al. in review). An ALS thereby facilitates the recording of networks of songbirds and allows us to evaluate how the singing behaviour 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 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

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their territories against former flockmates and males from nearby flocks, forming neighbourhoods of breeding pairs that contain high-quality (high-ranking) and low-quality (low-ranking) males. Males engage in countersinging contests with their neighbours to repel rivals and also to attract social and/or extra-pair mates (Mennill & 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 neighbouring males (Mennill et al. 2002). A network model has the potential to enhance our understanding of chickadee communication, as each neighbourhood contains several males and females within signaling range of one another.

Interactions, the specific relations between the signals of two or more individuals, are rarely studied beyond a dyadic context, although the dynamics within a dyadic context are increasingly well understood (Todt & Naguib 2000). During black-capped chickadee countersinging interactions, males adjust the frequency and timing of their songs with respect to their opponent (Reed et al. in review). Males sing a single song type, a tonal two-note *fee bee*, and are capable of frequency-matching opponents by transposing their song across a continuous frequency range of approximately 860 Hz (Mennill & Otter 2007). Interactive playback experiments (Mennill & Ratcliffe 2004b) and observational studies (Reed et al. in review) 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 opponents to direct future antagonistic and reproductive decisions (Mennill et al. 2002; Mennill et al. 2003; Mennill & Ratcliffe 2004a). Similar results have been found in other songbird species including

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nightingales (*Luscinia megarhynchos*; Naguib & Todt 1997) and great tits (*Parus major*; Peake et al. 2001). To date, however, few studies have focused on how countersinging interactions may influence other individuals in a communication network.

To evaluate neighbourhood-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 neighbourhood would respond to these simulated interactions. In each of ten neighbourhoods, we used stereo playback to broadcast two types of simulated song contests that differed only in the intensity of aggressive signaling. One playback treatment simulated a highly aggressive exchange between two unknown rivals, involving frequency matching and overlapping, and the other simulated a low intensity exchange between two unknown rivals, involving no matching or overlapping. Under the communication network model, we predicted that males in the neighbourhood 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 behaviour 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 & Ratcliffe 2004a); we expanded the scope of the investigation of eavesdropping to test if males also

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

Methods

Field methods

We conducted 20 playback trials in 10 black-capped chickadee neighbourhoods at the Queen's University Biological Station near Kingston, Ontario, Canada (44° 34' N, 76° 19' W) between 0810 and 0945 hours, 30 April to 15 May, 2005 and 2006. At this time of year, females are fertile and male-male countersinging interactions are common (Mennill & Otter 2007). We banded adult chickadees in the winter of each year with aluminum Canadian Wildlife Services bands as well as unique combinations of coloured leg bands (N = 149 individuals in 2005, 236 individuals in 2006). We determined the winter dominance ranks of males by observing pairwise interactions at feeding stations (N = 2811 interactions in 2005, 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 (see Ratcliffe et al. 2007 for details). We classified "high-ranking

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males" as the top-ranking male in flocks with two or three males, or the top two males in flocks with four or five males. We classified "low-ranking males" as the bottom-ranking male in flocks with two or three males or the bottom two males in flocks with four or five males. We classified "mid-ranking males" only in flocks with three or five males.

Our ALS consisted of an array of 16 omni-directional 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 multi-channel data acquisition card (National Instruments DAQ-6260) and stored as 16-channel AIF 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 m^2 and encompassed the territories of 7-10 male chickadees. We define a neighbourhood as a cluster of breeding territories with multiple males defending adjacent territories against one another. The neighbourhoods we recorded were often bounded by natural boundaries (e.g. lake shoreline, large fields). Recorded neighbourhoods consisted of birds familiar with one another from the previous winter, either from the same winter flock or adjacent winter flocks.

Playback Design

Our playback apparatus consisted of two loudspeakers (Sony SRS-77G) mounted on 1.8 m poles and separated from each other by 24 m. Small undefended gaps between territories are relatively common in black-capped chickadee neighbourhoods. We

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positioned the two loudspeakers inside such gaps, outside the territories of resident males, in order to simulate a countersinging interaction between birds attempting to insert themselves in an undefended space.

