The Ecology and Behavior of Chickadees and Titmice

An integrated approach

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CHAPTER 14

Status signaling and communication networks in chickadees: Complex communication with a simple song

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14.1 Introduction

Black-capped chickadees produce an extensive variety of calls, including the versatile *gargle* call (Chapter 11) and the namesake *chick-a-dee* call (Chapter 13). In contrast to these complex calls, the song of black-capped chickadees demonstrates a remarkable simplicity. Males sing a tonal, two-note phrase: *fee-bee*[1] (Fig. 14.1a). The fine structure of the chickadee song is highly conserved across the species' range throughout North America, with noteworthy exceptions described in a few isolated populations (Hailman 1989; Kroodsma *et al.* 1999; Gammon and Baker 2004; Chapter 12). Although the black-capped chickadee song is simple, young males inherit songs culturally, and nestlings raised in absence of adult tutors do not develop normal adult song (Kroodsma *et al.* 1995). In this chapter, we explore the ways in which male black-capped chickadees use this simple, learned song to achieve remarkably complex forms of communication. After a brief description of the ways in which male chickadees vary their songs over time, we evaluate two singing contexts: diurnal countersinging interactions and the dawn chorus. We then evaluate chickadee singing behavior within the new communication network model and highlight recent research on chickadees which has generated exciting insights into the ecology and evolution of sexual signaling in songbirds.

14.2 The *fee-bee* song: Variation on a two-note theme

In contrast to birds where each individual possesses a repertoire of song types, male black-capped chickadees typically have just one song type. However, male chickadees vary their songs by transposing the two-note *fee-bee* up and down a frequency continuum (Fig. 14.1b; Horn *et al.* 1992). Originally, black-capped chickadees were understood to have two song variants: a "normal song" at one frequency and a "shifted song" at another (Ratcliffe and Weisman 1985; Hill and Lein 1987; Chapter 10). Today we understand that male black-capped chickadees sing across a continuous frequency range of approximately 860 Hz (Horn *et al.* 1992; Christie *et al.* 2004b). Among songbirds, frequency transposition of an otherwise invariant phrase is an uncommon strategy, although it does occur in other species of birds, including the male songs of stripe-breasted wrens *Thryothorus thoracicus* (D. J. Mennill, personal observation) and eastern whipbirds *Phsophodes olivaceous* (Mennill and Rogers 2006). In other songbirds, including

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[1] Several mnemonics have been used to describe the chickadee's two-note song. Odum (1941) described the song as *phoebe*, while Desfayes (1964) suggested *dee-düh*. Brewer (1961) and then Ficken *et al.* (1978) opted for the more intuitive spelling of *fee-bee*. Kroodsma *et al.* (1999) suggest the mnemonic *hey sweetie*, which nicely describes the amplitude break in the second half of the chickadee song but also suggests that male song is directed at females, which we know to be only half of the singing male's audience. Among these options, we favor *fee-bee*, which is easily extended to *fee-bee-ee* when the amplitude break in the second syllable is of particular interest.

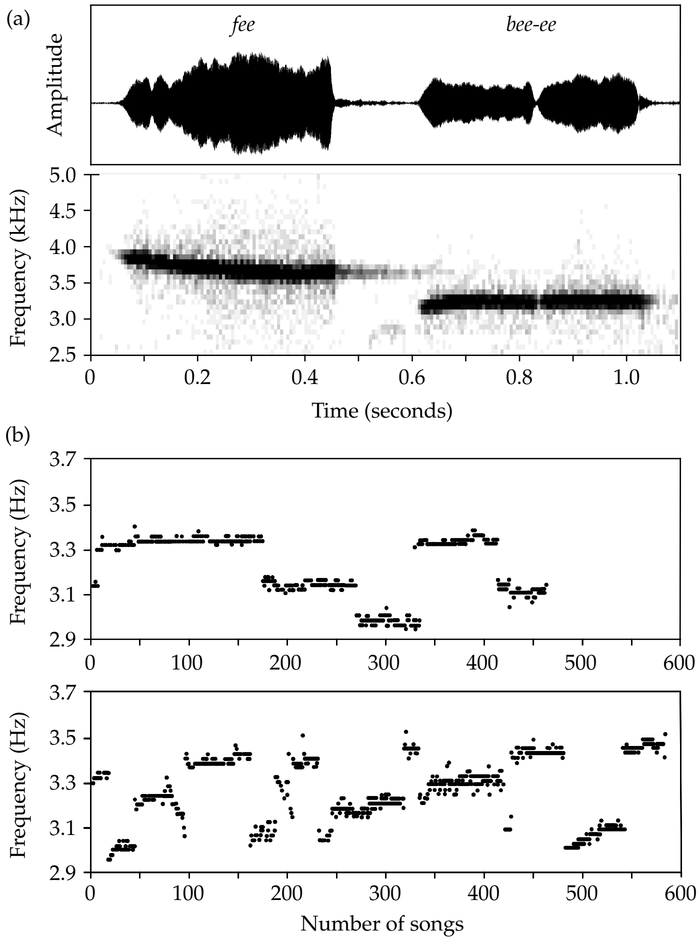

Figure 14.1 (a) Waveform and sound spectrogram of a black-capped chickadee *fee-bee* song. The *fee* note is higher in frequency and contains a subtle downslurred glissando. The *bee* note is relatively constant in pitch and contains a very short amplitude break which is audible at close range, i.e. *fee-bee-ee*. (b) Frequencies of all songs sung at dawn by two males, arranged along the x-axis in the order they were sung. Males transpose the *fee-bee* song across a frequency continuum, singing bouts of song at one frequency and then "pitch shifting" their song by intervals >80 Hz. Part b redrawn with permission from *The Auk*.

European nightingales *Luscinia megarhynchos*, Harris' sparrows *Zonotrichia querula*, and Kentucky warblers *Opornis formosus*, males emphasize certain frequency components within their songs (reviewed in Mennill and Ratcliffe 2004) even though they do not transpose the entire phrase.

The songs of black-capped chickadees, despite their simplicity and extreme similarity throughout most of North America, nevertheless show substantial variation in fine structure. This variation may—in conjunction with other vocal cues (Chapters 10, 11, and 13) aid individual recognition. Christie *et al*. (2004a) analyzed nine songs recorded from each of 46 male black-capped chickadees from eastern Ontario and measured five fine structural features: (1) song length, (2) relative length of the *fee* note, (3) relative loudness of the *fee* note, (4) the frequency ratio of the beginning to the end of the *fee* note (also known as the glissando frequency ratio), and (5) the frequency interval between the *fee* and the *bee* note. All five song features showed more variation between males than within males.

Multivariate analyses demonstrated that the fine structure of chickadee songs is sufficiently distinctive to allow individual identification (Christie *et al*. 2004a). In a test of laboratory-reared chickadees, Phillmore *et al*. (2002) confirmed that chickadees can indeed discriminate between the songs of at least eight different males. By using a sound transmission experiment, Christie *et al*. (2004a) demonstrated that these cues of individual identity persist over long broadcast distances, and Phillmore *et al*.'s (2002) laboratory test demonstrated that birds continue to distinguish between different individuals' songs when they are degraded by distance.

