

Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis

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Males of many songbird species participate in a distinct chorus beginning before sunrise. Despite its ubiquity, the function of dawn chorusing remains poorly understood. We tested the social dynamics hypothesis, which states that males sing at dawn to mediate their social relationships with neighbors through interactive communication. Using a 16-microphone acoustic location system, we recorded 29 entire dawn choruses in 10 neighborhoods of 6–10 territorial male black-capped chickadees (*Poecile atricapillus*) of known dominance rank. We analyzed song frequency matching and overlapping between neighboring males in 10 choruses and compared the intensity of these behaviors with social factors. Chickadees matched the frequency of their neighbor's songs more often than expected by chance. The level of matching was higher between neighbors who belonged to different flocks during the previous winter than between neighbors who had been flockmates. Males of the same dominance rank matched each other more than males of disparate ranks. There was no relationship between matching and pairing status or distance between opponents. Overlapping was used less than expected by chance. No measures of song overlapping were related to measured social factors. Our results show that neighboring male chickadees interact vocally at dawn by frequency matching. This is the first study to show that the intensity of songbird vocal interactions at dawn varies with social factors, supporting the social dynamics hypothesis. *Key words:* black-capped chickadee, dawn chorus, frequency matching, social dynamics, vocal interactions. [*Behav Ecol* 19:1192–1199 (2008)]

In many breeding animals, individuals participate in a pronounced dawn chorus when all territorial individuals sing at a high rate in the early hours of the morning (Henwood and Fabrick 1979; Staicer et al. 1996; Sueur 2002). Despite its ubiquity, the functions of the dawn chorus are not well understood. The dawn chorus of songbirds is thought to serve one or more intrinsic or social functions and may also be explained by environmental constraints (Mace 1987) and/or conditional constraints (Barnett and Briskie 2007). Staicer et al. (1996) have pointed out that several of the hypotheses for the function of the dawn chorus are not mutually exclusive, whereas a good functional explanation for chorusing should explain the phenomena in a large number of species. They proposed the social dynamics hypothesis to explain chorusing behavior, arguing that male singing behavior during the dawn chorus mediates social relationships with territorial neighbors through interactive communication.

In birds, male song serves the dual function of mate attraction and territory defense (Catchpole and Slater 1995). Both song and singing interactions (Todt and Naguib 2000) may convey information about male quality (e.g., Otter et al. 1997), motivation (e.g., Vehrencamp et al. 2007), and condition (e.g., Saino et al. 1997) to both male and female receivers. Evidence that males sing at dawn for intrasexual communication comes not from observations of interactions between individuals but from observations of individual behaviors. Males use specific song types or vary the pattern of

song type delivery in ways that are typical of intrasexual countering interactions later in the day (Morse 1989; Nelson and Croner 1991; Spector 1992; Trillo and Vehrencamp 2005; Liu and Kroodsma 2007). Males may perform the dawn chorus near their mate (Otter et al. 1997; Gorissen and Eens 2004) in many species, leading some authors to suggest that the chorus is directed at females, yet most male chorus songs travel across territory boundaries (e.g., Mennill and Otter 2007) such that their songs could impart information to neighboring males as well. Males of some species sing near territorial boundaries or approach specific neighbors while chorusing (Willis 1960; Staicer 1989; Burt and Vehrencamp 2005; Trillo and Vehrencamp 2005; Liu and Kroodsma 2007). In Eastern kingbirds (*Tyrannus tyrannus*), chorus length and song rate increase with the number of territorial neighbors (Sexton et al. 2007). Dawn singing may also continue well into the breeding season when females are no longer fertile, which suggests an intrasexual function (Staicer 1989; Amrhein et al. 2004a; Kunc et al. 2005; Liu and Kroodsma 2007), at least in single-brooded species. In winter wrens (*Troglodytes troglodytes*), males defend nonbreeding season territories and continue to sing at dawn. Simulated intrusions in autumn result in increased dawn chorus activity on subsequent days, suggesting that dawn singing is important for territory defense (Amrhein and Erne 2006). As nightingales (*Luscinia megarhynchos*) sing throughout the night, territorial vacancies may become apparent to nonresident males overnight (Thomas 2002), who then prospect for territories mainly at dawn (Amrhein et al. 2004b). These findings suggest that the breeding season dawn chorus is also an important time for territorial defense. Male chipping sparrows (*Spizella passerina*) do not perform a dawn chorus when their neighbors have been experimentally removed, suggesting that interactions between males are important at dawn (Liu 2004).

