

Black-capped chickadee dawn choruses are interactive communication networks

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Summary

The dawn chorus of songbirds provides an ideal opportunity to study communication networks because multiple singers are within signalling range of each other, permitting eavesdropping by both males and females. Using an Acoustic Location System, we examined the dawn chorus singing behaviour of male black-capped chickadees (*Poecile atricapillus*) in 15 neighbourhoods to determine whether singing behaviour is consistent with the communication network model. We calculated levels of frequency matching for 19 focal males and all of their neighbours. The observed level of frequency matching was greater than expected by chance. All males were involved in multi-way matching at dawn and often matched two or three neighbours simultaneously. The identity of individuals involved in three-way matches was related to both previous winter-flock membership and the relative dominance rank of the interacting males. We show that male black-capped chickadee dawn choruses are interactive communication networks where males are involved in high levels of matching with neighbours, and they match multiple individuals both simultaneously and sequentially. Additionally, the existence of multi-way matching and the identities of individuals involved suggest that individual males may eavesdrop at dawn. This is the first study to quantify network communication during the dawn chorus in multiple neighbourhoods.

Keywords: dawn chorus, communication network, vocal interactions, black-capped chickadee, eavesdropping.

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Introduction

Animal communication mediates many important social behaviours, though attention has only recently shifted to the broader social environment in which communication occurs (McGregor & Dabelsteen, 1996; McGregor, 2005). Traditionally, communication has been studied using dyadic models in which there is a single signaller and a single receiver (e.g., Bradbury & Vehrencamp, 1998). However, the signals of many territorial animals transmit over relatively long distances placing many signallers and receivers within range of each other. Communication networks are possible whenever groups of animals are within signalling and receiving range of multiple conspecific individuals, providing a new context for examining the ecology and evolution of animal communication behaviour (McGregor & Dabelsteen, 1996).

The first to realize the importance of using a network perspective were those that studied insect and anuran choruses where individuals adjust the timing of their signals relative to several other individuals (reviewed by Otte, 1974; Grafe, 2005). Network communication in birds was challenging to study until recently, due to the logistical constraints of recording multiple individuals on large territories (Kramer & Lemon, 1983). Eavesdropping, a network specific behaviour by which an individual uses the relative information available in singing interactions, has been demonstrated using multi-speaker and interactive playback experiments in both male songbirds (Naguib & Todt, 1997; Peake et al., 2001, 2005; Mennill & Ratcliffe, 2004a) and female songbirds (Otter et al., 1999a; Mennill et al., 2002; Leboucher & Pallot, 2004). These pioneering studies of eavesdropping as network-based phenomenon have focused on one or two territories at a time, and studies that simultaneously monitor multiple animals in a communication network are rare.

Vocal interactions in birds are often characterized by two opponents that exchange songs using pattern-specific behaviours (Todt & Naguib, 2000; Searcy & Beecher, 2009). One commonly studied pattern-specific behaviour is song matching, where a male sings the same song type as an opponent (e.g., Stoddard et al., 1992). Matching is associated with increased aggression and has been studied in a number of species during daytime singing (e.g., Krebs et al., 1981; Vehrencamp, 2001). Matching may also occur during the intense period of singing at dawn (Burt & Vehrencamp, 2005; Foote et al., 2008a) but the importance of interactive communication at this time of day has received relatively little attention.

In many species of songbirds, territorial males participate in a distinct dawn chorus beginning 30–60 min before sunrise and characterized by high singing rates and singing diversity (Staicer et al., 1996). During the dawn chorus, male singing behaviour likely mediates social relationships among males through interactive communication (social dynamics hypothesis; reviewed in Staicer et al., 1996). Because all males are singing simultaneously during the dawn chorus and because the dawn chorus probably includes an intra-sexual signalling function, it is an ideal time of day to examine potential network communication behaviours. Additionally, a better understanding of the network properties of the dawn chorus will contribute to identifying both male and female related functions of dawn chorusing.

Six lines of evidence from studies of various species of songbirds suggest that males singing at dawn are communicating with other males. First, males use specific song types or vary the pattern of song type delivery in ways that are typical of intra-sexual counter-singing interactions later in the day (e.g., Morse, 1989; Trillo & Vehrencamp, 2005). Second, males sing near territorial boundaries or approach specific neighbours while chorusing (e.g., Willis, 1960; Burt & Vehrencamp, 2005; Liu & Kroodsma, 2007), and may cease chorusing altogether when their neighbours are experimentally removed (Liu, 2004). Third, dawn singing may continue well into the breeding season when females are no longer fertile (e.g., Staicer, 1989; Amrhein et al., 2004). Fourth, males increase dawn chorusing activity following simulated territorial intrusions (Erne & Amrhein, 2009). Fifth, males may prospect for vacant territories primarily at dawn (Amrhein et al., 2004). Lastly, in two recent studies, males have been shown to interact vocally with neighbours during the dawn chorus by matching the type of song a neighbour sings in banded wrens (*Thryothorus pleurostictus*; Burt & Vehrencamp, 2005) and the frequency of a neighbour's song in black-capped chickadees (*Poecile atricapillus*; Foote et al., 2008a).

While dawn chorus singing may be especially important for intra-sexual interaction among males, absolute features of male dawn choruses honestly indicate male quality (Otter et al., 1997; Poesel et al., 2001; Christie et al., 2004a; Murphy et al., 2008) or condition (Barnett & Briskie, 2007; Grava et al., 2009), and correlate with paternity (Suter et al., 2009). Females can also likely obtain information about the relative quality of mates and neighbours from the dawn chorus by eavesdropping on their interactions (Peake, 2005). Given both the amount of song in the chorus, and the links between chorus

behaviour and individual quality, the avian dawn chorus provides a rich opportunity for information exchange in a network context.

Black-capped chickadees are an ideal species in which to study dawn chorus network communication because their singing behaviour has been studied from an individual, a dyadic, and a network perspective. Black-capped chickadees sing a well-defined dawn chorus, repeating songs at a single frequency on average 30 times before shifting to another frequency (Christie et al., 2004a). Chickadees use song frequency matching when interacting with other males both during daytime singing interactions (analogous to song-type matching in other species; Otter et al., 2002; Mennill & Ratcliffe, 2004b; Fitzsimmons et al., 2008a) and during the dawn chorus (Foote et al., 2008a). Frequency matching occurs in 37% of daytime singing interactions (7.7% of songs are matches; Fitzsimmons et al., 2008a) but occurs at higher rates during the dawn chorus (100% of neighbours frequency match at dawn, 23.6% of songs are matches; Foote et al., 2008a). A variety of experimental findings suggest that matching is an aggressive signal for chickadees, and that the dawn chorus and diurnal countersinging are distinct contexts with very different levels of matching (reviewed in Mennill & Otter, 2007). Males respond more strongly to matching playback than to non-matching playback (Mennill & Ratcliffe, 2004b), and may match playback songs (Otter et al., 2002).