In addition to providing information on singer identity, the fine structure of black-capped chickadee songs may convey cues of singer quality. Males do not show rank-related differences in the fine structural features of their songs (Christie *et al*. 2004a). However, high-ranking males maintain more consistent frequency ratios between their *fee* and *bee* notes when singing at low frequencies (Christie *et al*. 2004b). Therefore, by listening to an extended song bout which contains songs sung at multiple frequencies, a listening chickadee may be able to identify the singer and also extract cues to the quality of the singer. In this regard, the ability to alter song frequency could allow chickadees to signal individual condition, which is conveyed via repertoire size in other species of Parids (McGregor *et al*. 1981; Lambrechts and Dhondt 1988; Lambrechts 1992). The difference, however, appears to be in how that information is encoded. In black-capped chickadees it appears to be the use of different frequencies and the control of fine structure across those frequencies, rather than the absolute number of song type variants, that indicate male quality. Frequency shifting and the ability to maintain consistent frequency ratios may be analogous to the ability to regulate and control strophe length in great tits (Lambrechts and Dhondt 1988; Lambrechts 1992) or the incorporation of particular note types into songs (Forstmeier *et al*. 2002). As we discuss below, frequency shifting in chickadees also allows for other signaling patterns typically associated with repertoires, but it is important to first investigate the contexts in which chickadees sing.

14.3 Context of singing in chickadees

Black-capped chickadees sing in two primary contexts: males sing an extended bout of song in the early morning dawn chorus and males sing during diurnal song bouts, which are often manifest as countersinging interactions between multiple males. Although birds sing throughout the year (Ficken *et al*. 1978), singing activity increases dramatically in late winter when birds break out of their winter flocks and begin defending territories against their former flock-mates. In our eastern Ontario population, where the first egg is typically laid around April 30, diurnal countersinging interactions are common as early as late February, especially on sunny days. Pronounced dawn choruses, on the other hand, do not begin until mid-April. Both diurnal countersinging interactions and dawn choruses persist into the breeding season, but decrease substantially when parents begin offspring care. Near identical patterns occur in our Northern BC population, although egg-laying and the onset of the other activities occur about a week later, suggesting the influence of photoperiod and weather on controlling these behaviors (see Chapter 4). Black-capped chickadee communication appears to operate differently in these two contexts, so we discuss each context separately. We first discuss communication during diurnal countersinging interactions, where the intricacies of chickadee communication are better understood, and then discuss communication during the dawn chorus.

14.3.1 Singing context 1: Diurnal countersinging interactions

Before migratory birds return to North America's temperate forest, the quiet of a crisp, sunny spring morning is often interrupted when a male black-capped chickadee begins to sing from a high song post. A moment later, a distant male may respond with his own songs and the forest becomes the site of a vocal duel. Intense dyadic countersinging interactions are especially common during the period of territory establishment and egg-laying (Dixon and Stefanski 1970). Participants in these interactions are typically neighboring territorial males (Shackleton and Ratcliffe 1994), or else territorial males and interlopers in search of mating opportunities (Smith 1989; personal observations). Contestants typically exchange songs from a substantial distance from one another, although countersinging interactions sometimes escalate to extremely aggressive physical encounters (Dixon and Stefanski 1970); in the weeks prior to female fertility, song contests may escalate to the point where the two males, feet locked, tumble to the ground in a burst of feathers, usually with a crowd of observers close at hand. During countersinging interactions, contestants vary both the pitch of their songs and rhythm of their singing relative to their opponent (Fig. 14.2). Both the relative timing and relative frequency of contestants' songs are salient features of song contests.

14.3.1.1 Variation in song frequency during countersinging interactions

Several experimental studies have helped elucidate the signal function of frequency variation during diurnal countersinging interactions. Both loop playback and interactive playback techniques have been used to simulate the songs of a chickadee intruding into a male subject's territory. Horn *et al.* (1992) broadcast chickadee songs at low, moderate, or high frequencies (3130, 3380, or 3630 Hz—measured at start of *bee* note) from a loudspeaker positioned near the center of the territories of 24 male chickadees. Territorial males responded with songs that fell within 120 Hz of the frequency of the playback-simulated intruder (Horn *et al.* 1992). Otter *et al.* (2002) expanded on this approach and

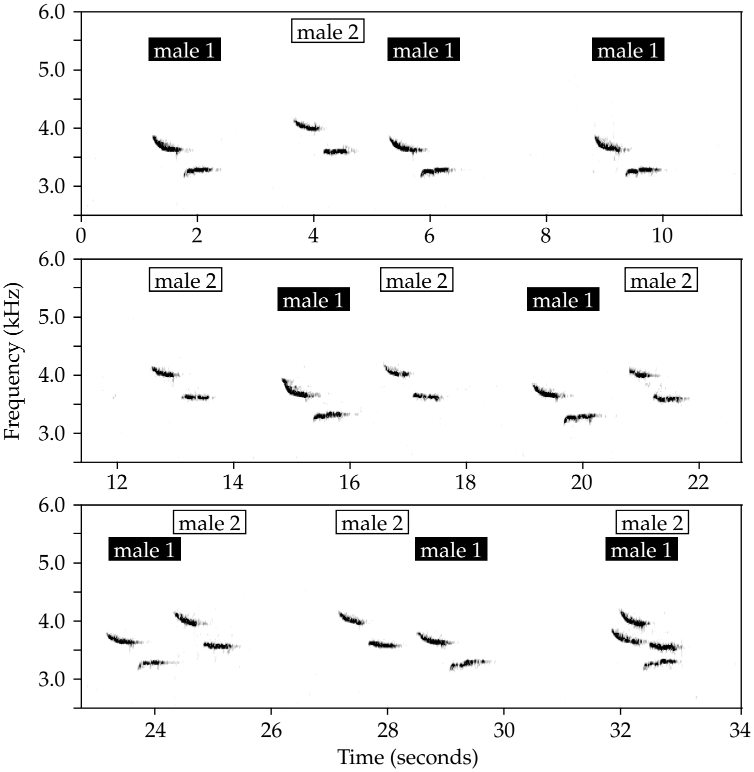

Figure 14.2 Sound spectrogram of a countersinging interaction between two neighboring territorial male black-capped chickadees. The spectrogram is shown in three consecutive stretches, depicting 34 seconds of countersinging. The two opponents are not frequency matched; male 1 sings at a frequency approximately 330 Hz lower than male 2. The two birds alternate songs until the final exchange (at second 32) where male 2 overlaps the song of male 1.

gave playback to 24 territorial males using three different treatments: (1) loop playback of a 3200 Hz song played every 5 seconds; (2) interactive playback of a 3200 Hz song played immediately after every song sung by the territorial male; and (3) interactive playback of songs that matched the frequency of the subject's songs (matching accuracy: 24 ± 11 Hz) and immediately followed the subject's songs. These treatments incited increasingly close approaches from the territorial male, indicating that chickadees perceive frequency matching, in concert with one-to-one temporal correspondence, as a threatening signal (Otter *et al*. 2002). Interestingly, males in treatment 2 often shifted to frequency match the playbacks, thus effectively becoming treatment 3 although not through our intervention; these males showed heightened levels of response compared to those that did not frequency match the playback.