We conducted a two-treatment playback experiment within each neighbourhood after recording a control period in which no playback was broadcast. Each neighbourhood received one treatment where we attempted to broadcast a highly "aggressive" interaction between the two simulated rivals, and another treatment where we attempted to broadcast a more "submissive" interaction between the two simulated rivals (Fig. 3.1). Song overlapping and frequency matching are directed signals of aggression in naturally-occurring chickadee song contests (Mennill & Otter 2007; Reed et al. in review). 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 two 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 of his songs at the higher frequency, and the other simulated male sang all of 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 half-way through the simulated interaction (one bird shifted from the high frequency to the low frequency after 7 songs, 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 one minute without any chickadee singing activity across the entire neighbourhood, which we monitored at the central computer. Each playback treatment lasted one minute and was followed by a ten minute observation period. Once 30 minutes had elapsed after the first treatment was broadcast, we began the second treatment upon observing one minute without chickadee any singing activity across the entire neighbourhood (average delay between playback treatments: 54.80 ± 4.11 minutes).

Playback stimuli were created using an established protocol (Mennill & Ratcliffe 2004a). We used recordings of six different chickadees recorded in our study population in 2000 to create songs for three different simulated intruders, pairing the *fee* note of three songs with the *bee* note of the other three songs at population-typical frequency and time differences. Using CoolEdit 2000 (Syntrillium, Phoenix AZ), we subtly modified the three recordings so they were the same length, amplitude, and frequency. We used CoolEdit to create two-channel stimuli, putting the contributions of each of the simulated rivals in either the left or right channel. We created 12 two-channel sound files which included all combinations of interactions between the three 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. Additionally, each simulated male was represented in the left and right channel an equal number of times. 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

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broadcast the same number of songs for each simulated male (15 songs per male), 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 SPL, 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 two 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 two treatments.

Analysis of Playback Responses

We examined singing activity in each neighbourhood at three time points: during the ten minutes immediately preceding the first round of playback (control period), during the first round of playback and the ten minutes immediately following playback, and during the second round of playback and the ten minutes immediately following 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 calculated eight variables: (1) song output at the neighbourhood level (total number of songs produced by all individuals in the recording area, per minute), (2) song output for each individual (number of songs produced, per minute), (3) intersong interval for each individual (delay between the start of one song and the start of the next song, excluding pauses longer than 15 sec), (4) number of pauses longer than 15 sec

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within the song bouts of each individual, (5) mean song frequency (measured one-quarter of the way through the *bee* note, following Christie et al. 2004), (6) the number of frequency shifts greater than 50 Hz for each male, and (7 & 8) the difference in frequency between a focal male's songs and the two frequencies broadcast during playback (3620 and 3124 Hz). 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 three of 118 song bouts; singing data from these three males were included in all analyses except for the analysis of rank, as the rank information was unknown for these unidentified males. Males were classified by location relative to playback; "adjacent" males had territories bordering the playback apparatus, while "distant" males had at least one male's territory between their territory and the playback area.

Statistical Analyses

We conducted a one-way analysis of variance (ANOVA) to examine the effect of playback treatment (aggressive, submissive) on the number of males singing within the ten recorded neighbourhoods. We conducted three-factor ANOVA to examine the effects of playback treatment (aggressive, submissive), male proximity to playback (adjacent, distant), and male dominance rank (high, mid, low) on measures of singing behaviour (song rate, mean intersong interval, number of pauses, mean frequency, number of frequency shifts, and frequency with respect to playback stimuli). We considered song rate both at the individual and neighbourhood level (song output of all individuals within the recorded neighbourhood). 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 ± SE. All tests are two-tailed.

Results

At the neighbourhood level, we found no difference in the number of males singing before playback and following the two playback treatments (Fig. 3.2a; ANOVA: $F_{2,27} = 0.94$, $P = 0.40$). However, neighbourhood song output following aggressive playback was more than double that following submissive playback (Fig. 3.2b; ANOVA: $F_{2,27} = 3.78$, $P = 0.04$). In total, we analyzed 118 bouts of singing 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, showed a near significant pattern with respect to playback treatment (Fig. 3.3;), 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 sang more songs after aggressive playback than submissive playback, and males with territories bordering the playback apparatus sang more songs than distant males.