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Taken together, there is accumulating evidence that the dawn chorus may serve an intrasexual function. To test the social dynamics hypothesis, however, naturally occurring interactions between territory holders must be studied. Two commonly studied ways in which birds may interact during countersinging interactions involve varying the type of signal used (pattern-specific responses) and varying the timing of their signal (time-specific responses, Todt and Naguib 2000). One commonly studied pattern-specific behavior is song matching, where a male sings the same song type as an opponent (e.g., Stoddard et al. 1992). Males may vary the timing of their songs such that their songs overlap an opponent's song or they may alternate songs with an opponent (e.g., Hultsch and Todt 1982). Both matching and overlapping are associated with increased aggression and have been well studied in a number of species during daytime singing (Krebs et al. 1981; Vehrencamp 2001; Otter et al. 2002; Vehrencamp et al. 2007).

The study of singing interactions at dawn has been largely overlooked due to the technical challenge posed by the large number of singers, the amount of background noise, and the low light levels that make it difficult to track individuals. Until recently, recording multiple individuals in the field was not feasible. To date, the only study of dawn interactions is from a single morning's recording of neotropical banded wrens (*Thryothorus pleurostictus*, Burt and Vehrencamp 2005). Acoustic location systems (ALSs) are arrays of simultaneously recording microphones that can be used to record multiple individuals. An ALS records information on timing and content of vocalizations as well as location of singers. Vocalizations are recorded by 3 or more microphones that can then be used to triangulate male positions based on differential arrival times of sounds (Mennill et al. 2006). The advent of this technology presents a new opportunity to study the dawn chorus in neighborhoods of territorial individuals. In this investigation, we use an ALS to examine the dawn chorus of black-capped chickadees (*Poecile atricapillus*) to determine if males interact at this time of day and how these interactions may relate to social dynamics.

Chickadees are an ideal species with which to test the social dynamics hypothesis because both time- and pattern-specific singing interactions have been well studied, and the social relationships among birds in winter flocks can be ascertained prior to the breeding season. Black-capped chickadees are small (10 g) resident songbirds that form winter flocks of 2–12 individuals with stable linear dominance hierarchies (Ratcliffe et al. 2007). Once flocks break up in spring, pairs defend all-purpose breeding territories within their former flock home range against former flockmates and males from other winter flocks (Mennill and Otter 2007). Black-capped chickadees sing a simple 2-note *fee-bee* song that they shift up and down a continuous frequency range of 860 Hz (Horn et al. 1992). During the breeding season, male chickadees sing a pronounced dawn chorus beginning before sunrise and lasting 40–50 min in duration. Honest information about male quality is signaled by chorus start time, chorus length, and song rate (Otter et al. 1997). Chickadees sing with eventual variety, repeating a song at a given frequency on average 41 times before switching to a different frequency during the dawn chorus (Horn et al. 1992). Unlike species with repertoires that match by singing the same song type, chickadees match relative to the frequency of an opponent's song. Chickadees use both matching and overlapping behaviors in response to playback (Otter et al. 2002) and in naturally occurring daytime interactions (Shackleton and Ratcliffe 1994; Fitzsimmons et al. 2008).

In this study, we asked whether male chickadees use frequency matching and overlapping to interact during the dawn chorus. To determine if interaction intensity is related to social dynamics of male territorial neighbors, we compared

the amount of matching and overlapping during dawn chorus performance with social factors we predicted might be important in chickadee neighborhoods. First, we examined the relationship between the amount of matching and overlapping and winter flock membership. Studies of neighbor–stranger discrimination suggest that males should behave more aggressively toward less familiar individuals (Stoddard et al. 1990). If mediation of social relationships is a function of the dawn chorus, we predicted increased interaction between birds that were not flock mates during the previous winter (and who are therefore less familiar with each other), compared with former flockmates. Second, we determined whether the amount of matching and overlapping related to the relative dominance ranks of the interacting males. Given that contest duration tends to be longer between more evenly matched opponents (Enquist et al. 1990), we predicted that males of similar rank would match and overlap more often than males of different ranks. Third, we investigated how pairing status related to levels of matching and overlapping between neighbors. We predicted that paired males should match and overlap other paired males at a higher level because unpaired individuals (typically of lower quality) may pose a reduced territorial threat and are less likely to compete successfully for extrapair copulations (Otter et al. 1998). Last, we predicted that males singing close together would match and overlap each other more often than those further apart, if matching at dawn is a signal of aggressive intention to escalate a contest (Vehrencamp 2001). Additionally, we tested whether high levels of matching by neighbors were the result of increased bout duration, more matching events, or both.