Mennill and Ratcliffe (2004c) employed a fully-interactive approach to engage 81 territorial males in countersinging interactions with a playback-simulated intruder. In half of the trials, the simulated intruder matched the frequency of the resident male (matching accuracy: 7 ± 15 Hz). In the other half of the trials, the intruder sang at a frequency 346 ± 16 Hz higher than the resident male. All males who received interactive playback responded very aggressively to playback, exhibiting closer average approach distances than had been reported in any previous study. However, birds who were frequency matched during playback retreated away from the loudspeaker and spent more time singing from a greater distance from the simulated intruder, indicative of an aversive response (Mennill and Ratcliffe 2004c). Taken together, these three playback studies indicate that frequency variation has important consequences during countersinging interactions. Frequency matching during diurnal countersinging interactions appears to be a directed signal of aggression and functionally similar to song-type matching in other birds.

Many birds who sing with a repertoire of discrete song types communicate aggressive signals by tactically choosing songs that match their opponent's song type (Vehrencamp 2001). Type matching, as an aggressive countersinging strategy, has been demonstrated in many birds, including great tits (Krebs *et al*. 1981; McGregor *et al*. 1992). As with type matching, our analyses of chickadee singing strategies suggest that frequency matching is a directed signal of aggression. Thus, the ability to frequency shift songs compensates black-capped chickadees for the lack of song-type variation found in other Parids. Innovative, interactive playback experiments with repertoire singing birds have revealed a complex system of graded signals based on the relative song choice of countersinging birds, which have helped the understanding of the evolutionary pressures responsible for the evolution of repertoires (reviewed in Beecher and Brenowitz 2005). Further research on the subtleties of chickadee countersinging behavior is needed to answer questions about the importance of frequency variation during song contests. For example is high-frequency singing more or less aggressive than low-frequency singing, and are changes in song frequency signals of aggression *per se*?

14.3.1.2 Variation in song timing during countersinging interactions

Although frequency variation during diurnal countersinging interactions is well studied, variation in song timing is more poorly explored. Detailed studies of the function of song overlapping require tight regulation of the timing of signals broadcast during playback, and only since the proliferation of interactive playback software have researchers rigorously applied an experimental approach to field studies of overlapping. The topic of overlapping of song was originally studied in association with the repetitive phrasing of great tit song strophes, which can lengthen or shorten a song bout. Male great tits increase variation in song timing (Dabelsteen *et al*. 1996) and stop songs short (Langemann *et al*. 2000) when overlapped by playback. Blue tits show higher song rates when overlapped (Poesel 2004). Territorial males respond in like fashion in other, non-Parid songbirds including nightingales, European robins *Erithacus rubecula* (Todt 1981), and blackbirds *Turdus merula* (Brindley 1991).

Mennill and Ratcliffe (2004c) used interactive playback to simulate a singing chickadee who either overlapped every song given by each playback subject or avoided overlapping by singing 1.5 seconds after the playback subject's song was complete. In response to an overlapping opponent, territorial males sang significantly more shortened songs, dropping the *bee* note from significantly more songs when they were overlapped by an opponent. Furthermore, overlapped males sang with significantly more variation in the silent interval between consecutive songs. These responses of male black-capped chickadees to an overlapping opponent mirror the responses of other songbirds to overlapping opponents outlined above. This cross-taxa similarity of response to overlapping playback suggests that the very nature of overlapping, as a signal that masks an opponent's signal, is a more antagonistic countersinging approach than non-overlapping. Both the increase in shortened songs and the increase in variable song timing exhibited by black-capped chickadees may be strategies used by countersinging birds to avoid having their songs masked by an opponent.

To further quantify the occurrence of frequency matching and overlapping during chickadee countersinging interactions, we transcribed 68 naturally-occurring song contests heard between March 21 and May 6, 2001 and 2002 (D. J. Mennill, unpublished data). Using a different symbol for each contestant, we noted the relative pitch and relative timing of each song by the relative position of the symbols on graph paper. (One challenge with documenting song overlap during naturally-occurring countersinging interactions is that the observer's perception of overlapping signals may differ from the birds' perceptions of those signals owing to the slow speed of sound propagation through air. During the transcriptions we describe here, the observer was typically in relatively close proximity to the countersinging males, such that the perception of overlapping likely matched the perception of overlapping by the counter-singing chickadees.) From these transcriptions, we extracted the following variables for each song contest: (1) the number of song overlaps; (2) whether or not the contestants were frequency-matched with one another; and (3) whether or not the countersinging contest escalated (as indicated by the contestants approaching each other and giving extended bouts of *chick-a-dee* and *gargle* calls; sample sizes vary depending on how reliably overlapping and frequency matching could be determined in each contest). Song contests that escalated tended to contain more song overlaps (3.9 ± 0.7 overlaps per contest; mean ± SE) than song contests that did not escalate (3.0 ± 0.7 overlaps per contest) but this difference was not significant (Wilcoxon: $Z = 1.1$, $P = 0.11$, $N = 61$). Frequency matching, on the other hand, showed a significant relationship with contest outcome: 25 of 32 contests (78%) that escalated contained frequency matching between the contestants, whereas only 20 of 36 contests (56%) that did not escalate contained frequency matching (Fisher exact: $p = 0.04$; birds were considered to be frequency-matched if the musically trained transcriber could detect no difference in their song frequency). These results mirror those of Shackleton and Ratcliffe (1994) who found that frequency matching was associated with contest escalation in 27 interactions recorded in 1991. Therefore, observations of natural contests support the idea that song overlapping and frequency matching are directed signals of aggression, important during the diurnal countersinging interactions of black-capped chickadees. These results also suggest that song overlapping and frequency matching serve distinct signal functions. Mennill and Ratcliffe's (2004c) interactive playback experiment showed that overlapping primarily influenced the birds' singing rhythm and frequency matching influenced the birds' movement behavior. Our observations of naturally occurring countersinging interactions support this idea; song contests that involved frequency-matching usually resulted in the opponents approaching one another, whereas song contests that involved overlapping did not.

14.3.2 Singing context 2: The dawn chorus

In the early twilight before sunrise, when dark treetops can just barely be distinguished from the dark sky, male black-capped chickadees begin an extended period of singing. The *fee-bee* of one male penetrates the still dawn air, then two more males join the chorus, and soon the entire neighborhood comes alive with song. Each male may continue to sing for as long as 70 min, singing an average of 282 ± 36 songs (Horn *et al.* 1992; Christie *et al.* 2004b). Song output during the chorus varies with male dominance status. Males with high-ranking dominance status begin singing earlier, they sing for longer, and they sing at a higher rate than their low-ranking counterparts (Otter *et al*. 1997). Therefore, during the chorus, males broadcast cues to their quality not only through the fine structure of their songs (see above) but also through song output (Otter *et al*. 1997). Male chorus output also reflects male pairing status. Following experimental removal of the female, male chorus length dramatically increases (Otter and Ratcliffe 1993). During the chorus, males pitch shift their song by an interval of ≥80 Hz every 30.7 ± 3.7 songs (Christie *et al*. 2004b). The rate of pitch shifting varies dramatically, both between males and between the choruses from any particular male, where some chorus performances featuring a pitch shift after nearly every song while others contain no pitch shifts whatsoever. In general, however, male choruses consist of bouts of songs at similar frequencies punctuated by marked changes in frequency (Fig. 14.1b).