Black-capped chickadees form winter flocks of 2–12 individuals structured by stable linear dominance hierarchies (Ratcliffe et al., 2007). In spring, flocks break up and males defend all-purpose breeding territories (Smith, 1991). High-ranking males have greater reproductive success and sire extra-pair offspring with nearby females (reviewed in Ratcliffe et al., 2007). Both flock identity and dominance rank influence the way males sing and interact with others. High-ranking male chickadees begin the dawn chorus earlier, have higher song rates (Otter et al., 1997), and have more consistent song structure (Christie et al., 2004a; Hoeschele et al., 2010) than low-ranking males. High-ranking males respond more strongly than low-ranking males to playback (Mennill & Ratcliffe, 2004a,b). Compared to males from the same winter flock, males that spent the winter in different flocks are involved in more dyadic interactions during the dawn chorus (Foote et al., 2008a). Additionally, males of similar rank match each other during the dawn chorus more often than do males of disparate ranks (Foote et al., 2008a).

Table 1. Summary of behaviours expected to occur in communication networks and in the absence of communication networks (i.e., where communication occurs only in the context of a signaller/receiver dyad).

	Communication within a network of individuals	Communication solely within a signaller/receiver dyad
Multi-way matching between multiple neighbours (simultaneous matching)	Yes	No
Dyadic matching between neighbours (sequential matching)	Yes	Yes
Eavesdropping on dyadic interactions between others	Yes	No

In this study we used an Acoustic Location System to study communication behaviour of male black-capped chickadees from a network perspective. Our Acoustic Location System consisted of an array of 16 simultaneously recording microphones that allowed us to record 6–10 singing males at a time across adjacent breeding territories. We examined the song frequency patterns within chickadee dawn chorus performances to determine whether social cues influence frequency matching within the dawn chorus. We examined the singing behaviour of each male with respect to all of his neighbours, focusing on song frequency matching, to determine if communication during the dawn chorus extends beyond the dyad. We thereby tested whether breeding neighbourhoods constitute communication networks. A summary of behaviours predicted to occur in dawn chorus communication networks is provided in Table 1. We describe how male chickadees communicate with multiple neighbours at dawn, and how this behaviour relates to both flock membership (whether individuals were in the same flock during the preceding winter) and social dominance (the relative rank of males). By recording birds in a natural context, this work stands apart from previous studies of eavesdropping which have typically involved experimental manipulation.

Methods

Study area, population, and recording methods

We studied a banded population of black-capped chickadees at Queen's University Biology Station (44°34'N, 76°19'W), near Kingston, ON, Canada

from January to July, 2005–2007. Adult birds were captured in winter using treadle-traps baited with sunflower seeds and banded with a unique combination of three coloured bands and a numbered aluminum Canadian Wildlife Service band ($N = 149$ birds in 2005, $N = 236$ in 2006, $N = 61$ in 2007). We determined the dominance hierarchies in winter flocks by observing pair-wise aggressive interactions at feeding stations ($N = 2811$ interactions in 2005, $N = 8423$ in 2006, $N = 1100$ in 2007). Behaviours of dominant birds included supplanting or chasing subordinates; behaviours of subordinate birds included waiting to feed and displaying submissive postures (see Ratcliffe et al., 2007 for details). We classified males into three rank categories: (1) high-ranking males were the top two males in flocks of four or five males and the top male in flocks of two or three males; (2) mid-ranking males were the middle male in flocks of three or five males; and (3) low-ranking males were the bottom two males in flocks of four or five males and bottom male in flocks of two and three males (Mennill et al., 2004).

We collected focal recordings of males using directional microphones (Sennheiser MKH-70) and solid-state digital recorders (Marantz PMD660 or PMD670) between April 25 and May 24, 2005 and 2006. Chickadee songs differ between males in temporal, frequency, and relative amplitude characteristics, making male songs individually distinctive (Christie et al., 2004b; Wilson & Mennill, 2010). We used these focal recording to confirm male identities in the Acoustic Location System recordings when identification on the basis of relative territorial position or field observations was in doubt.

From April 27 to May 15, 2005 to 2007, we recorded neighbourhoods encompassing 6–10 territorial male black-capped chickadees (average 7.2 ± 0.3 territories, $N = 15$) using a 16-microphone Acoustic Location System. A neighbourhood consisted of a cluster of breeding territories with males who were familiar with each other either from sharing membership in the same winter flock or by interacting with individuals from nearby flocks. We recorded 15 different neighbourhoods of up to 160 000 m², five in each of 2005, 2006 and 2007. The Acoustic Location System consisted of 16 omni-directional microphones housed in polyvinyl chloride (PVC) tube rain covers and mounted on 3 m long wooden poles that were elevated and attached to small trees using bungee cords. Microphones were connected to a central computer using 2200 m of cable. Input from all microphones was digitized using a multi-channel data acquisition card (National Instruments DAQ-6260) and recorded as 16-channel AIFF files using Chickadee v1.9

recording software (J. Burt, Seattle, WA, USA). This setup was an extension of the 8-microphone system described by (Mennill et al., 2006). We recorded from 0425 to 1130 EST on two to four consecutive days in each neighbourhood. During all recording sessions, three or four observers noted the activities of individual birds within the recording area, including details of male singing locations and identities.

Sound analysis

From the 46 mornings recorded with the Acoustic Location System, we chose one from each of the 15 neighbourhoods for analysis. We analyzed the first morning of recording for 10 neighbourhoods; for the remaining five, we analyzed the second morning because weather or technical difficulties with the Acoustic Location System on the first morning reduced the quality of those recordings. There was no significant difference among years in any of the variables measured: dawn chorus length (2005: 47.4 ± 2.7 min; 2006: 46.6 ± 2.1 min; 2007: 44.1 ± 3.6 min; ANOVA: $F_{2,12} = 0.35$, $p = 0.71$), average song rate of males (2005: 11.4 ± 0.4 songs/min; 2006: 10.7 ± 0.6 songs/min; 2007: 10.6 ± 0.6 songs/min; $F_{2,97} = 0.62$, $p = 0.54$), or the amount of matching between neighbours (2005: $21.6 \pm 2.1\%$ of exchanges; 2006: $25.7 \pm 2.2\%$ of exchanges; 2007: $24.0 \pm 2.5\%$ of exchanges; $F_{2,97} = 0.84$, $p = 0.44$). For the 15 dawn chorus recordings analyzed, we annotated all songs sung by all males recorded within the 15 neighbourhoods ($N = 92$ males, $N = 41\,071$ songs) from the start of recording until approximately 0630 EST. Annotations were made using the time and frequency cursors in Syrinx-PC sound analysis software (J. Burt). We used a combination of field notes, fine structural details of male songs, and location information to confirm male identities. As described by Mennill et al. (2006) we used software written in MATLAB (Mathworks, Natick, MA, USA) to localize male songs on the basis of time delays in recordings of songs at multiple microphones. We determined the location of each male for every 20th song. If males moved distances of more than 10 m, we determined the location of the singer before and after each movement as well. We considered every 20th song appropriate given that chickadees do not move extensively during the dawn chorus and tend to remain in one area for many songs in a row (Otter & Ratcliffe, 1993). For songs that were not localized, we assigned the location of the previous localization to those songs for determining mean distance of males.