METHODS

Study area, population, and recording methods

We studied a banded population of black-capped chickadees at Queen's University Biology Station, near Kingston, Ontario, Canada (44°34'N, 76°19'W) from January to July, 2005 and 2006. Adult birds were captured in winter using treadle traps baited with sunflower seeds and banded with a unique combination of 3-colored bands and a numbered aluminum Canadian Wildlife Service band ($N = 149$ in 2005, $N = 236$ birds in 2006). We determined the dominance hierarchy in winter flocks by observing pairwise interactions at feeding stations ($N = 2811$ interactions in 2005, $N = 8423$ interactions in 2006). Behaviors of dominant birds included supplanting or chasing subordinates, whereas behaviors of subordinate birds included waiting to feed and displaying submissive postures (Ratcliffe et al. 2007). We classified males into 3 rank categories: 1) high-ranking males were the top 2 males in flocks of 4 or 5 males and top male in flocks of 2 or 3 males; 2) mid-ranking males were the middle male in flocks of 3 or 5 males; and 3) low-ranking males were the bottom 2 males in flocks of 4 or 5 males and bottom male in flocks of 2 and 3 males (Mennill et al. 2004).

We collected focal recordings of all 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. 2004a). We used these focal recording to confirm male identities in the ALS recordings when identification was in doubt.

From April 27 to May 15, 2005 and 2006, we recorded neighborhoods encompassing 6–10 black-capped chickadee territories using a 16-microphone ALS. We recorded in 10 different areas of approximately 160 000 m², 5 in each of 2005 and 2006. The ALS consisted of 16 omni-directional microphones

housed in polyvinyl chloride 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 multichannel data acquisition card (National Instruments DAQ-6260) and recorded as 16-channel AIFF files using Chickadee v1.9 recording software (John Burt, Seattle, WA). This setup was an extension of the 8-microphone system described by Mennill et al. (2006). We recorded from 0425 to 1130 eastern standard time (EST) on 2 or 3 consecutive days in each ALS configuration. During recording sessions, 2 or 3 observers transcribed the activities of individual birds within the recording area, including details of male singing locations and identities.

Sound recording analysis

From the 29 dawn choruses recorded (13 in 2005 and 16 in 2006), we analyzed one dawn chorus from each of the 10 neighborhoods. There was no significant difference between 2005 and 2006 in any of chorus length (t -test: $t_8 = 0.22$, $P = 0.83$; 2005: 47.4 ± 2.7 min; 2006: 46.6 ± 2.1 min), average song rate of males ($t_{70} = 0.94$, $P = 0.35$; 2005: 11.4 ± 0.4 songs/min; 2006: 10.7 ± 0.6 songs/min), the amount of matching between neighbors ($t_{66} = 1.39$, $P = 0.17$; 2005: $21.6 \pm 2.1\%$ of exchanges; 2006: $25.7 \pm 2.2\%$ of exchanges), or the amount of overlapping between neighbors ($t_{66} = 0.98$, $P = 0.33$; 2005: $18.3 \pm 0.5\%$ of exchanges; 2006: $17.2 \pm 0.7\%$ of exchanges). We analyzed the first morning of all recordings in 2006 because subsequent mornings were part of a separate playback study. In 2005, we analyzed the first morning of recording unless recording was stopped early due to technical difficulties or high levels of wind, which makes localization difficult. For each chorus, we annotated all songs sung by all males recorded ($N = 72$ individual choruses, $N = 32\ 341$ songs) from the start of recording until approximately 0630 EST using the time and frequency cursors in Syrinx PC (J. Burt, Seattle, WA). We used a combination of field notes, fine structural details of male songs, and location information to confirm male identities. Using software written in MATLAB (Mathworks Inc., Natick, MA) to localize male songs, as described by Mennill et al. (2006), we determined the location of each male for every 20th song. When males moved long distances (>20 m), we located the song before and after each movement as well. We considered every 20th song appropriate given that chickadees do not move extensively during the chorus and tend to remain in one area for long periods (Otter and Ratcliffe 1993). We calculated the minimum, average, and maximum distance between neighboring males during the chorus. 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 3 min. Morning countersinging interactions typically begin as the dawn chorus diminishes (Foote J, personal observations), so we did not count males rejoining the dawn chorus after they had been silent for 3 min, 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; Foote J, Fitzsimmons LP, Mennill DJ, Ratcliffe LM, unpublished data). In 3 of 10 dawn choruses, males started singing again after long pauses after 40 min had passed since the beginning of the chorus. Neighborhood dawn choruses ranged in length from 39 to 56 min.

For each pair of neighboring males ($N = 68$ pairs), we calculated the difference in frequency of subsequent songs

in their choruses. We determined whether songs were frequency matched for all potential exchanges that occurred while males were separated by a distance of 150 m or less. We had distance data for 57 of 68 male pairs; for the additional 11 male pairs, where positions for one male were missing because they sang from the edge of the microphone array, 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.