Egg-laying female black-capped chickadees sleep inside their nest cavities, and males typically sing much of the dawn chorus in close proximity to their nest (Otter and Ratcliffe 1993; Gammon 2004; Mennill and Ratcliffe 2004b). Males often pause or stop singing upon the female's emergence from the nest cavity (Otter and Ratcliffe 1993; Gammon 2004). Upon the emergence of the female from the nest cavity, males often switch from singing to giving *variable see* and *gargle* calls (Gammon 2004; personal observation). Both withinpair copulations (Otter and Ratcliffe 1993; Gammon 2004) and extra-pair copulations (Smith 1988; Mennill *et al*. 2004) commonly follow the end of the dawn chorus. Based on the observation that males tend to give their dawn chorus in close proximity to the nest cavity, several authors have suggested that the male chorus is "directed at the female" (Otter and Ratcliffe 1993; Gammon 2004). We encourage a cautious approach to this interpretation for several reasons. First, male dawn song is far louder than necessary to communicate with a female inside the nest cavity; indeed, males accomplish this task with the remarkably quiet *faint fee-bee* vocalization later in the breeding season (Smith 1991). Instead, males sing songs at a high amplitude, such that a human observer listening to the dawn chorus can consistently hear more than one male and often as many as four males (Hansen *et al*. 2005). Second, males may benefit by remaining near their nest cavity for reasons that are independent of communication with the female. Most notably, females often solicit copulations, both withinpair and extra-pair, upon exiting the nest cavity at dawn. Males may find an advantage in remaining near the nest cavity so that they can either copulate with their partner or mate guard her when she emerges. This idea could be tested by conducting a pair-wise comparison of the position of males during the dawn chorus when their partner is fertile and when she is not, or by comparing the chorus locations of high-ranking males (whose females seldom follow a mixed reproductive strategy) versus low-ranking males (whose females often follow a mixed reproductive strategy). Third, males may sing the dawn chorus near their nest cavity to mask their partner's ability to hear the dawn chorus performance of neighboring males. Analyses of recordings made with microphones mounted inside nest boxes suggest that this sort of masking comes into play in the dawn chorus of great tits (see below; K. A. Otter, T. M. Peake, A. M. R. Terry, and P. K. McGregor, unpublished data).

The interactive nature of chickadees' diurnal countersinging contests is obvious, but the processes that govern the timing and frequency of chorusing male chickadees' songs are very poorly understood. Upon hearing the apparent cacophony of a busy black-capped chickadee chorus, which includes the dissonant harmonies of multiple song frequencies and the irregular overlaps and alternations between many males' songs, a human listener may be inclined to believe that chorus singing is non-interactive. To test whether the dawn chorus was interactive, Shackleton and Ratcliffe (1994) simultaneously recorded three males in neighboring territories during two mornings of dawn chorus. They found little evidence for correspondence in the frequency of songs given by neighboring males. However, analysis of larger groups of birds over a much longer periods of time is required to rigorously determine whether song frequency and timing show any correspondence between neighbors during the chorus. As Burt and Vehrencamp (2005) have demonstrated using multichannel array recordings of banded wrens *Thryothorus pleurostictus*, the dawn chorus can involve interactive behavior with complex processes of tactical song choice.

14.4 Communication networks

Conventionally, animal communication has been understood as a dyadic process of information exchange involving one signaler and one receiver: a songbird may defend his territory by signaling to a male receiver and he may attract a breeding partner by signaling to a female receiver (e.g. Kroodsma and Byers 1999). The dyadic model of communication is useful for understanding pitch matching and overlapping during dyadic countersinging contests of black-capped chickadees (see above). However, chickadees share two characteristics, in common with many other songbirds, which are not easily accounted for within the dyadic model. First, chickadee songs are long-range signals that may convey information across broad distances to multiple receivers simultaneously. Second, each breeding neighborhood of chickadees consists of multiple males and females who may all benefit by assessing the quality of their neighbors. A communication network model, which accounts for multiple signalers and multiple receivers exchanging information simultaneously (McGregor 2005), may therefore provide an enhanced understanding of communication in black-capped chickadees in particular, and in songbirds in general.

Within a communication network, individuals may transmit information in novel ways that occur outside of the traditional dyadic model. Eavesdropping is a network-based receiver behavior, whereby an individual gathers information from a signaling interaction between conspecifics without being directly involved in that interaction (McGregor and Dabelsteen 1996; *sensu* "social eavesdropping" Peake 2005). Eavesdropping on the diurnal countersinging contests of male songbirds may facilitate low-cost and direct comparisons of the relative quality of countersinging contestants. Female black-capped chickadees, who are genetically promiscuous (Otter *et al*. 1998; Mennill *et al*. 2004) and are quick to divorce their partner if a higher-status male becomes available (Otter and Ratcliffe 1996; Ramsay *et al*. 2000), might eavesdrop on male–male countersinging interactions to evaluate the quality of potential partners. Male chickadees might benefit from eavesdropping on the countersinging interactions of other combatants; this information could then be used to adjust his own willingness to escalate in subsequent interactions with one or the other of these rivals. We tested these ideas using multispeaker playback and interactive playback approaches.

14.4.1 Male eavesdropping in black-capped chickadees

To test whether male black-capped chickadees eavesdrop, Mennill and Ratcliffe (2004a) used a multispeaker experiment to evaluate the responses of territorial males to a countersinging contest between two simulated intruders. Playback was given through three loudspeakers arranged in an equilateral triangle with 24 m between each loudspeaker. Playback occurred in three stages (Fig. 14.3a). In stage 1, the territorial male was attracted to within 5 m of a loudspeaker broadcasting *chick-a-dee* calls, thereby bringing the male to a position equidistant from the remaining two loudspeakers. In stage 2, *fee-bee* songs were broadcast from the other two loudspeakers, simulating a countersinging contest between two unknown males. The two simulated males sang songs at the same frequency, the same rate, and the same amplitude; the only difference between the two loudspeakers was that the songs of one male consistently overlapped the other (after Naguib and Todt 1997). During playback, an observer evaluated which loudspeaker the subject approached first. In stage 3, a postplayback assay, songs were broadcast from the loudspeaker that the male did not first approach in stage 2, to confirm that both loudspeakers were positioned in such a way as to elicit a territorial response from the subject.

The responses of territorial males to the multispeaker playback demonstrated that male black-capped chickadees do eavesdrop on the countersinging interactions between others. High-ranking males preferentially approached the overlapping loudspeaker (Fig. 14.3b). Because there were no absolute differences in information broadcast by the two loudspeakers, only relative