We defined the start of the dawn chorus as the time when the second male in the recorded area started singing. We defined the end of the dawn chorus as the time at which only one male remained singing for at least three minutes. Morning counter-singing and solo-singing typically began as the dawn chorus diminished (J. Foote, pers. obs.), so we did not count males rejoining the dawn chorus after they had been silent for three minutes, providing it was 40 min or longer from the start of the dawn chorus, which is the average dawn chorus length of individual males in this population (Otter et al., 1997).

For frequency analyses, conducted in Syrinx-PC, we used a 1024 FFT Blackman window to measure the frequency of the end of the *fee* note (fee_{end}) and the start of the *bee* note (bee_{start} ; one quarter of the way into the *bee* note; Christie et al., 2004a) which was repeatable to ± 2 Hz. We considered songs to be matched if the *fee* or *bee* notes of two males were ≤ 50 Hz different. However, if the average frequency difference of two males' fee_{end} for a bout of song was > 100 Hz, we considered the songs not to match, even if $bee_{start} \leq 50$ Hz (see Foote et al., 2008a for a more detailed explanation). We used a 50 Hz cut-off based on previous interactive playback studies where subjects responded agonistically, as though matched, when the playback song frequency was within 50 Hz of the subject's song (Mennill et al., 2002; Otter et al., 2002; Mennill & Ratcliffe, 2004b). We considered a male to be involved in a matching interaction with a neighbour when its song matched the frequency of that neighbour according to these criteria.

We conducted comparisons of 100 pairs of neighbouring birds within the 15 recorded neighbourhoods. For all pairs we calculated the difference in frequency of subsequent songs in their dawn choruses. Neighbours were defined as individuals who shared a territory boundary. We determined whether songs of neighbours were frequency matched for all potential exchanges that occurred while males were separated by a distance of 150 m or less (likely maximum sound transmission distance at dawn; Christie et al., 2004b; J. Foote, pers. obs.). We had accurate location data from the Acoustic Location System for 86 of 100 male pairs. For the additional 14 male pairs, where positions for one male were missing because they sang from the periphery of the Acoustic Location System setup, we determined if males were within 150 m using the positions for one male and calculating the distance from that male's localized position to the mapped position of the second male determined from our field notes and territory maps from that morning.

From our sample we selected all males who were near the center of the array recordings and, therefore, had all of their neighbours recorded that morning, without repeating males who had been present in more than one year near an array centre. For these 19 males, from their dyadic matching comparisons calculated above, we looked at each of their songs sung during the dawn chorus and determined whether it was matched by one or more neighbours. We defined communication network size as the number of contiguous neighbours who sang within 150 m for at least a portion of the dawn chorus. As an additional measurement, we considered the average number of males singing within 10 s of each song males sang during the dawn chorus (a measure of the average number of neighbours singing for each song of the focal male). For each song, we identified the number of neighbours that matched that song frequency as described above and from this calculated the proportion of dawn chorus songs that were matched by one neighbour (dyadic matches), two neighbours (three-way matches), and three neighbours (four-way matches).

For the 19 focal males we calculated the difference in frequency between each male's subsequent songs to identify changes in frequency, referred to as frequency shifts. When the difference in frequency from the preceding song was ≥ 80 Hz, we considered the male to have changed frequency (Horn et al., 1992). When a male switched back and forth between two frequencies repeatedly on a short time scale we counted it as a single frequency shift (it is typical for some chickadees to switch back and forth between two frequencies several times before singing exclusively at the second frequency; J. Foote, pers. obs.). We compared the average frequency of each bout between shifts (referred to as song frequency bouts) to all other bouts to determine how many different frequencies males used during the dawn chorus. As for matching between individuals, if the average frequency of the fee_{end} or bee_{start} of two bouts was ≤ 50 Hz then these bouts were considered to be at the same frequency. We calculated the average number of songs males sang before shifting to a new frequency (referred to as shifting rate).

Statistical analysis

We used JMP 7 (SAS, Cary, NC, USA) for all statistical analysis at $\alpha = 0.05$. All tests were two-tailed and results are presented as mean $\pm$ standard error. We did not conduct Bonferroni corrections because our small sample size

increases the likelihood of making a Type II error (Nakagawa, 2004). Effect sizes (ES) for *t*-tests were calculated using Cohen's *d* (Cohen, 1988); the parametric, independent *t*-test statistics were used to calculate ES for non-parametric and paired analyses (Dunlop et al., 1996). For χ^2 tests ES were calculated using Cramer's phi (Φ).

It is difficult to establish what levels of interactive behaviours should occur by chance during the complex counter-singing interactions of birds (Todt & Naguib, 2000; Searcy & Beecher, 2009; Naguib & Mennill, 2010). To control for relationships that may have occurred by chance in our analysis of frequency matching in chickadee dawn choruses, we constructed 'virtual dawn choruses' for an equal number of males ($N = 19$) to provide a comparison dataset involving songs where frequency matching would occur by chance alone. We term the virtual dawn chorus singers as 'chance' males, to distinguish them from our observed 'focal' males. This was an extension of an approach we used in a previous study (Foote et al., 2008a), where we calculated dyadic matching comparisons among 10 dawn choruses recorded in 2005 and 2006; each of the 59 males in those dawn choruses was randomly paired with one male from each of the nine other dawn choruses (i.e., recordings collected on different days). To construct a comparison set of virtual dawn choruses of chance males, we randomly selected 19 of these 59 males. We randomly assigned the number of neighbours to each of the 19 chance males such that it matched the distribution of focal males (our focal male sample had 5 males with 2 neighbours, 9 males with 3 neighbours, 4 males with 4 neighbours, and one male with 5 neighbours). We then randomly selected the dawn chorus numbers to assign neighbours from the 9 dyadic comparisons that each chance male had previously been subject to. Because the chance males in the virtual dataset do not move in and out of each others' hearing range as actual focal males do, the average number of neighbours singing was significantly higher in the virtual dataset (*t*-test: $t_{36} = 2.13$, $p = 0.040$; 1.99 ± 0.14 neighbours singing). This value (average number of neighbours singing) is important in later analyses (see below). Therefore, to permit comparisons between chance and focal males, we adjusted this value by removing the last neighbour added in all chance males whose average number of neighbours singing was higher than the maximum for actual focal males. Once these males had been adjusted the 75th percentile was higher for the chance sample so we followed the same procedure for males in that percentile until the distributions of the two samples matched and there was

Table 2. Mean $\pm$ standard error values for the number of neighbours (Ns) singing and the number of songs with 0–4 neighbours singing for focal male black-capped chickadees' dawn chorus performances (males recorded using a 16-channel Acoustic Location System) compared to chance males (males recorded on different days and combined to provide a comparison dataset).