To evaluate male song rate in response to playback treatments, we measured intersong interval, the time between the start of one song and the start of the next song. Intersong interval was not influenced by playback treatment, male proximity to playback, or dominance rank (Table 3.1; ANOVA: $F_{5,101} = 1.71$, $P = 0.14$). Males did, however, interrupt their song bouts with significantly more long pauses (silent intervals longer than

15 seconds between songs) following aggressive playback than during the control period (number of pauses per minute: control = 0.12 ± 0.02, aggressive playback = 0.21 ± 0.02, submissive playback = 0.13 ± 0.03; ANOVA: whole model: $F_{5, 103}$ = 3.22, P = 0.01; playback treatment: $F_{2, 103}$ = 4.68, P = 0.01; proximity to playback: $F_{1, 103}$ = 1.62, P = 0.20; rank: $F_{2, 103}$ = 1.98, P = 0.14).

Males sang across a broad range of frequencies in response to both playback treatments (aggressive: 2902-3781 Hz; submissive: 2938-3692 Hz). There was no significant difference in the mean song frequency with respect to playback treatment, male proximity to playback, or dominance rank (Table 3.1; ANOVA: $F_{5, 103}$ = 0.24, P = 0.94). Similarly, the number of frequency shifts greater than 50 Hz was not influenced by any of these factors (Table 3.1; ANOVA: $F_{5, 103}$ = 1.03, P = 0.40). Males did not shift their song frequencies to match or to avoid matching the frequencies broadcast during playback; we examined the frequencies at which males were singing with respect to the playback stimuli, and found no effect of playback treatment, male proximity to playback, or dominance rank for either the high or low frequency stimuli (high: ANOVA: $F_{5, 101}$ = 0.35, P = 0.88; low: ANOVA: $F_{5, 101}$ = 0.20, P = 0.96).

Discussion

Our neighbourhood-level recordings support the prediction, under the communication network model, that male black-capped chickadees respond to simulated dyadic interactions in their neighbourhood, even when these interactions take place outside their breeding territory. Territorial males responded differentially to playback treatments varying only in aggressive signaling intensity; males responded with higher

song output to simulated aggressive countersinging interactions which featured frequency matching and song overlapping and with lower song output to submissive countersinging interactions featuring neither matching nor overlapping. Neighbourhood song output was higher following aggressive playback treatments than following submissive treatments. Individual song output following playback was influenced by proximity to playback; males with territories bordering the playback apparatus had higher song output than more distant males in the neighbourhood. In using an ALS to record an entire neighbourhood of black-capped chickadee territories, this study is the first to quantify the distance of effect that dyadic exchanges have on a communication network in free-living animals.

Increased song output, both at the neighbourhood and 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 & Todt 1997; Mennill & Ratcliffe 2004a) and match (reviewed in Vehrencamp 2001) during countersinging interactions. Upon hearing an aggressive interaction between two strangers, males may have increased song output to assert their presence and to prevent direct threats to their own territories. Additionally, males may have increased song output in response to their neighbour's increasing singing activity. Not surprisingly, males bordering the playback area had higher song output than more distant males in the neighbourhood. 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 hence did not alter singing behaviour with respect to playback. Indeed,

many distant males were further than 80 m from playback, beyond the distance that chickadee song is estimated to travel (Christie et al. 2004). In addition to increased song output, males throughout the recorded neighbourhoods inserted more long pauses during song bouts following aggressive contests. This change in singing rhythm may indicate arousal; increasing variability in song timing makes it more difficult for rivals to anticipate the next song from an individual and may thereby decrease the potential for song overlap. Alternatively, this change in singing rhythm may arise from males changing song perches more often during the silent breaks between songs, a behaviour that is also thought to signal heightened arousal in chickadees (Mennill & Ratcliffe 2004b).

Our results corroborate previous findings which demonstrate that male black-capped chickadees eavesdrop on countersinging interactions between rivals (Mennill & Ratcliffe 2004a), and, importantly, our results provide the first evidence that male chickadees eavesdrop on interactions that occur outside of their territory boundaries. Because the playback treatments differed only in the singing strategies used by the two 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 increased song rate and increased number of pauses between songs that we observed in response to aggressive treatments, but not submissive treatments, therefore demonstrate that males were eavesdropping on the exchanges between the simulated rivals (*sensu stricto* social eavesdropping; Peake 2005). 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

two strangers outside of a focal male's territory boundary. Following 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 two simulated strangers (Peake et al. 2001). Taken together, these studies of eavesdropping and communication networks demonstrate that birds are attentive to the behaviour of conspecific individuals outside of their territory boundaries.