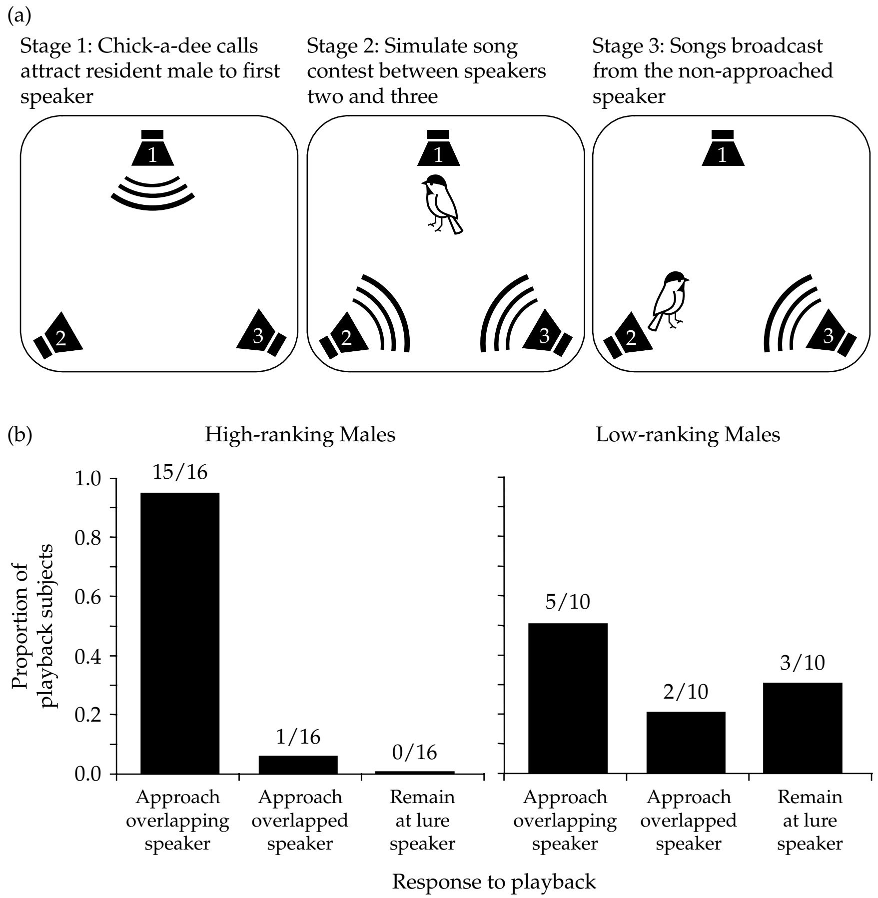

Figure 14.3 (a) Schematic representation of a multispeaker playback experiment designed to test whether male black-capped chickadees eavesdrop on the countersinging interactions of other males. Stage 2 simulated a countersinging interaction between two males where one bird consistently overlapped the other's songs. (b) High-ranking males preferentially approached the loudspeaker broadcasting overlapping songs, demonstrating that males eavesdrop on male–male interactions. Reprinted with permission from *Behaviour*.

information in the form of song overlapping, the high-ranking males' responses indicate that males extract relative information from rivals' countersinging interactions. This result adds to a growing body of research documenting male eavesdropping in great tits and other species (see Peake 2005 for review). In contrast to the strong directional response exhibited by high-ranking male black-capped chickadees, low-ranking males showed a mixed response. Although low-ranking males approached the overlapping loudspeaker most often, they sometimes approached the overlapped loudspeaker and, in three cases, approached neither loudspeaker. These differential responses of high and low-ranking males support the idea that responses to conspecific rivals varies with the quality of the territorial male: high-ranking males, who are better able to dominate other birds during physical encounters, preferentially approach a loudspeaker broadcasting a more aggressive signal. Future playback studies expanding on this multispeaker experimental design may shed insight into the signal function of pitch matching and pitch shifting behavior, and may even help to tease apart which signals are most salient to eavesdroppers.

14.4.2 Female eavesdropping in black-capped chickadees

Using a modified version of Otter *et al.* (1999) interactive playback study, Mennill *et al.* (2002, 2003) engaged male chickadees in countersinging contests with a simulated intruder to test whether female black-capped chickadees eavesdrop on male–male song interactions. The experiment involved playback to groups of four birds: two pairs of breeding partners in neighboring territories, where the males had been flock-mates during the previous winter, one high-ranking and one low-ranking. Playback was conducted at the onset of female fertility and occurred in four successive stages (Fig. 14.4a). In stage 1, one male was engaged in a 6-min countersinging contest with a playback-simulated intruder. In stage 2, an hour later, the other male was engaged in a 6-min countersinging contest with the same playback-simulated intruder. We used the same catalogue of songs to interact with both males, but with one male we simulated an aggressive opponent (one who overlapped and pitch-matched all of the subject's songs) and to the other male we simulated a submissive countersinging opponent (one who avoided overlapping and sang at a frequency 300–400 Hz higher than the subject) (Fig. 14.4b). There were no absolute differences in the song output of the playback between aggressive and submissive trials, only relative differences between the pitch and timing of the songs of the resident male and the simulated intruder. Stages 1 and 2 of playback were repeated to each male on two subsequent days. In the final two stages of the experiment, we assessed females' responses to playback. In stage 3, a behavioral assay, we followed each pair for 30 min on the day following playback in the early morning, a time when chickadee extrapair copulations are common (Smith 1988; Mennill *et al.* 2004). In stage 4, a genetic assay, we used microsatellite paternity analyses to sample the broods of both females for extrapair offspring.

The genetic assay (stage 4) confirmed that female black-capped chickadees eavesdrop on male–male vocal interactions. The proportion of nests containing extrapair young was significantly greater in the broods of females paired to high-ranking males who received aggressive playback, compared to the broods of females paired to high-ranking males who received submissive playback or to males who received no playback (Fig. 14.4c, Mennill *et al.* 2002). In other words, after hearing their high-ranking partner "lose" a song contest to an opponent, females paired to high-ranking males changed from a monogamous mating strategy to a promiscuous mating strategy. Surprisingly, the behavioral assay (stage 3) yielded no evidence that female black-capped chickadees eavesdrop on male–male song contests; neither female behavior nor male behavior showed any difference on the morning following aggressive or submissive playback manipulations (Mennill *et al.* 2002, 2003). Although no extraterritorial forays were observed during the observation period, one extrapair copulation was observed outside the observation period. A female paired to a high-ranking male who had received aggressive playback had an extrapair copulation with a low-ranking male who had received submissive playback (Mennill *et al.* 2004). Genetic assignment of extrapair fathers demonstrated two more cases where females paired to aggressive-playback high-ranking males had extrapair copulations with submissive-playback low-ranking males. No other study of the black-capped chickadee mating system (Smith 1988; Otter *et al.* 1998; Mennill *et al.* 2004) has documented a female seeking an extrapair copulation from a low-ranking male from the same winter flock as her high-ranking partner. The three cases that followed Mennill *et al.*'s playback experiment therefore indicate that eavesdropping on male–male song contests influences not only the female's decision about whether or not to follow a mixed reproductive strategy (Mennill *et al.* 2002) but also whom to target as an extrapair sire (Mennill *et al.* 2003).