There were no significant differences between chance and focal males.

	Chance males	Focal males	<i>t</i> -test statistic
No. Ns singing	1.65 $\pm$ 0.089 (<i>N</i> = 19)	1.64 $\pm$ 0.090 (<i>N</i> = 19)	(<i>t</i> ₃₆ = 0.088, <i>p</i> = 0.93)
No. songs 0 Ns	49.90 $\pm$ 13.62 (<i>N</i> = 19)	41.42 $\pm$ 6.53 (<i>N</i> = 19)	(<i>t</i> ₃₆ = 0.56, <i>p</i> = 0.58)
No. songs 1 N	142.21 $\pm$ 20.67 (<i>N</i> = 19)	164.26 $\pm$ 22.61 (<i>N</i> = 19)	(<i>t</i> ₃₆ = 0.72, <i>p</i> = 0.48)
No. songs 2 Ns	209.84 $\pm$ 19.85 (<i>N</i> = 19)	184.26 $\pm$ 22.62 (<i>N</i> = 19)	(<i>t</i> ₃₆ = 0.85, <i>p</i> = 0.40)
No. songs 3 Ns	116.00 $\pm$ 13.64 (<i>N</i> = 9)	125.82 $\pm$ 22.72 (<i>N</i> = 11)	(<i>t</i> ₁₈ = 0.35, <i>p</i> = 0.73)
No. songs 4 Ns	28.50 $\pm$ 11.5 (<i>N</i> = 2)	8.50 $\pm$ 1.5 (<i>N</i> = 2)	(<i>t</i> ₂ = 1.72, <i>p</i> = 0.23)

no longer a significant difference between the two groups (Table 2). For 8 of the chance males we arbitrarily removed one neighbour in order to make the distributions of the chance dataset and actual dawn chorus data match (2.58 ± 0.16 neighbours per male). Following these adjustments, the virtual dataset (involving 'chance' males) and the actual dawn chorus dataset (involving 'focal' males) did not differ in the average number of neighbours singing or in the number of songs when 0, 1, 2, 3 or 4 neighbours were singing (Table 2).

Results

Communication network size

The 19 black-capped chickadees in our analysis had an average of 3.10 ± 0.19 neighbours that sang within 150 m for at least a portion of the dawn chorus (range 2–5, *N* = 19 males). On average, 1.64 ± 0.09 of those neighbours sang within 10 s of any given song in the dawn chorus (range 0.91–2.41, *N* = 19 males). For the remaining songs, these neighbours were either silent or were more than 150 m away.

High-ranking males did not have significantly more neighbours than low-ranking males (high-ranking: 3.18 ± 0.27 ; low-ranking: 2.86 ± 0.33 ; t -test: $t_{16} = 0.76$, $p = 0.46$, ES = 0.38). Additionally, high-ranking males did not have a significantly different number of neighbours singing within 10 seconds of any song time than low-ranking males (t -test: $t_{16} = 0.70$, $p = 0.50$, ES = 0.35; high-ranking: 1.70 ± 0.12 ; low-ranking: 1.57 ± 0.15). Consequently, high-ranking and low-ranking male black-capped chickadees shared similar sized communication networks.

Neighbourhood singing frequency

To determine whether social cues early in the morning might influence the singing behaviour of animals in a neighbourhood later in the dawn chorus, we examined whether the starting frequency of the first male to start singing, or the frequency of the first match of the morning, influenced the dominant frequency of the dawn chorus (most commonly sung frequency by all males recorded) using regression. To calculate the dominant frequency of the neighbourhood we plotted the distribution of all songs sung during the dawn chorus in 50 Hz bins (measurement for fee_{end}). The dominant frequency of that dawn chorus was identified as the bin with the highest frequency of occurrence and assigned the middle value for the bin (e.g., the 3900–3950 Hz peak would be represented by 3925 Hz). We found no relationship between the first song sung by the earliest starting male and the dominant frequency of the neighbourhood during the dawn chorus ($r^2 = 0.0044$, $F_{1,13} = 0.057$, $p = 0.82$). Similarly, we found no relationship between the frequency of the first matching interaction in a neighbourhood and the dominant frequency of the neighbourhood during the dawn chorus ($r^2 = 0.0037$, $F_{1,13} = 0.049$, $p = 0.83$).

Frequency matching

When we compared actual dawn chorus interactions with a chance dataset involving virtual dawn chorus performances (pairs of chorus performances randomly combined from separate recording days), we found that focal male black-capped chickadees matched neighbours significantly more often than expected by chance (t -test: $t_{36} = 4.21$, $p = 0.00020$, ES = 1.44; Figure 1). Focal males matched at least one neighbour for a greater proportion of their songs during the dawn chorus than did chance males. The proportion of

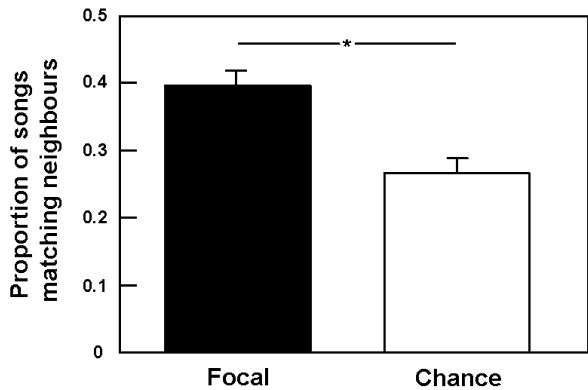


Figure 1. Comparison of the amount of time spent matching at least one neighbour between 19 focal males and 19 chance males during the dawn chorus of black-capped chickadees. Focal males were recorded with a 16-channel Acoustic Location System; chance males were individuals recorded on different days and combined to provide a comparison dataset. Focal males matched neighbours significantly more often than expected by chance. Error bars show standard error; asterisk indicates significant differences at $p < 0.05$.

Table 3. Pearson correlation coefficients (r) among matching (proportion of songs matching at least one neighbour), number of neighbours (No. Ns), average number of neighbours singing (No. Ns singing), switching (average number of songs before switching), and number of frequencies used for focal males (above the diagonal line; $N = 19$) and chance males from virtual dawn choruses (below the diagonal line; $N = 19$).