Singing strategies in different social contexts are under different selection pressures; males may behave very differently when faced with a rival intruding directly into their territory compared to an indirect, but nearby, interaction between two strangers. We did not simulate an intrusion or attempt to actively engage a territory holder as in most playback experiments (e.g. Naguib & Todt 1997; Peake et al. 2001; Mennill & 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 presently. Future studies should expand the approach we have used here by engaging territorial males directly in a countersinging exchange. Such an interaction may have a broader influence on the communication network because neighbours may be able to gain more information from overhearing a known neighbour interacting with a stranger than they can from two strangers interacting with each other.

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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 behaviour when males actively engage rivals, but both high- and low-ranking males may behave in a similar fashion when they sing in response to a nearby but indirect threat. Similarly, the lack of frequency effects in male playback responses may also be due to the indirect challenge posed in this playback design. Previous playback experiments that were designed to actively engage focal males (Horn et al. 1992; Otter et al. 2002) demonstrate that frequency matching is a directed signal used by male black-capped chickadees to address songs to rivals during dyadic contests within territory boundaries. When males respond to rivals outside their territory boundary (present study), they do not frequency match those rivals, whereas males do frequency match rivals when they are challenged within their territory (Horn et al. 1992; Otter et al. 2002).

In many territorial songbirds, individuals settle within signaling 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 to the individuals directly involved in these interactions, and also to nearby eavesdropping individuals. Only one other study has investigated countersinging exchanges at a network level: Burt & Vehrencamp's (2005) study of one morning of countersinging interactions in banded wrens (*Thryothorus pleurostictus*). They found a high level of song matching between neighbours during the dawn chorus, indicating that males adjust their singing strategies

with respect to their neighbours' songs, and that they do, in fact, interact with one another at dawn. Our results complement the findings of Burt & Vehrencamp (2005) by showing that interactions between neighbours 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 & Vehrencamp 2005). Our study reveals that dyadic interactions have an immediate effect on adjacent neighbours, but may also have a ripple effect and cause more distant neighbours to adjust their singing behaviour. 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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Acknowledgments

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Table 3.1. Singing behaviours that did not vary with playback treatment

Song feature	Control period	Aggressive treatment	Submissive treatment
Intersong interval (s)	5.59 ± 1.32	5.20 ± 1.12	5.07 ± 1.22
Mean frequency (Hz)	3380 ± 24	3366 ± 29	3397 ± 26
Frequency shifts/min	0.43 ± 0.07	0.43 ± 0.06	0.28 ± 0.07
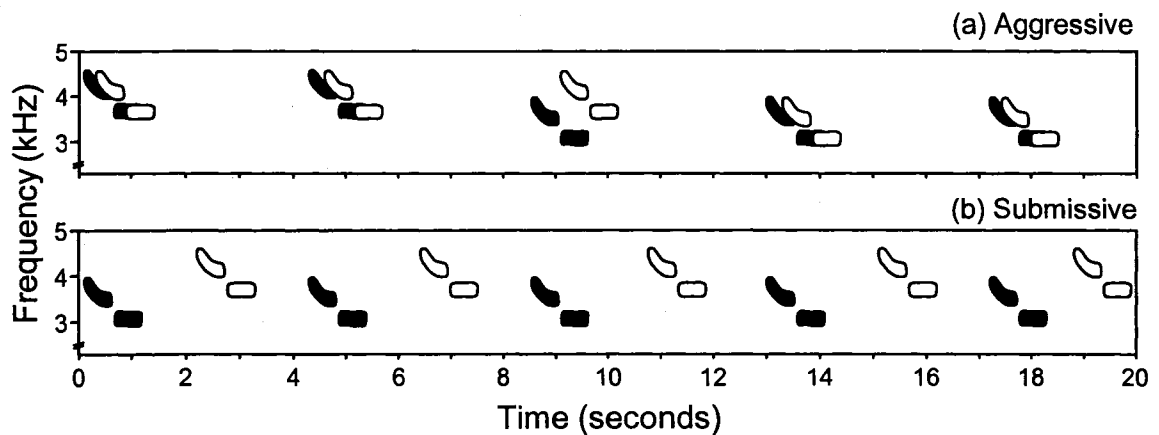
Figure 3.1. Stylized sound spectrograms of playback stimuli that simulated countersinging interactions between two male black-capped chickadees, one shown in black and the other shown in white. (a) In aggressive treatments, the songs of one simulated male overlapped the songs of the other, and the simulated 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.