Females paired to high-ranking male chickadees are typically genetically monogamous (Otter *et al.* 1998; Mennill *et al.* 2004), yet these females increased the proportion of extrapair young in their broods after hearing their partner lose an aggressive countersinging contest. In contrast, females paired to low-ranking males continued to produce similar proportions of extrapair young regardless of the playback treatment given to their partner (Fig. 14.4c). Why were aggressive playback sessions

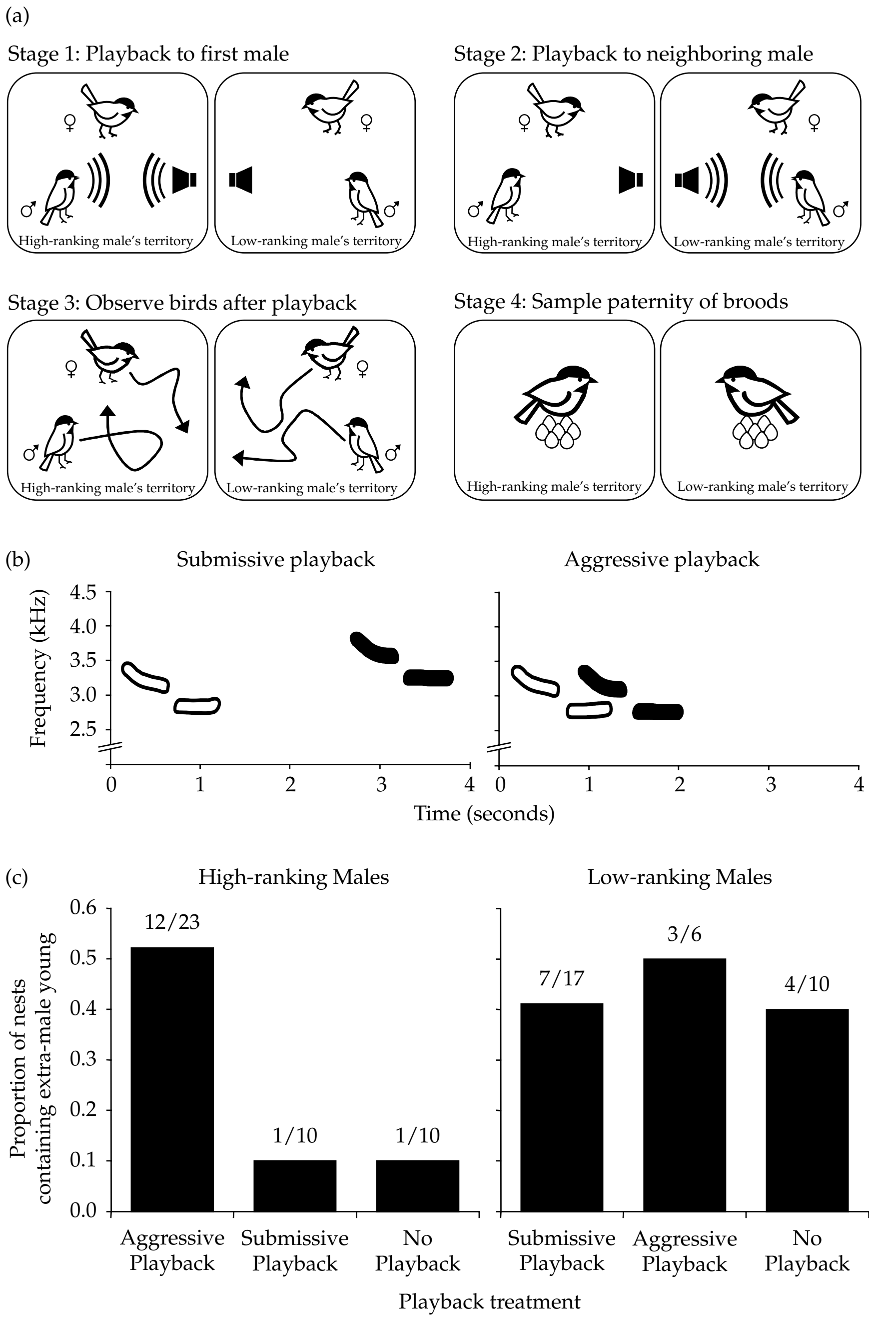

Figure 14.4 (a) Schematic representation of an interactive playback experiment designed to test whether female black-capped chickadees eavesdrop on male–male countersinging interactions. (b) During submissive playback interactions, interactive playback simulated an opponent (black) who avoided overlapping the subject (white) and sang at a higher frequency than the subject. During aggressive playback interactions, the playback-simulated intruder overlapped and pitch matched the subject. (c) High-ranking males who received aggressive playback lost paternity significantly more often than high-ranking males who received submissive playback or no playback. Low-ranking males lost paternity at equivalent levels regardless of the playback treatment they received. Parts b and c reprinted with permission from *Science*.

sufficient to increase the proportion of extrapair young in the broods of high-ranking males whereas submissive playback sessions did not reduce the proportion of extrapair young in the broods of low-ranking males? In complex systems, Gould (1998) suggests that a "great asymmetry" exists between the perception of constructive and destructive forces, where the apparent severity of one negative event outweighs the product of many positive events. Such an asymmetry may influence the mate choice decisions of eavesdropping female black-capped chickadees. Females paired to high-ranking males are accustomed to observing their partner dominate contests over food resources throughout the winter and dominate territorial countersinging interactions during the breeding season. Therefore, the poor vocal performance of high-ranking males during aggressive playback trials was unusual and may have been sufficiently extraordinary to call into question previous female assessments. Females paired to low-ranking males, in contrast, observe their partner dominate some contests (e.g. with interlopers of even lower quality) and be dominated in other contests (e.g. with a higher-ranking neighbor). Consequently, the strong performance of low-ranking males during the playback manipulated song contests may not have been outside the normal experience of females paired to low-ranking males.

Otter *et al*. (1999) evaluated female eavesdropping in great tits using a similar interactive playback experiment. Two differences between the great tit studies and those described above for chickadees may be salient in comparing results. As great tits do not have cohesive flock membership or strict dominance hierarchies, males were randomly assigned to receive aggressive or submissive playback during playback interactions. Further, because great tits do not pitch shift and song type matching does not appear to have an additive effect to overlapping alone (Dabelsteen *et al*. 1996), overlapping versus non-overlapping was the primary difference between aggressive and submissive treatments.

Like the results with chickadees, the evidence from interactive playback sessions with great tits suggests that breeding females eavesdrop on the vocal interactions of males. Female great tits paired to males who received aggressive playback readily forayed into the territories of neighboring males who had received submissive playback, presumably to assess alternative mating opportunities (Otter *et al*. 1999). Genetic analyses demonstrated that these extraterritorial forays did not, however, translate into extrapair fertilizations (Otter *et al*. 2001).

Otter *et al*.'s (1999, 2001) experiments with great tits and Mennill *et al*.'s (2002, 2003) experiments with black-capped chickadees demonstrate that female Parids eavesdrop. Both experiments documented a change in female reproductive activities following manipulation of male signals. However, the reproductive activities of females changed in different ways for these two species. Great tit females readily forayed into neighboring territories but did not change their genetic mating strategy, whereas black-capped chickadee females did not readily foray outside of their territory and yet they changed their genetic mating strategy. These differences may be related to differences in the behavioral ecology of chickadees and tits. Black-capped chickadees spend the winter in small cohesive flocks with stable flock membership where interactions follow a strict linear dominance hierarchy (Smith 1991). In contrast, great tit flocks are larger, flock membership is transitory, and rank relationships are more labile (Dent *et al*. 2002). For female great tits, surrounded by breeding males whose relative quality is less resolved, eavesdropping may be a means of initial assessment of male quality, which females follow up with forays into neighbors' territories. If detailed assessments fail to confirm the information gained through eavesdropping, female great tits may forgo extrapair copulations (Otter *et al*. 2001). Female black-capped chickadees, however, are expected to be intimately familiar with the relative status of all males singing within earshot. Consequently, information gained through eavesdropping may be especially important to female black-capped chickadees when that information reveals quality differences that contrast the females' previous assessments. Having lost confidence in her mate's status after hearing him dominated in a song contest with an aggressive opponent, female chickadees may adopt the next best strategy of seeking an extra-pair fertilization from another nearby, high-ranking male (Mennill *et al*. 2003). Despite their differences, these two studies of Parid eavesdropping behavior demonstrate that female eavesdropping is an important means of female assessment of male quality.