For frequency analyzes, we used a 1024-Fast Fourier Transform (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. 2004b) that was repeatable to ± 2 Hz. We considered songs to be matched if the *fee* or *bee* notes of 2 males were ≤ 50 Hz different. However, if the average frequency difference of 2 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. We included this additional criterion because one male's song had an atypical interval ratio (ratio between fee_{end} and bee_{start} notes, Weisman et al. 1990). The interval ratio is highly conserved across individuals and populations; however, some males may sing songs with atypical interval ratios at extremes of their frequency range (Christie et al. 2004b). We chose to include fee_{end} in this study because the *fee* note is sometimes sung alone (3.2% of songs at dawn were just *fees*) and were used by 96% of males in the population. Using both fee_{end} and bee_{start} to determine the amount of matching was comparable to using just bee_{start} (Spearman: $r^2 = 0.55$, $N = 68$, $P < 0.0001$).

We considered a song to overlap if it overlapped $\geq 33\%$ of an opponent's song. Songs overlapped by $<33\%$ are unlikely to be perceived as an overlap by both signaler and receiver at the average distance between males during the dawn chorus. This criterion minimized the chance of including "false" or ambiguous overlaps (Naguib 2005). To determine overlapping, we calculated the length of each male's song and the time difference between the end of the first male's song and the start of the second male's song. If this number was negative, it overlapped at least a portion of the song. To determine if songs overlapped by at least 33%, we determined if the overlap time was ≥ 0.33 times the first male's song length. To evaluate whether our 33% rule for determining overlapping affected our results, we also calculated $\geq 50\%$ overlapping, $\geq 25\%$ overlapping, and all overlapping (any portion of opponent's song overlapped, $>0\%$ overlapping). For both matching and overlapping, for each pair of males, we calculated the proportion of subsequent songs that were either matches or overlaps (number of matches or overlaps/total number of subsequent songs). We refer to this proportion as the amount or level of matching/overlapping.

Statistical analysis

To determine a null distribution of chance matching/overlapping at dawn, we randomly paired each male in each ALS recording to another male in each of the other 9 ALS recordings from different days ($N = 259$ comparisons). We then determined both matching and overlapping for these pairs of males over the duration of the chorus in the same manner as we did for real pairs of neighbors (above). Data for matching were square root transformed to meet the assumptions of normality for parametric statistics. We compared matching and overlapping with chance expectation by taking a random subset of values from our chance comparisons that equaled our sample size for real neighbors ($N = 68$). We compared observed matching/overlapping with chance levels using t -tests.

We compared matching and overlapping of males who were in the same flock with those in different flocks as well as instances where both males were paired to those where only one male was paired using *t*-tests. We assigned a rank disparity score to each neighbor pair, where a rank disparity of 0 represented males of the same rank, rank disparity of 1 represented males of 1 rank difference (high- and mid-ranking males, and mid- and low-ranking males), and rank disparity of 2 represented males of 2 rank differences (high- and low-ranking males). To compare matching and overlapping among rank disparities, we used analysis of variance (ANOVA). We did not have sufficient winter flock membership and rank data for one or both males in 3 of 68 neighbor pairs for our flock analysis and for 9 of 68 neighbor pairs for rank analysis. For pairing analysis, 2 instances where both males were unpaired were not included due to small sample size for this category. To compare amount of overlapping and matching to distance, we used Pearson correlation to determine the relationship between amount of matching and the mean, minimum, and maximum distance between males during the chorus. We also compared the minimum distances between unpaired males and their paired neighbors with the distance between 2 paired neighbors.

Because chickadees typically sing at one frequency for many songs in a row before changing to a different frequency (Horn et al. 1992), matching between countersinging males tended to occur in bouts where both males sang at the same frequency. To determine whether the amount of matching was related to bout duration, we calculated the length of each matching bout by subtracting the time of the first match from the end of the song that was the last match. To determine whether the amount of matching was related to the number of occurrences of matching during the chorus, we used the residuals of number of matching bouts versus number of subsequent song comparisons to control for combined chorus duration. We used Pearson correlation to determine the relationship between the amount of matching and the maximum and median duration of matching bouts and residuals of number of matches. We then compared duration of matches between flockmates and non-flockmates using a *t*-test and among-rank disparities using ANOVA. We used JMP 7.0 for all statistical analysis. All analyses were 2 tailed with $P = 0.05$. All data are reported as mean \pm standard error.

RESULTS

Males used frequency matching at dawn significantly more often than expected by chance (*t*-test: $t_{134} = 3.66$, $P = 0.0002$). Males matched each other $23.6 \pm 1.5\%$ of the time during the chorus whereas matching by chance would occur only $17.3 \pm 0.6\%$ of the time. Overlapping and matching were not significantly correlated (Pearson: $r^2 = 0.002$, $N = 68$, $P = 0.70$) and overlapping of matched and nonmatched songs occurred with similar frequency (paired *t*-test: $t_{67} = 1.17$, $P = 0.25$), so overlapping was, therefore, analyzed separately from matching. Overlapping ($17.8 \pm 0.5\%$ of exchanges) was used slightly but significantly less frequently than expected by chance ($19.6 \pm 0.4\%$ of exchanges) during the dawn chorus (*t*-test: $t_{134} = 3.13$, $P = 0.002$). Overlapping was also used less frequently than expected by chance if the criterion for an overlap was changed to greater than 50% overlapping (*t*-test: $t_{134} = 2.66$, $P = 0.008$), greater than 25% overlapping (*t*-test: $t_{134} = 3.32$, $P = 0.001$), or greater than 0% overlapping (*t*-test: $t_{134} = 2.52$, $P = 0.013$). For subsequent overlapping analyses, we used only the 33% overlapping level.