	Matching	No. Ns	No. Ns singing	Switching	No. frequencies
Matching		0.17	0.56*	0.46*	0.50*
No. Ns	0.36		0.59**	-0.04	0.005
No. Ns singing	0.55*	0.59**		0.38	-0.31
Switching	-0.10	0.05	0.31		0.46*
No. frequencies	0.07	0.19	-0.05	-0.48	

* $p < 0.05$; ** $p < 0.01$.

songs that matched at least one neighbour increased with the average number of neighbours singing in both focal males and chance males (Table 3), but not simply with the number of neighbours. Both high- and low-ranking male chickadees were involved in matching for a similar proportion of their dawn choruses (high-ranking: 0.40 ± 0.03 ; low-ranking: 0.37 ± 0.04 ; t -test: $t_{16} = 0.64$, $p = 0.53$, $ES = 0.32$). Males who matched at a high rate sang more

songs before switching to a new frequency than males who matched at a lower rate (Table 3). We did not find this relationship in the virtual chorus dataset (Table 3). Additionally, males who sang at fewer frequencies matched at a higher rate than males who sang many frequencies, a relationship that did not occur by chance (Table 3).

Frequency shifting

Neither the number of frequencies males used at dawn nor shifting rate (i.e., the rate at which males changed to a song frequency that was different by >80 Hz) were related to either the number of neighbours or the average number of neighbours singing (Table 3). However, males who sang at a large number of frequencies also shifted at a high rate. This relationship was not found in our comparison dataset (Table 3). Neither shifting rate nor the number of frequencies used was related to social rank (*t*-test: shifting: $t_{16} = 0.030$, $p = 0.98$, $ES = 0.015$; number of frequencies: $t_{16} = 0.40$, $p = 0.70$, $ES = 0.2$); high-ranking males shifted frequency every 24.8 ± 3.1 songs and sang at 4.7 ± 0.4 frequencies during the dawn chorus whereas low-ranking males shifted frequency every 24.9 ± 3.9 songs and sang at 5.0 ± 0.5 frequencies. Males were equally likely to shift to match another male as they were to shift to a non-matching frequency (paired *t*-test: $t_{18} = 0.50$, $p = 0.62$, $ES = 0.20$). Frequency shifts resulted in matching $38.4 \pm 2.5\%$ of the time and non-matching $40.5 \pm 2.6\%$ of the time. In the remaining $21.0 \pm 2.7\%$ of the time, no neighbours were singing during a shift or when shifting from a match, only the matched neighbour was singing. Following a match with one neighbour, males were no more likely to shift to match another neighbour than to a non-matching frequency (when another neighbour was singing; paired *t*-test: $t_{18} = 1.37$, $p = 0.19$, $ES = 0.42$). In total, $23.8 \pm 2.9\%$ of frequency shifts were from a match to another frequency. Of these frequency shifts, $13.6 \pm 2.0\%$ of the time males shifted from a match with one neighbour to another match (either with the same male or another neighbour) and $10.2 \pm 1.9\%$ of the time males shifted from a match to a non-matching frequency. When neighbours were singing, $66.0 \pm 0.03\%$ of song frequency bouts during the dawn chorus were matches to at least one neighbour, or were matched by at least one neighbour. The remaining 34% of song frequency bouts were not matches to any neighbour.

Multi-way matches

For each male in both focal and chance datasets we counted the number of songs matched by neighbours that were dyadic (two-way) and the number that were multi-way (three-way or four-way). Dyadic (t -test: $t_{36} = 3.64$, $p = 0.0009$, $ES = 1.21$), three-way (Mann–Whitney test: $U_{36} = 464$, $p = 0.0066$, $ES = 0.88$), and four-way matching (Mann–Whitney test: $U_{36} = 52$, $p = 0.013$, $ES = 0.95$) occurred significantly more often than expected by chance (Figure 2). Four-way matches occurred rarely, however the opportunity for four-way matches was also rare; only 10 males had 3 or more neighbours singing within 150 m at one time during our recordings; six of these 10 males were involved in four-way matching. None of the 8 males in the chance dataset with more than 3 neighbours singing had instances of 4-way matching. All of the 19 focal males were involved in at least one multi-way match. Matches involving three males were the most common type of multi-way singing interaction. No matches involving more than four males were observed. Of the five males who had four or more neighbours, only two had four neighbours singing at one time, one for only 7 of his songs and the other

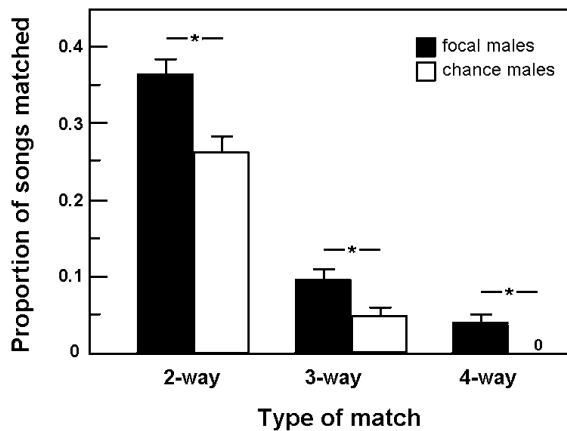


Figure 2. Proportion of dawn chorus songs that were two-way (No. songs that were two-way matches/No. songs where at least one neighbour was singing), three-way (No. songs that were three-way matches/No. songs where at least two neighbours were singing), and four-way matches (No. songs that were four-way matches/No. songs where at least three neighbours were singing) for chance and focal male black-capped chickadees. Focal males were involved in significantly more two-way, three-way, and four-way matches than expected by chance.

Error bars show standard error; asterisk indicates significant differences at $p < 0.05$.

for 10. As such, the opportunity for matches involving more than four males was very small.

When at least two neighbours were singing, dyadic matching among focal males occurred significantly more often than multi-way matching ($44.86 \pm 2.84\%$ of songs were dyadic matches while $10.70 \pm 1.79\%$ of songs were multi-way matches; Mann–Whitney test: $U_{36} = 193$, $p < 0.0001$, $ES = 3.66$). Given that dyadic matching occurs most often, and dyadic matching was greater in the focal male sample, the finding that three-way matching occurs more often than by chance may not be surprising. However, the ratio of dyadic-to-multi-way matching when two or more neighbours were singing was 10.7:1 in our focal male sample versus 18.4:1 in our chance matching sample, suggesting that multi-way matching was even more common in our focal males.

Eight of the 19 focal males matched two neighbours by switching back and forth between two different frequencies. Two of the males did this on two separate occasions. Three of 10 occurrences were the result of the male matching one neighbour at a given frequency and switching to match the other neighbour, before switching back. In the remaining 7 instances, the male switched back and forth between the two neighbours more than once (Figure 3). We observed instances of switching between two neighbours only twice in the chance dataset.