14.4.3 Nest cavities and male singing behavior

Communication network theory suggests that females should position themselves in order to maximize assessment of the males around them (Otter and Ratcliffe 2005). The nesting behavior of black-capped chickadees provides support for this theory. Black-capped chickadees routinely construct their nests closer to the edges of their territories than would be expected by chance (Ramsay *et al*. 1999). Nests typically fall within 20 m of territory edges, despite the large size of chickadee territories (Fig. 14.5; average territory diameter: 152 ± 27 m; Mennill *et al*. 2004). Detailed investigation of food abundance and vegetation features show no marked differences between nest sites at territory edges versus comparison sites at territory centers, suggesting that chickadees nest at territory peripheries based on conspecific attraction

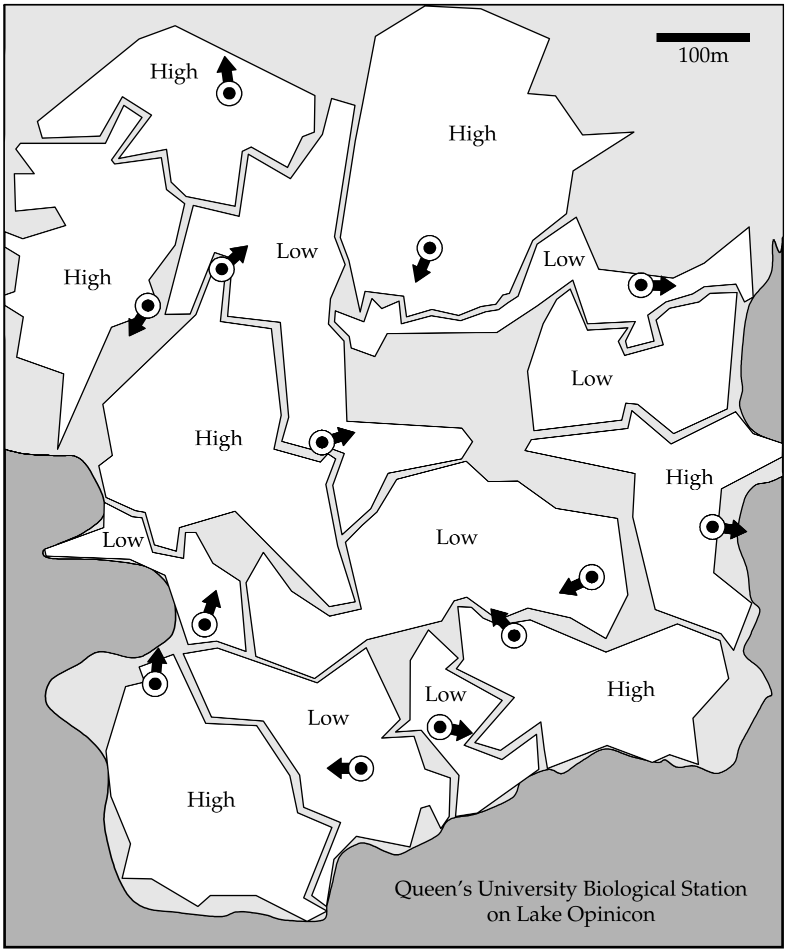

Figure 14.5 Territory map of part of the breeding population of black-capped chickadees at Queen's University Biological Station in 2000. Nest cavities are shown as circles. Arrows indicate the orientation of the nest cavity entrance. Territories were assessed by spot mapping the birds' movement patterns (see Mennill *et al*. 2004). The rank of the territorial male is shown for each territory.

(Ramsay *et al*. 1999). Female chickadees, who remain inside of the nest cavity for much of the dawn chorus, may be better able to hear the dawn chorus performance of neighboring males by nesting near territory boundaries. Given that black-capped chickadee song transmits over a minimum distance of 80 to 100 m (Christie *et al*. 2004a; Fotheringham and Ratcliffe 1995), females maximize the number of males audible to them during the chorus by nesting near territory edges. Analyses of black-capped chickadee nest positions in 190 territories over 5 years showed that nest sites fell within 100 m of more chorusing positions of neighbors than did comparison sites at territory centers (Mennill *et al*. 2004). Females may also nest at territory edges to facilitate early morning extrapair copulations with neighbors (Ramsay *et al*. 1999). However, although extrapair copulations do often occur shortly after female emergence from the nest (Smith 1988), they do not usually occur in close proximity to the nest (Mennill *et al*. 2004), suggesting that the edge-nesting behavior of female chickadees maximizes acoustic contact rather than physical contact with neighbors.

Recordings made inside the nest boxes of great tits provide further support for the idea that roosting female Parids may monitor the dawn chorus performance of neighboring males while they roost inside the nest cavity. Microphones were placed inside the nests of seven different females in a

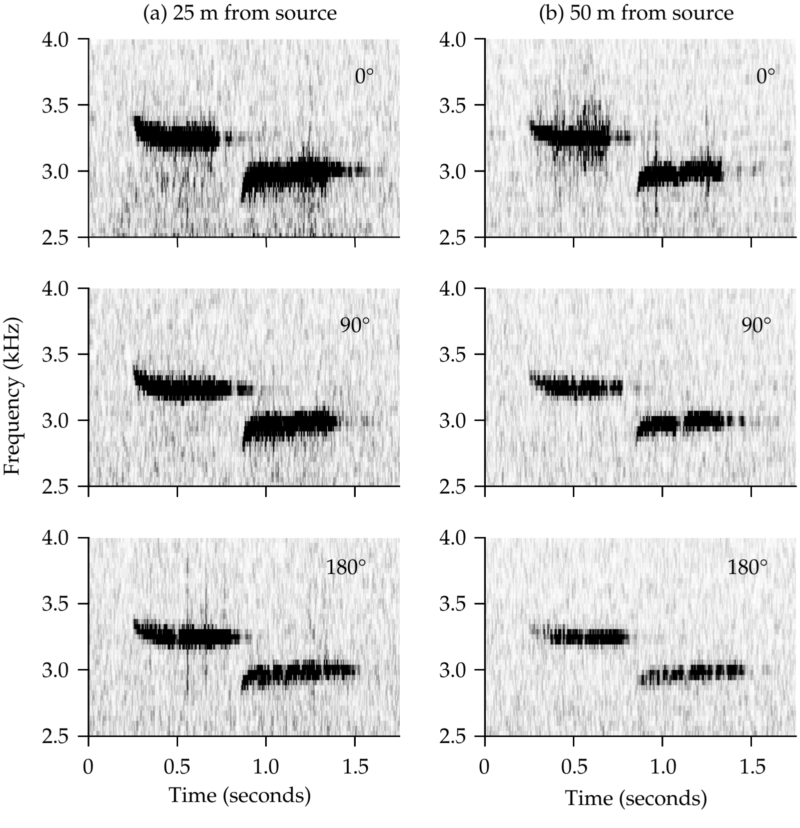

Figure 14.6 Sound spectrograms of black-capped chickadee songs recorded by a microphone mounted inside an abandoned nest cavity. Songs were broadcast through a loudspeaker positioned either 25 m from the nest cavity (a) or 50 m from the nest cavity (b). The nest was rotated so that the entrance to the nest cavity was oriented facing the loudspeaker (0°; top), at a right-angle to the loudspeaker (90°; middle), or away from the loudspeaker (180°, bottom). The nest cavity demonstrated acoustically directional properties, such that a female chickadee roosting inside the cavity will be better able to hear a male in front of her nest than a male singing behind her nest. Reprinted with permission from *Journal of Avian Biology*.

population of breeding great tits at Strødam Biological Station near Hillerød, Denmark. For all seven recordings, the dawn chorus of both the pair male plus at least one neighboring male were audible (K. A. Otter, T. M. Peake, A. M. R. Terry, and P. K. McGregor, unpublished data). The recordings further showed that songs from males singing more than 75 m away from the roosting female were clearly audible. Similarly, in black-capped chickadees, recordings made with microphones placed inside nest cavities could clearly detect males singing more than 50 m away (Mennill and Ratcliffe 2004b). Although cavity nesting may impede the transmission of some signals, these findings of the acoustics of Parid nest cavities demonstrate that cavity nesting does not impair female assessment of distant male dawn chorus performances.