The proportion of exchanges that were matches during the chorus was significantly greater between males who had been in different winter flocks compared with males who had been

members of the same winter flock (Figure 1a; *t*-test: $t_{63} = 2.27$, $P = 0.027$). However, the amount of overlapping was not related to flock membership (Figure 1b; *t*-test: $t_{63} = 0.18$, $P = 0.86$).

The proportion of songs matched varied with disparity in rivals' winter dominance ranks as predicted (Figure 2a; ANOVA: $F_{2,56} = 2.72$, $P = 0.07$), although not significantly over the 3 categories. There was a 9% difference in the amount of matching between males in the same rank category (rank disparity of 0) and pairs of males of high and low rank (rank disparity of 2); males of the same rank matched significantly more than males of high and low rank (*t*-test: $t_{34} = 2.45$, $P = 0.02$). Rank category 0 combines neighbors who are of high-high, mid-mid, and low-low rank. All categories of males of equal rank matched songs at high levels (high-high choruses: $30.5 \pm 4.4\%$, mid-mid choruses: $24.4 \pm 8.8\%$, low-low choruses: $28.7 \pm 6.2\%$; ANOVA: $F_{2,11} = 0.12$, $P = 0.89$). The amount of overlapping was not related to rank disparity (Figure 2b; ANOVA: $F_{2,56} = 1.16$, $P = 0.32$).

Neither the amount of matching (*t*-test: $t_{64} = 0.86$, $P = 0.40$) nor the amount of overlapping (*t*-test: $t_{64} = 0.45$, $P = 0.65$) between neighbors was related to pairing status. Paired males

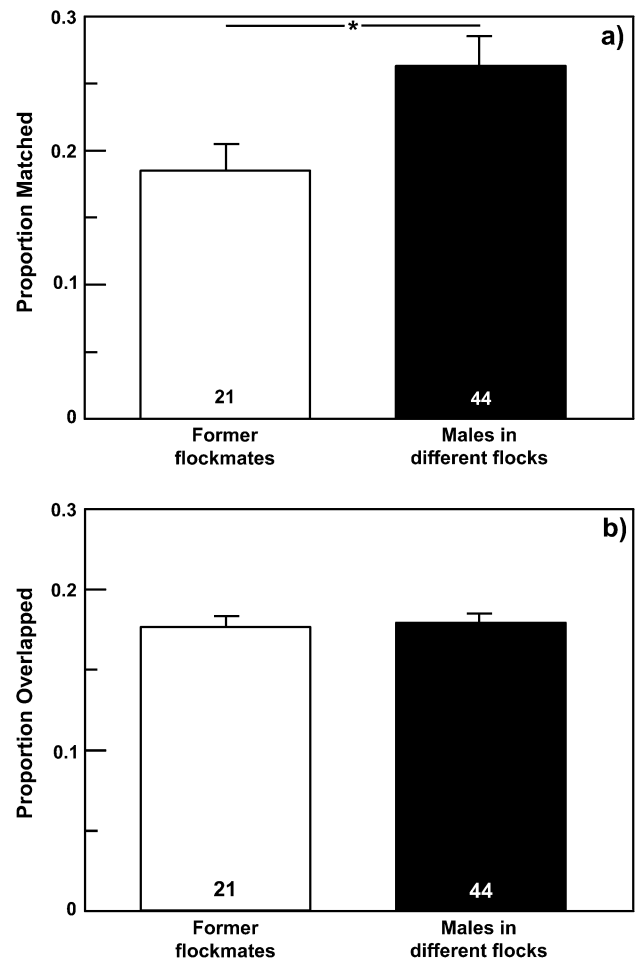


Figure 1
The average proportion of opponent's songs that were (a) frequency matched and (b) overlapped during dawn chorus countersinging exchanges between former flockmates and between males who had been in different winter flocks. Males from different winter flocks matched each other significantly more often than did former flockmates. Asterisk shows significant difference between groups at $P < 0.05$. Error bars show standard errors.