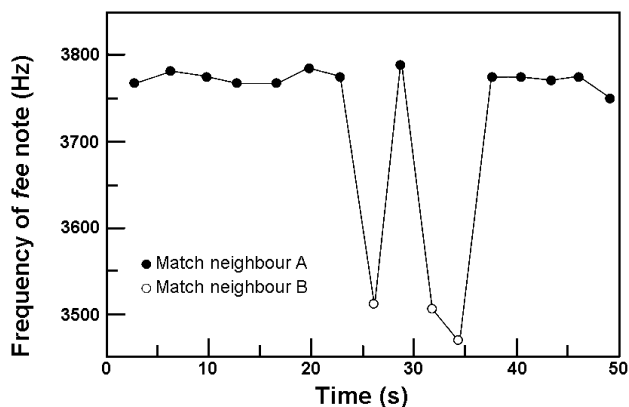


Figure 3. Example of a male black-capped chickadee shifting back and forth between frequency matches with two different neighbours. Each circle represents one of the focal male's songs during a 50 s segment of the dawn chorus. Black circles represent songs where the male is frequency matched with neighbour A; white circles represent songs where the male is frequency matched with neighbour B.

Three-way matches typically occurred in the sequence of: (1) two males matching dyadically, (2) a third male matching, and then (3) one of the three males switching to end the three-way match while the other two males continued to match dyadically. We examined who terminated three-way matches: the male who initiated the preceding dyadic match, the male who was matched in the dyadic match, or the third male to match. In 37.1% of three-way matches, the third male to match also ended the match; in 40.0% of three-way matches, the male who had been originally matched dyadically was the first to end the three-way match; and in 22.9% of three-way matches, the male who initiated the dyadic match was the first to end the three-way match; the identity of the male to terminate the match did not differ statistically between the three alternatives ($\chi^2_2 = 3.54$, $p = 0.17$, $ES = 0.24$; $N = 26, 18$ and 16 , respectively).

For three-way matches, we determined whether the first two individuals to match had been in the same previous winter flock (referred to as 'flock-mates') or had been in different flocks during the previous winter (referred to as 'non-flockmates') and we compared the flock membership of the third male to match relative to the two original males. Interactions between two flockmates and one non-flockmate were the most common type of interaction. Three-way matches were significantly more likely to be the result of two non-flockmates matching and a flockmate of one male joining the match rather than the result of a non-flockmate joining an interaction between flockmates ($\chi^2_1 = 10.67$, $p = 0.0011$, $ES = 0.44$; Figure 4a). Similarly, all four-way matches began between non-flockmates. For three-way matches where two non-flockmates began the match and the third male to match was a flockmate of one of the original males, we investigated whether the third male was more likely to be a flockmate of the male who initiated the dyadic match or of the male who was matched. The third male to match was equally likely to be the flockmate of the male who was matched as the male who initiated the match ($\chi^2_1 = 0.10$, $p = 0.75$, $ES = 0.05$, $N = 19$ and 18). Additionally, we looked at whether the flockmate that was third to match was high- or low-ranking compared to the flockmate that was already involved in the interaction. When the third male to match was a flockmate, it tended to be a high-ranking flockmate rather than a low-ranking flockmate ($\chi^2_1 = 3.10$, $p = 0.078$, $ES = 0.28$; Figure 4b), although the relationship was not significant. When males of high-rank joined interactions of flockmates we examined whether their flockmate was matching a non-flockmate

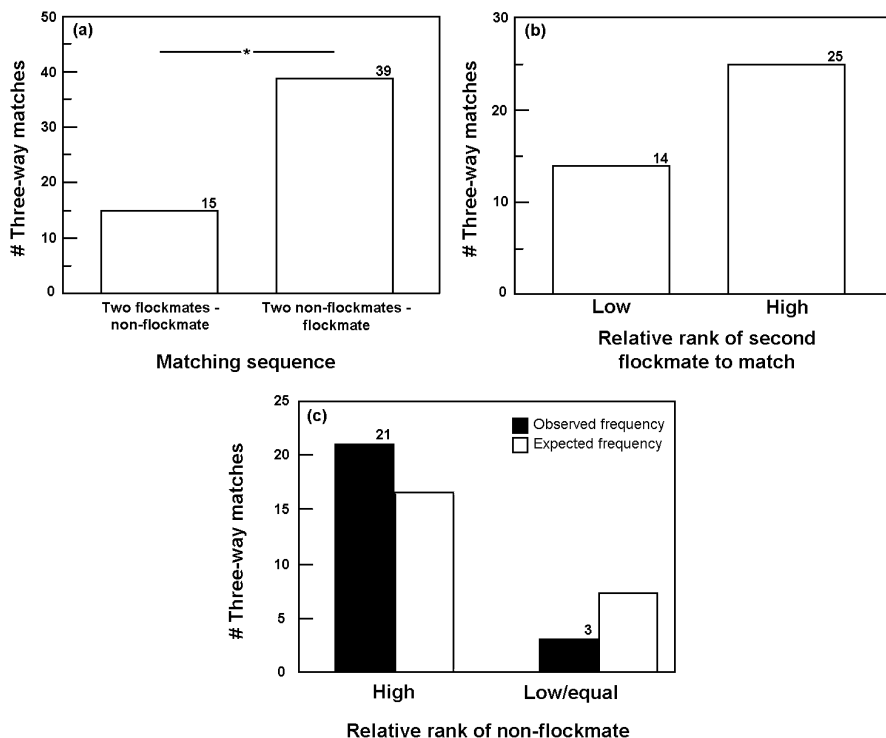


Figure 4. Comparison of the three-way matches that occurred during the dawn chorus of black-capped chickadees. (a) Three-way matches that were initiated in the sequence of two flockmates matching dyadically that were then matched by a non-flockmate or two non-flockmates matching dyadically matched by a flockmate of one male. (b) Three-way matches between two non-flockmates matched by a low-ranking or high-ranking flockmate. (c) Three way matches where the third male to match was a high-ranking flockmate and (1) the non-flockmate was of low- or equal-rank to the first male of the flock involved in the match, or (2) the non-flockmate was of high-rank or low/equal rank compared to the first male of the flock involved in the match; asterisk indicates significant differences at $p < 0.05$.

male of high or equal/low relative rank. The likelihood of a low-ranking male having a non-flockmate neighbour of high-rank in our sample was 69.2% and the likelihood of a male having a neighbour of low/equal-rank was 30.8%. Controlling for the likelihood of having high- or low-ranking neighbours, when high-ranking flockmates joined interactions of their low-ranking flockmates, the flockmate was more likely to be involved in a match with a male of high-rank than a male of equal or low-rank, though the relationship was not significant ($\chi^2_1 = 3.76$, $p = 0.052$, $ES = 0.39$; Figure 4c).

Discussion

During the dawn chorus of black-capped chickadees, males had an average of 3.1 neighbours with an average of 1.6 neighbours singing at any one time. Males spent an average of 40% of their dawn chorus matching other males, and they matched neighbours' song for at least one exchange during 66% of their song frequency bouts. The amount of time a male spent matching increased with the average number of neighbours singing. Dyadic matching was more common than multi-way matching; however, all males were involved in multi-way matches. Multi-way matching suggests that males may have eavesdropped on dyadic interactions of their neighbours; moreover, our data suggest that males may have preferentially joined dyadic interactions involving flockmates who were of low-rank and who were matching males of high-rank. Given that we have shown that chickadees interact with several neighbours simultaneously (multi-way matching) and that they may eavesdrop on interactions of others (in concordance with previous experimental work; Mennill & Ratcliffe, 2004b; Fitzsimmons et al., 2008a), and given that we did not find that matching only occurred sequentially (dyadic matching of each neighbour in turn), we conclude that chickadee dawn choruses can be understood as communication networks.