Black-capped chickadee nest cavities have acoustically directional properties. Recordings made with microphones placed inside a chickadee nest demonstrate that a female is better able to hear males singing in front of her nest cavity than males singing behind her nest cavity (Fig. 14.6; Mennill and Ratcliffe 2004b). Analyses of the orientation of 132 chickadee nests in eastern Ontario demonstrated that chickadee nests have random compass orientation and are not specifically directed at the territories of high-ranking neighbors (e.g. Fig. 14.5). However, the nest cavities of females who nested in the soft wood substrate of birch, *Betula papyrifera*, and aspen, *Populus tremuloides*, were oriented towards their extrapair partner's territory (n = 17; Mennill and Ratcliffe 2004b). Consequently, the drive to monitor the singing behavior of neighbors may influence not only nest cavity location (Ramsay *et al*. 1999, Mennill *et al*. 2004) but also nest entrance orientation (Mennill and Ratcliffe 2004b). These intriguing results demonstrate how communication network thinking may provide new insights into the breeding biology of songbirds.

14.5 Singing behavior in other North American Parids

The male songs of North American Parids vary substantially between each species. The other North American *Poecile* chickadees demonstrate two major themes of variation, both of which are distinct from the pitch-shifting behavior of black-capped chickadees. Mountain chickadees *P. gambeli*, Carolina chickadees *P. carolinensis*, and Mexican chickadees, *P. sclateri*, appear to have repertoires of discrete song types. The songs of mountain chickadees are superficially similar to black-capped chickadees, but each male has a repertoire of four to seven song types, each consisting of two to four whistled notes (Wiebe and Lein 1999). Mountain chickadees engage in countersinging interactions, during which males use songs with lower frequency terminal notes in the most aggressive contests (Hill and Lein 1989). The songs of Carolina chickadees vary substantially from black-capped chickadee songs, although males of both species can learn the other species' song (Kroodsma *et al*. 1995). Studies of "pure" Carolina chickadees show that their songs usually possess four whistled notes (Hailman 1989), although the number can vary from one to 12 (Ward 1966), and individuals have at least two distinct song variants (Lohr *et al*. 1991), which may be important during countersinging interactions (D. J. Mennill, personal observation). The songs of Mexican chickadees are poorly understood. Two types of songs have been described for Mexican chickadees (Ficken 1990), at least one of which appears to occur as complex song types, but countersinging behavior has not been described. Thus, most North American chickadees possess song repertoires akin to those of European congeners, such as the marsh tit and willow tit. Similarly, the songs of male North American titmice (genus *Baeolophus*) also exhibit repertoires. Tufted titmice sing with a repertoires of up to 14 song types (Gaddis 1983) and during countersinging interactions males type-match their opponents (Duguay and Ritchison 1998). Oak titmice *B. inornatus* have repertoires of up to 11 song types (Dixon 1969) and certain song types are associated with countersinging interactions between males (Gaddis 1983). From a communication network perspective, North American Parids with song repertoires are expected to behave in a way similar to Eurasian Parids with song repertoires. So far, however, black-capped chickadees appear unique in the use of frequency shifting to achieve functions associated with multiple song types in other Parids.

The remaining two North American *Poecile* chickadees, chestnut-backed chickadees and boreal chickadees, are (along with their Eurasian congener the Siberian tit) anomalous songbirds: none exhibit a long-range, male song. Male boreal chickadees produce a varied "warbling song" in aggressive situations with other males (McLaren 1976) and chestnut-backed chickadees give modified gargle calls in aggressive situations (Dahlsten *et al*. 2002), but neither of these vocalizations travel sufficient distances to be used in long-range advertising. Hailman *et al*. (1994) studied the dawn behavior of Siberian tits, and found that these birds center their activity around the nest, as do chorusing black-capped chickadees, but use *chick-a-dee* and *gargle* calls in place of song. Like black-capped chickadees, male Siberian tits cease their vocalizations when the female emerges from the nest cavity, but the lack of a long-range signal coupled with the highly dispersed spacing of this species would seemingly preclude the ability of a communication network to form around dawn calling activity. Similar patterns of dawn activity using *chick-a-dee* calls have been noted in the boreal chickadee (C. T. Naugler, personal communication), but these are yet to be formally studied. These species therefore represent an interesting opportunity to test the importance of communication networks for songbirds. If other female Parids use male chorus performance for assessing male quality, do females in brown-headed chickadee species suffer a loss of network-based assessment? Alternately, do females use different mechanisms of assessing the relative quality of their mates, such as the extreme levels of copulation solicitation by females seen in crested titmice (Lens *et al*. 1997)?

14.6 Summary and future studies

The two-note *fee-bee* song of black capped chickadees ranks among the simplest learned songs of oscine songbirds. Male chickadees vary the timing and pitch of this vocalization during both extended dawn chorus performances and interactive countersinging exchanges with rivals. Since the publication of Susan Smith's book on the behavioral ecology of black-capped chickadees in 1991, our knowledge of chickadee singing behavior has expanded dramatically and the complex processes of communication between breeding males and females have become a model system in animal communication. Our research with black-capped chickadees, taken together with research on communication networks in other Parids, demonstrates that male singing behavior is a network-based process that can convey information about male quality to rival males and choosy females simultaneously.

Many aspects of chickadee communication require further research. Within the context of the dawn chorus, the interplay between broadcast communication and directed communication is poorly understood. Within the context of diurnal countersinging interactions, overlapping is relatively well understood, although future studies should evaluate how often birds overlap during natural contests and whether partial overlap is functionally equivalent to complete overlap. Communication through pitch variation, in contrast, is poorly understood. During non-matched countersinging, is singing at a lower frequency a more or less aggressive communication strategy? Is pitch shifting a signal *per se*? The continuity between the dawn chorus and diurnal singing merits further investigation. Poesel *et al*.'s (2004) study of blue tits demonstrated that dawn chorus performance predicted male performance during male–male countersinging contests. Other singing contexts in chickadees also merit more careful study. During the late winter and early spring it is not uncommon to hear a lone male belt out a song bout that is unanswered by other males. Are these solo bouts unchallenged contest proclamations, or do these song bouts serve a separate function? These and other questions will allow us to better understand the dyadic and network-based dynamics of communication and the complex ways in which chickadees use their simple song.

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