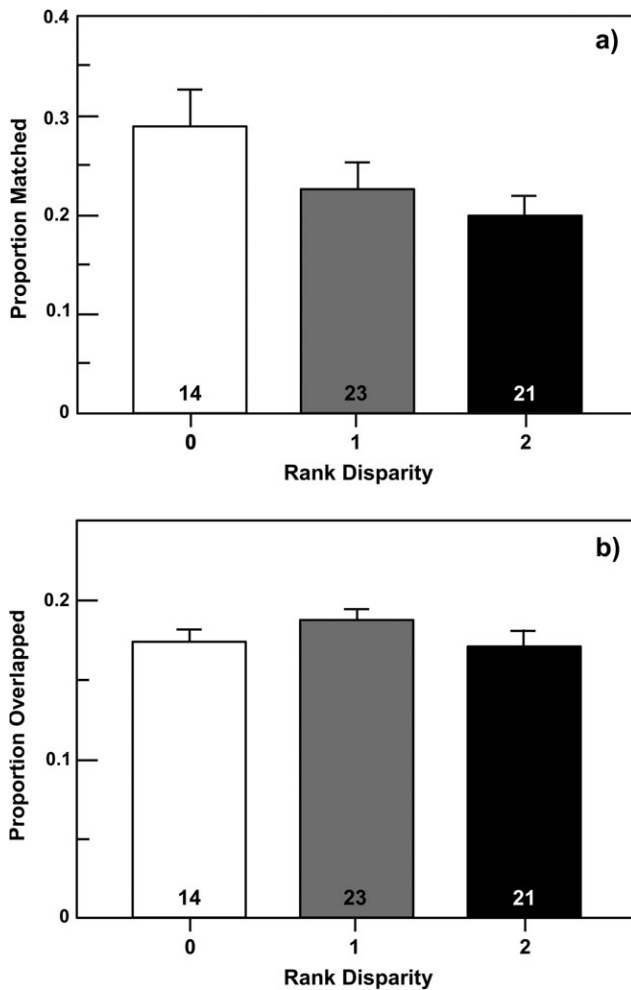


Figure 2
The average proportion of opponent's songs that were (a) frequency matched and (b) overlapped between males of different rank disparities (0 = opponents of same rank category, 1 = opponents of 1 rank category difference, 2 = opponents of 2 rank differences). Error bars show standard errors.

matched each other $24.3 \pm 1.9\%$ and overlapped each other $17.8 \pm 0.6\%$ of the time. When one male was unpaired, neighbors matched each other $21.3 \pm 2.4\%$ of the time and overlapped $17.3 \pm 0.9\%$ of the time.

There was no relationship between amount of matching (Pearson: mean: $r^2 < 0.0001$, $N = 57$, $P = 0.94$; minimum: $r^2 = 0.04$, $N = 57$, $P = 0.11$; maximum: $r^2 = 0.03$, $N = 57$, $P = 0.23$) or the amount of overlapping (Pearson: mean: $r^2 = 0.03$, $N = 57$, $P = 0.23$; minimum: $r^2 < 0.0001$, $N = 57$, $P = 0.96$; maximum: $r^2 = 0.01$, $N = 57$, $P = 0.43$) and any measure of distance between opponents. Mean distance between males was 109.3 ± 5.3 m (range 25.0–214.5 m), minimum distance between males was 58.7 ± 4.6 m (range 2.8–133.6 m), and maximum distance between males was 164.5 ± 7.9 m (range 63.2–338.2 m). Unpaired males tended to have lower minimum distances from opponents than did paired males, although this difference was not significant (t -test: $t_{54} = 1.70$, $P = 0.09$). Unpaired males sang as close as 47.5 ± 7.5 m to their paired neighbors whereas neighbors who were both paired sang at minimum distances of 64.4 ± 5.9 m.

Both median and maximum duration of matching bouts of neighbors were significantly positively correlated with the total amount of matching (Pearson: median duration: $r^2 = 0.27$,

Table 1

Average of median and maximum duration (\pm SE) of matching bouts of neighboring males of the same and different winter flocks and of different rank disparities

	Median duration (s)	Maximum duration (s)
Flockmates	18.2 ± 4.0	71.6 ± 6.8
Non-flockmates	39.0 ± 8.5	98.6 ± 11.4
Rank disparity 0	35.8 ± 12.2	125.5 ± 21.3
Rank disparity 1	43.3 ± 13.8	99.4 ± 14.8
Rank disparity 2	18.0 ± 3.3	65.6 ± 8.1

$n = 68$, $P < 0.0001$; maximum duration: $r^2 = 0.37$, $n = 68$, $P < 0.0001$) whereas the number of matching events controlled for number of exchanges was not (Pearson: $r^2 = 0.04$, $n = 68$, $P = 0.09$). Non-flockmates had significantly longer matching bouts on average than flockmates, although their maximum bout lengths did not differ (Table 1; median: t -test: $t_{63} = 2.0$, $P = 0.049$; maximum: unequal variances t -test: $t_{56.94} = 0.89$, $P = 0.38$). Males of disparate social ranks (level 2, or high vs. low) had significantly shorter maximum matching bout lengths than males of the same social rank (level 0), whereas their average bout lengths did not differ significantly (Table 1; ANOVA: maximum: $F_{2,56} = 4.54$, $P = 0.015$, Tukey's honestly significant difference test $P < 0.05$; median: $F_{2,56} = 1.1$, $P = 0.18$). Males of one rank difference (level 1) did not differ significantly in bout duration from males of rank differences of either level 0 or level 2.