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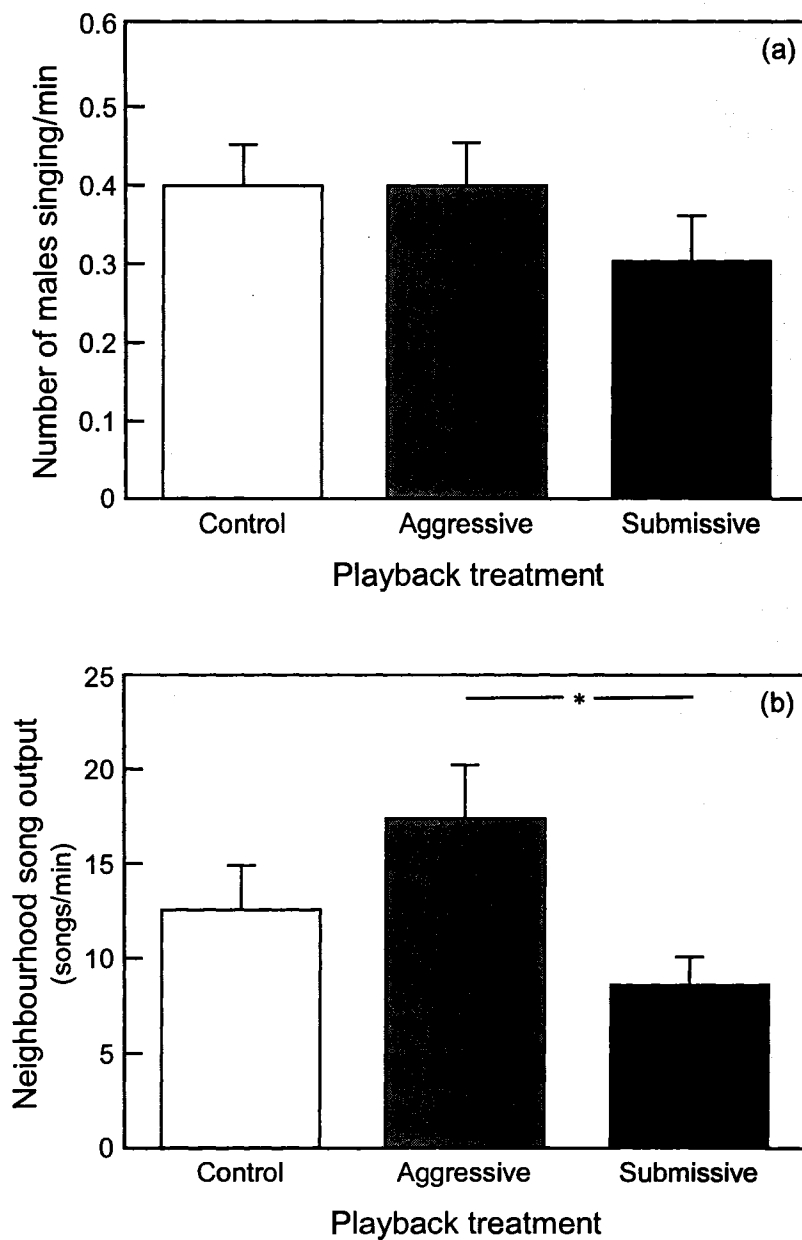
Figure 3.2. The influence of playback treatment on the number of males singing and neighbourhood song output. (a) The mean number of males singing in the neighbourhood. (b) The mean neighbourhood song output; song output was significantly higher following aggressive playback treatments than following submissive treatments. Asterisk shows significant difference between groups at $P < 0.05$. Error bars show standard errors.
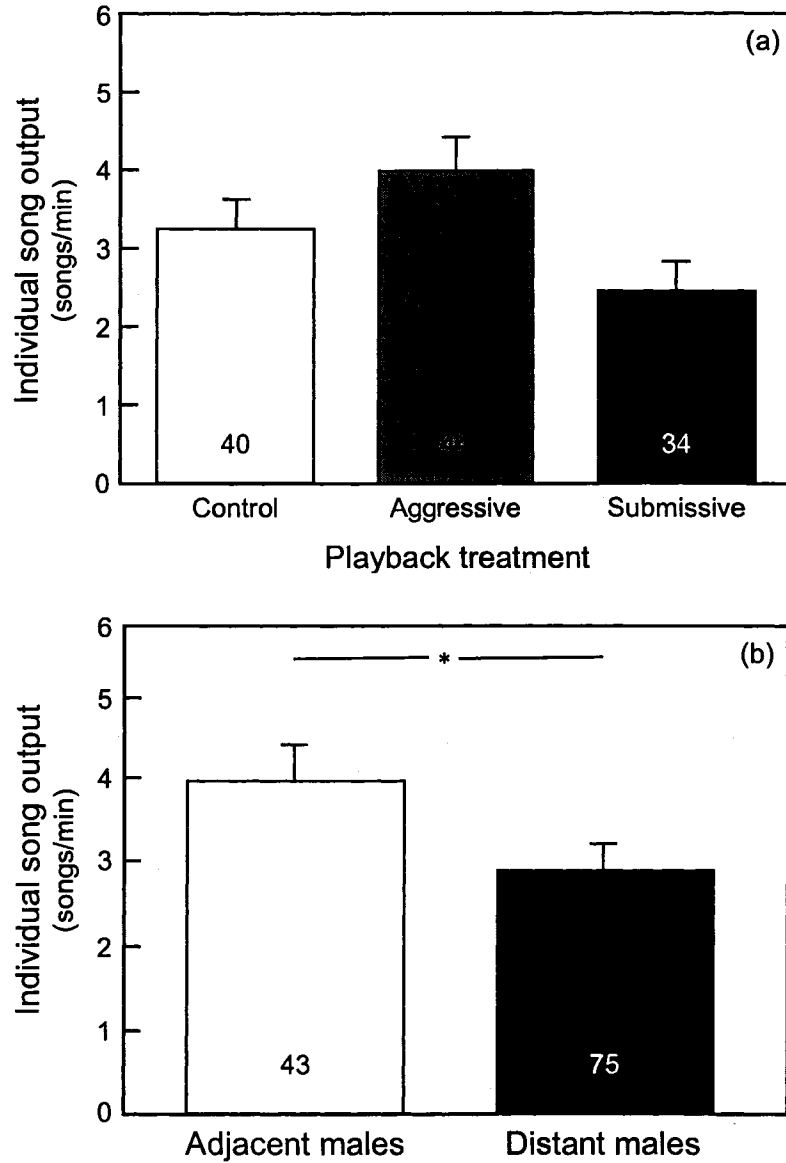
Figure 3.3. The influence of playback treatment and male proximity to playback on individual song output. Numbers of song bouts are shown at the base of each bar. (a) Individual song output was higher following aggressive playback treatments than following submissive treatments. (b) Song output was higher for males with territories bordering the playback area than for distant males in the neighbourhood. Asterisk shows significant difference between groups at $P < 0.05$. Error bars show standard errors.

Summary

1. Song matching and overlapping are directed aggressive signals in many songbird species. In chapter 2, I examine the use of two aggressive signals, frequency matching and song overlapping, in 100 naturally-occurring song contests among male black-capped chickadees (*Poecile atricapillus*) using a 16-microphone Acoustic Location System. I quantify the distance between opponents and examine male movement behaviour during contests. Matching is associated with overlapping, and contests in which opponents approach each other contain higher levels of matching than contests in which the males retreat. My results support the idea that chickadees use graded signals to indicate their level of aggression during song contests.

2. Male chickadees eavesdrop on countersinging interactions occurring outside of their territory boundaries. In chapter 3, I use stereo playback to simulate two types of song contests that differ only in the timing and patterning of the songs. I examine the singing activity of males in the neighbourhood surrounding the playback apparatus, which was positioned in undefended space between resident males. Territorial males respond more intensely to the aggressive treatments than the submissive treatments; both neighbourhood and individual song output was higher following aggressive treatments. Males bordering the playback apparatus responded more intensely than males distant to playback. My playback experiment provides important empirical support for communication networks in free-living animals.

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