In developing 'virtual dawn choruses' made up of recordings of males collected on separate days and combined for comparison to actual dawn choruses, we found that some level of frequency matching occurs purely by chance. While we refer to any time when focal birds are frequency matching as an interaction, we are, thus, unable to discriminate between chance matching and true interactive communication. Nevertheless, the levels of matching were higher in the dawn choruses we recorded than the virtual choruses we developed for comparison. Additionally, the relationships between matching and flock membership/social dominance in our data suggest that a large part of the frequency matching at dawn was in fact the result of singing interactions between males.

Network behaviour and dominance rank

Both high- and low-ranking male chickadees had similar sized communication networks when both the total number of neighbours and the average number of neighbours singing were considered. Additionally, both high- and low-ranking males had similar frequency shifting rates, sang at a similar

number of frequencies, and matched at similar levels during the dawn chorus. Christie et al. (2004a), using single-channel recordings, also found that high- and low-ranking males shifted at similar rates and made pitch shifts of similar size. Despite disparities in reproductive success (Otter et al., 1998, 1999b; Mennill et al., 2004) and singing quality (Otter et al., 1997; Christie et al., 2004a; Hoeschele et al., 2010) between high- and low-ranking males, our analysis reveal that both high- and low-ranking males compete in similarly sized network settings during the dawn chorus and use their ability to match and shift frequency in similar ways. Logue & Forstmeier (2008) predicted that low quality singers should avoid matching because matching increases an eavesdropper's ability to compare the two males' singing performance. At present, our data do not support this prediction. Both high- and low-ranking chickadees were engaged in similar levels of matching, whether considered dyadically (Foote et al., 2008a) or in a network fashion (present study), despite the fact that low-ranking males are understood to have lower quality songs. Additional studies examining whether low-ranking birds avoid matching at the extremes of the frequency range, where the ratio between the *fee* and *bee* notes becomes unstable (Christie et al., 2004a) may better address this question. Our results support the hypothesis that the dawn chorus functions to mediate social relationships among males (Staicer et al., 1996), in that all territory holders may need to renegotiate their relationships with neighbours each morning, regardless of social rank.

Neighbourhood singing frequency

There was no relationship between either the first song sung in the dawn chorus or the first match of the morning and the peak frequency of the network. There was, however, variation in peak frequency between mornings, suggesting that the common frequency of the morning was not just a by-product of all males singing at a most common frequency (e.g., in the middle of the frequency range) but was determined each day by some undetected properties in the network. Possible undetected factors driving frequency could include: the first match between two males whose interactions are particularly intense, or the first song sung by a male who was involved in frequent and aggressive daytime interactions the day before. Alternatively, if matching and song overlapping follow a graded system of aggression, it may be the frequency of songs that are used in overlaps that dictates the frequency currency of the

network. At dawn, we found no evidence of a graded system, with matching songs no more likely to be overlapped than non-matching songs (Foote et al., 2008a). However, during daytime counter-singing interactions, matching and overlapping behaviour is consistent with a graded system of aggressive signals (Fitzsimmons et al., 2008a), where overlapping precedes matching during diurnal contests. Social characteristics determining peak frequency could also differ over time and between neighbourhoods.

Frequency matching

Males were involved in matching on average for 40% of their dawn chorus, significantly more often than expected by chance. For the remaining time, when males were singing at a non-matching frequency, they might not have been interacting with neighbours or they could have been interacting in ways that do not involve frequency matching. Males could use non-matching time to eavesdrop on the interactions of others or to listen to neighbours to determine whom to match next. While eavesdropping also likely occurs while matching, it would presumably be an easier perceptual task when the male is not involved in a matching interaction when attention must be divided between listening to the surrounding interactions while simultaneously attending specifically to the songs of one neighbour. The perceptual complexities of communication networks await further study.

Males matched their neighbours both sequentially by matching each neighbour in turn and simultaneously by matching two or more neighbours at one time, either at the same frequency or by alternating between two different frequencies. When matching, 38% of the time males switched to match another neighbour while 41% of the time they switched to a non-matching frequency (21% of the time either no neighbours were singing or the neighbour originally matched was the only male singing). The proportion of songs that match at least one neighbour increased with the average number of neighbours singing such that males with more neighbours singing had a more complex perceptual task during the dawn chorus. These findings support the hypothesis that the dawn chorus is an interactive communication network. High levels of matching at dawn implies that the delivery of songs is influenced by other birds and that males are interacting (Burt & Vehrencamp, 2005).

Dyadic matching was significantly more common than multi-way matching. Multi-way matching was, however, a commonly observed phenomenon

in black-capped chickadee communication networks. Multi-way matches have also been observed in banded wren dawn choruses (Burt & Vehrencamp, 2005). Banded wrens match neighbours sequentially to a higher degree than chickadees during the dawn chorus; however they have more flexibility to match sequentially, in that they switch song types more often than chickadees switch frequencies (Burt & Vehrencamp, 2005). Banded wrens more commonly match multiple neighbours by alternating between song types and matching each neighbour separately, rather than matching both neighbours with the same song type. Because chickadees share the same frequency range with all neighbours, all males should be able to match a given song frequency (Christie et al., 2004a). Additionally, males repeated songs at a given frequency 24 times (this study) on average before switching, which may explain why multi-way matching at the same frequency was relatively common in this species, compared to banded wrens where males share 82% of their repertoire with a given neighbour and switch rapidly between song types. Frequency matching in black-capped chickadees makes it relatively easy to have multi-way matches because the constraint of song type sharing by all three participants is lifted. We did observe chickadees switching back and forth between neighbours as described for banded wrens, but the behaviour was observed in only 42% of males, while multi-way matching at the same frequency was observed in all males. We demonstrate evidence of multi-way competitive interactions in black-capped chickadee communication networks, supporting the prediction that the dawn chorus is an interactive network, as was also found in banded wrens (Burt & Vehrencamp, 2005).

Frequency shifting

Males who shifted at a high rate and males who sang at many frequencies matched at a lower rate than males who shifted at a lower rate or sang at fewer frequencies. High song type switching rates (which may be analogous to frequency shifting in chickadees) during daytime singing are associated with higher levels of aggression (e.g., Kramer et al., 1985). Some males may switch at a high rate at dawn as an alternate form of interaction with neighbours. However, shifting may not be as useful as a directional signal during the dawn chorus as frequency matching because the high levels of singing at dawn may create ambiguity in the intended recipient (Burt & Vehrencamp,

2005). Alternatively, shifting at a high rate and/or singing at many frequencies may represent different signalling strategies, either to avoid matching or the singing style may make matching at a high level difficult. Although these males matched at a lower level, they were still involved in matching (lowest level of matching was 22% of songs). Interestingly, neither switching rate nor the number of frequencies sung was related to network size. Males did not alter their singing style based on the number of other males with whom they interact. Examining the behaviour of males that switch at a high rate over the course of the breeding season and across seasons could identify whether this style is used consistently or whether it varies with dawn chorus characteristics.