DISCUSSION

Male black-capped chickadees frequency matched their neighbors during the dawn chorus, indicating that the dawn chorus is a dynamic network of interacting territory holders. Recordings made with a 16-channel ALS revealed that the amount of matching between males was related to both flock membership and rank disparity, supporting the social dynamics hypothesis. These differences in matching were the result of longer duration matching bouts and not the relative number of times males engage in bouts of matching. Results of 2 previous studies (Burt and Vehrencamp 2005; Liu and Kroodsma 2007) lent support to the social dynamics hypothesis, but the present study is the first to show that dawn interactions themselves are related to the social relationships between territorial neighbors. In contrast to our findings for frequency matching, song overlapping appears to be less important for black-capped chickadees at dawn, occurs less often than expected by chance, and is unrelated to any of the measured social factors.

Frequency matching in black-capped chickadees shares similarities with song type matching in other species (this study and Shackleton and Ratchiffe 1994; Fitzsimmons et al. 2008). Song type matching is a commonly used strategy in songbirds that share at least some portion of their repertoire with neighbors, whereas overlapping is possible in all birds regardless of whether they share song types. Matching has also been described in the vocal interactions of frogs (Gerhardt et al. 2000) and cetaceans (Janik 2000). Matching and overlapping in birds have primarily been considered in the context of daytime singing interactions. Our results, as well as those of Burt and Vehrencamp (2005), suggest that these behaviors are used at dawn as well as during the daytime.

Chickadees use matching more frequently at dawn (this study) than during daytime countersinging interactions in the same population, where matching does not differ from chance levels (Fitzsimmons et al. 2008). In banded wrens, matching was also more frequent at dawn than later in the

day (Burt and Vehrencamp, 2005). The dawn chorus may be an optimal time to engage in singing interactions because all territorial males participate in the chorus, and their attention is not divided among other tasks (e.g., foraging, preening, mate guarding), compared with later in the day when males may differ in their motivation to interact. Singing at dawn might allow males to determine survival, current condition, pairing status, and motivation levels of neighbors and to assert their competitiveness level for the coming day (reviewed in Staicer et al. 1996). Consistent with this hypothesis, flock membership and rank disparity were not related to matching or overlapping in chickadee daytime singing interactions (Fitzsimmons et al. 2008), suggesting that renegotiation of social relationships by interactive communication may occur mainly before sunrise. Male chickadees may avoid competitive singing interactions with neighbors after sunrise once females have emerged from nest sites and mate guarding becomes more important; although males still respond strongly to strangers after dawn (Otter et al. 2002; Mennill and Ratcliffe 2004a) and use matching in escalated encounters (Shackleton and Ratcliffe 1994).

Male chickadees from the same winter flock spent significantly less time matching at dawn than males from different flocks. Although males defend autonomous, all-purpose territories, familiarity, and individual recognition may play an important role in regulating the amount of interaction required each day to reestablish or maintain relationships. Males from different flocks have spent less time in close contact and may have prolonged interactions as a result. Aggressive behaviors tend to decrease with increasing familiarity in animals (reviewed in Marler 1976; Ward and Hart 2003). Song-type matching in neighboring male song sparrows (*Melospiza melodia*) declines seasonally from territory establishment, when males are less familiar, through breeding (Beecher et al. 2000). In chickadees, non-flockmates may settle contests only by fighting and, therefore, might spend more time matching at dawn in anticipation of later daytime contests over boundaries and nest sites.

Males of similar rank matched for a larger portion of their chorus than males of disparate rank. Males of similar rank matched at a high level regardless of the absolute ranks of the 2 opponents. Males of similar rank are likely of similar quality and more assessment time might be necessary to resolve social relationships each morning. Contest duration typically increases with decreasing asymmetry of opponents (e.g., Enquist et al. 1990; Schmitz and Baldassarre 1992; Hack et al. 1997; Kemp 2000). We found that matching bouts were longer between males of similar rank as predicted by the sequential assessment model (Enquist et al. 1990). Male chickadees might be either aware that they are the same rank or during interactions they might be detecting something about their relative quality through their opponent's persistence and the quality of their interchanges.