Multi-way matches

Three-way and four-way matches occurred significantly more often than expected by chance. Three-way matches were significantly more likely to be the result of two non-flockmates matching dyadically, joined by a flockmate of one of the males compared to two flockmates matching dyadically, joined by a non-flockmate. The third male to join was likely to be a flockmate of high-rank compared to the original participant, although this relationship was not significant. High-ranking flockmates tended to join interactions when their low-ranking flockmate was interacting with a male from another flock who was of high-rank. Females mated to low-ranking males are more likely to seek extra-pair copulations than females mated to high-ranking males, and extra-pair mates are typically high-ranking males (Otter et al., 1998; Mennill et al., 2004). High-ranking males may join into interactions of their low-ranking flockmates to display their continued current high level of quality to eavesdropping females. Female black-capped chickadees typically place their nests near territory boundaries (Ramsay et al., 1999; Mennill et al., 2004), and extra-pair copulations often occur during or just after the dawn chorus (Smith, 1988; Mennill et al., 2004). Additionally, males whose mates are non-fertile preferentially sing near territory boundaries of neighbours with fertile females and may be well placed to facilitate eavesdropping (Foote et al., 2008b). Males of similar quality are likely to be a greater threat to high-ranking males both in terms of territory and paternity and may be best kept at a distance.

In addition, male black-capped chickadees defend all-purpose breeding territories that fall within their former winter flock home range. High-ranking

flockmates may have an interest in joining together in territorial interactions against non-flockmates to defend any portion of their future winter home range from being usurped. If low-ranking males are less successful in interactions with males of high-rank, then high-ranking males may have an interest in joining matches to defend their winter flock home range. In winter, dominant males are responsible for the majority of flock home-range defence against males of other flocks (Smith, 1991), and may continue this role in part during the breeding season. Alliances in which individuals support each other in contests are common in primates (Harcourt, 1989), although most examples are of alliances between kin in interactions with other group members. It can be advantageous for territorial residents to form defensive coalitions to fight off potential usurpers (Getty, 1987). Established neighbouring rock pipits (*Anthus petrosus*) coordinate defence against intruders both at boundaries and within the territory boundary of one of the males (Elfström, 1997). Male long-tailed manakins (*Chiroxiphia linearis*) form alliances and co-ordinate displays to attract females (McDonald, 1989). While non-flockmates are established territory holders, in chickadees they clearly have a different relationship to their neighbours than do flockmates (Foote et al., 2008a). Experiments investigating how males respond to intruders, in the territories of flockmates and non-flockmates, could be used to further investigate the relationships of flockmates during the breeding season.

The existence of three-way matching suggests that male black-capped chickadees eavesdrop on interactions at dawn. Males may hear an aggressive interaction and match one or both of the opponents in that interaction. Additionally, males preferentially joined multi-way matches that involved flockmates. These results further support the hypothesis that the dawn chorus is an interactive communication network. Eavesdropping on competitive interactions among territory holders outside of experimental contexts has not been demonstrated. The relative information males may obtain from eavesdropping on interactions at dawn needs further study to confirm the behaviour; however, this behaviour will be challenging to document in natural populations with sufficient sample sizes to warrant statistical conclusions. Eavesdropping on simulated daytime interactions has been found in both male (Mennill & Ratcliffe, 2004a; Fitzsimmons et al., 2008b) and female (Mennill et al., 2002) chickadees. Alternatively, during three-way matches males may be matching only one male and ignoring the other.

Additionally, the observed trend that high-ranking males tended to join interactions in which their low-ranking flockmates were matching high-ranking non-flockmates demonstrates that males are likely aware of the relative rank of other individuals in their network. High-ranking males may be aware that their flockmates are involved in interactions with other high-ranking males by attending to cues that are available in the signalling interactions themselves; however, we have found no evidence that behaviour of high- and low-ranking males differ during dyadic interactions in the dawn chorus (Foote et al., 2008a). Males may also compare the relative quality of others using cues related to song quality; males of high- and low-rank vary in individual dawn chorus output (Otter et al., 1997) and fine structural details of songs (Christie et al., 2004a; Hoeschele et al., 2010). To determine whether males attend to these variables will require further experimentation. Alternatively, males may be using past experiences with both males to determine relative rank of flockmates and their neighbours. When pairs are establishing breeding territories in the spring, there are frequent interactions between neighbours that often extend beyond the dyad and involve additional flock members (J. Foote, pers. obs.), and males may use information obtained in these encounters to inform singing behaviour at a later time. Awareness of the relative relationships of other individuals in their network would suggest that male chickadees may be capable of transitive inference, an ability that has been documented in African grey parrots (*Psittacus erithacus*, Pepperberg, 2005), and pinyon jays (*Gymnorhinus cyanocephalus*, Bond et al., 2003). Because black-capped chickadees live in winter flocks with stable dominance hierarchies (Ratcliffe et al., 2007), they may show a level of social complexity that makes them amenable to transitive inference experiments. The trend of high-ranking males joining interactions of their low-ranked flockmates that were matching other high-ranking males could also be a function of high-ranking males having an increased likelihood of singing. High-ranking males begin singing earlier and sing longer dawn choruses than low-ranking males (Otter et al., 1997).

Interactive communication at dawn could provide opportunities for eavesdropping females to obtain up-to-date information on the relative quality of their mate and neighbouring males. Female chickadees eavesdrop on daytime interactions and may alter mate-choice decisions based on information in simulated interactions (Mennill et al., 2002). Whether females attend to variation in male singing quality at dawn needs further study. Male dawn

chorus characteristics correlate with mate choice (e.g., Suter et al., 2009) however, direct experimental evidence of mate choice based on dawn chorusing is lacking. Sound transmission experiments show that chickadee nest cavities have directional acoustic properties and that females could likely hear singing interactions 50 m or more from the nest cavity (Mennill & Ratcliffe, 2004c).

Summary

Using a 16-channel Acoustic Location System we studied the patterns of naturally occurring interactions of black-capped chickadees and found that males matched multiple neighbours at dawn both sequentially and simultaneously. Our results provide support for the social dynamics hypothesis that males sing at dawn to adjust their relationships with neighbours (Staicer et al., 1996), and that the dawn chorus is an interactive communication network (Burt & Vehrencamp, 2005). Additionally, we show that neighbours may eavesdrop on the interactions of other males in their communication network and preferentially join in interactions of their flockmates, particularly those of low-rank who are matching males of high-rank.

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