Contrary to our predictions, males did not match their paired neighbors more often than they did unpaired males. Unpaired chickadees often sing very near other males and sometimes move into other males' territories and sing later in the day (J. Foote, personal observation). Therefore, unmated males may still require a territorial response similar to that of mated males. We found that unpaired males had minimum distances that were on average 17 m closer to their neighbors than paired males were to each other. In rock ptarmigans (*Lagopus mutus*), fights with bachelors are even more intense than with other mated males (Brodsky and Montgomerie, 1987). Both paired and unpaired males could be a threat to a territorial male's paternity. Although unpaired male chickadees are often of low rank and unlikely to sire extrapair young (Otter et al. 1998), they can quickly fill territorial va-

cancies that arise as a result of mortality early in the breeding season.

Across animal signaling systems, matching is predicted to be a conventional signal of aggressive intentions, signaling the probability of approach and subsequent escalation (Molles and Vehrencamp, 2001; Vehrencamp 2001). The amount of matching between males during the chorus did not relate to the distance between individuals, suggesting that matching at dawn might not function as a conventional signal. Additionally, matching and overlapping may function as graded signals of aggression (Otter et al. 2002). We found that matched songs were no more likely to be overlapped than unmatched songs as would be predicted if they were graded signals of aggression at dawn. At dawn, chickadees move infrequently (Otter and Ratcliffe 1993); therefore, levels of matching may instead predict interactions with close approach or fights once the chorus is over. Males typically sing continuously through the chorus (Otter et al. 1997) and singing does not escalate to fights at dawn as it does later in the day, although males may be in close proximity. Absolute qualities of male chorusing behavior are honest indicators of quality that may be important for female choice (Otter et al. 1997; Poesel et al. 2006) and may signal competitiveness later in the day (Poesel et al. 2004) to nonterritorial males prospecting for territories (Amrhein et al. 2004b). These factors might make it risky for a male to take a break from singing in order to fight at dawn. Males with fertile mates remain close to their nest cavity while singing (Otter and Ratcliffe 1993), so movements of males at dawn may be constrained and neighbors far apart may still have an interest in prolonged matching.

Although matching may not signal immediate aggression at dawn, it may function to signal that a male is directing his song at a particular opponent (Brémond 1968). Males may also engage in prolonged matching to probe and reveal relative status (Nielsen and Vehrencamp 1995). We found that higher overall levels of matching at dawn were associated with increased bout length, with males from different flocks and of similar ranks engaging in longer bouts. Matching interactions of males may contain information that could be used by eavesdroppers such as floaters and females to evaluate relative quality of males (Otter and Ratcliffe 2005). Both male and female chickadees use information obtained from eavesdropping on countersinging interactions (Mennill et al. 2002; Mennill and Ratcliffe 2004b). Matching may also serve as a signal to other conspecific males. Males who take turns matching each other may signal a strong dyad to potential usurpers (Todt and Naguib 2000). If nonterritorial chickadees prospect territories at dawn like nightingales do (Amrhein et al. 2004b), signaling a strong dyad of experienced neighbors may be beneficial to both of the countersinging territorial males.

Males overlapped less than expected by chance, suggesting that avoidance of overlapping occurs at dawn. Signalers have been shown to avoid overlap by timing their songs to fall in periods of silence of other species or playback stimuli, in both birds (Ficken et al. 1974; Brumm 2006) and frogs (Zelick and Narins 1985). Avoiding overlap prevents masking of the signal to receivers but also permits mutual listening for assessment (Todt and Naguib 2000). In response to overlapping playback, males may alter the timing of song delivery or song length to avoid overlap (Hultsch and Todt 1982; Dabelsteen et al. 1996; Mennill and Ratcliffe 2004a; Hall et al. 2006; Osiejuk et al. 2007). Avoidance of overlap is small between each pair of neighbors but is likely significant because each male has several neighbors and interspecific signalers to consider when timing song delivery. Avoiding overlap at dawn may be part of the signaling strategy and signal attention during the chorus, potentially allowing individuals to assess subtle variations of an opponent's song characteristics (Todt and Naguib

2000). Because of the difficulty of timing songs relative to multiple neighboring singers, overlapping may not carry the same agonistic function at dawn as it does in dyadic counter-singing interactions occurring later in the day when background noise levels are lower. Some overlapping at dawn may be communicative; however, it is difficult to tease apart from chance in this study. We found no relationship between overlapping and any of the measured social factors, and overlapping was not associated with matching. Although Burt and Vehrencamp (2005) found a correlation between matching and overlapping, banded wren songs are 3 times as long as chickadee songs, so the relationship may be clearer in species where errors in perceived overlap are likely smaller. Overlapping during daytime singing interactions in chickadees is more common than during the dawn chorus, although it does not differ significantly from chance (Fitzsimmons et al. 2008).

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