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Frequency matching, overlapping and movement behaviour in diurnal countersinging interactions of black-capped chickadees

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Animal signalling contests are used by males to advertise to choosy females and to repel male competitors. During countersinging interactions in songbirds, males vary the type and timing of songs with respect to their opponent's behaviour. In black-capped chickadees, *Poecile atricapillus*, frequency matching and song overlapping appear to be important in territory defence and mate attraction. We studied frequency matching and overlapping behaviour during 100 naturally occurring diurnal song contests among male chickadees using an Acoustic Location System (ALS). The ALS consisted of 16 microphones that recorded countersinging interactions across multiple territories simultaneously, allowing us to triangulate the position of individuals based on delays in sound arrival at each microphone. We used the ALS to record 10 neighbourhoods of chickadees whose relative dominance status had been tabulated during the preceding winter. In 80% of contests there was at least one instance of overlapping between the contestants. In 37% of contests, the contestants were frequency matched within 50 Hz. Neither overlapping nor matching occurred at levels different from those expected by chance. However, contests that contained frequency matching had significantly more instances of overlapping than nonmatched contests. There were no rank-related differences in the proportion of opponents' songs that were frequency matched or overlapped. In using an Acoustic Location System to record entire neighbourhoods of territorial songbirds, this study is the first to quantify song matching and overlapping by free-living animals in the context of natural countersinging exchanges between familiar territorial neighbours.

Keywords: Acoustic Location System; black-capped chickadee; countersinging; male–male conflict; microphone array; overlapping; *Poecile atricapillus*; song matching; vocal communication

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

One well-studied pattern-specific response is signal matching, which occurs when an individual responds with the same type of signal as the preceding signal from his opponent (Stoddard et al. 1992). Song matching in birds is thought to be a directed signal of aggression and is associated with escalated encounters in species with song repertoires (Vehrencamp 2001) and in species that vary the patterns of their songs in other ways (Morton & Young 1986; Mennill & Ratcliffe 2004b). Evidence from

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interactive playback studies suggests that increased matching is perceived as an increased threat by males (Vehrencamp 2001; Mennill & Ratcliffe 2004b). Song overlapping, a time-specific response that occurs when a singer starts a song before the end of his opponent's song, has similarly been argued to be an aggressive signal (Todt & Naguib 2000). Overlapping masks part of an opponent's signal, impairs mutual listening, and, like song matching, is associated with escalated contests in several species (Dabelsteen et al. 1997; Mennill & Ratcliffe 2004b; Poesel & Dabelsteen 2005; Naguib & Kipper 2006). Interacting individuals may use these dynamic signalling strategies to communicate quality, motivation and intention during countersinging exchanges. Few studies have examined the interplay between pattern- and time-specific responses, and the relative signal function of matching and overlapping. Furthermore, most studies involve song playback to engage animals in simulated contests and, consequently, we know very little about variation in pattern- and time-specific responses during natural countersinging interactions. In this study, we investigate frequency matching and song overlapping in naturally occurring diurnal song contests of black-capped chickadees, *Poecile atricapillus*, using an Acoustic Location System to track the singing and movement behaviour of males.

The black-capped chickadee provides a model system for examining pattern- and time-specific variation in singing behaviour. Chickadees spend the winter in flocks structured by stable, linear dominance hierarchies, and winter dominance status serves as a proxy for individual quality (Ratcliffe et al. 2007). Early in spring, winter flocks break up and male chickadees establish breeding territories. Males defend their territories against former flockmates and males from nearby flocks, forming neighbourhoods of breeding pairs (Mennill & Otter 2007). Males engage in countersinging contests with their neighbours to defend territories and also to attract social and/or extrapair mates. Male dominance position in the winter influences singing behaviour during the breeding season: singing performance is an honest advertisement of male dominance status (Otter et al. 1997) and is used by females to assess both their partner and neighbouring males (Mennill et al. 2002). Although male chickadees have only a single song type, a tonal two-note 'fee bee', they are capable of frequency matching opponents by transposing their song across a continuous frequency range of approximately 860 Hz (Mennill & Otter 2007). Black-capped chickadees provide a unique system for investigating dynamic signalling strategies because dominance rank serves as a proxy for the quality of males who regularly interact through song contests involving frequency matching and overlapping.

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

In this study, we examined male movement behaviour and quantified frequency matching and song overlapping in naturally occurring chickadee song contests. Previous research allowed us to generate specific predictions about male behaviour during countersinging interactions. The use of songs in interactions may communicate a male's social status (Todt & Naguib 2000) and also convey information about a male's motivation and aggressive intentions (Vehrencamp 2001). We therefore predicted that a chickadee's social rank in his winter flock would be related to his singing behaviour in the spring, such that dominant males would use more aggressive signalling strategies during song contests. Given that frequency matching is a signal of directed aggression (Mennill & Ratcliffe 2004b), we predicted that males would match the frequency of neighbours of similar or lower rank, but would avoid matching the frequency of males with higher rank. Furthermore, given that overlapping is a signal of aggression (Mennill & Ratcliffe 2004a, b), we predicted that males would overlap neighbours of similar or lower rank, but would avoid overlapping males of higher rank. Based on the results of earlier playback studies in chickadees (Otter et al. 2002; Mennill & Ratcliffe 2004b), we predicted that male singing strategies would be associated with male movement behaviour during contests, whereby birds involved in aggressive contests would interact at close range. Lastly, based on the sequential assessment model (Enquist et al. 1990), we predicted that contests between males of similar dominance rank would involve more exchanges than contests between males of disparate dominance ranks.

METHODS

Field Methods

We studied black-capped chickadees at the Queen's University Biological Station near Kingston, Ontario, Canada (44°34′N, 76°19′W) between January and July 2005 and 2006. We captured adults in the winter using treadle traps baited with seeds. We banded each individual with an aluminium Canadian Wildlife Services band as well as a unique combination of coloured leg bands ($N = 149$ birds in 2005, $N = 236$ birds in 2006). We determined the dominance ranks of birds in winter flocks by observing pairwise interactions at feeding stations ($N = 2811$ interactions in 2005, $N = 8423$ interactions in 2006). A bird was scored as dominant if it supplanted or chased an opponent, resisted a supplanting attack by an opponent, elicited a submissive posture in an opponent, or fed while an opponent waited to approach a feeder (see Ratcliffe et al. 2007 for details). We classified 'high-ranking males' as the top-ranking male in flocks with two or three males, or the top two males in flocks with four or five males. We classified 'low-ranking males' as the bottom-ranking male in flocks with two or three males or the bottom two males in flocks with four or five males. We classified 'mid-ranking males' only in flocks with three or five males.

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

Our ALS consisted of an array of 16 omnidirectional microphones connected to a central computer by 2200 m of microphone cable. The microphones were housed in rain guards made of PVC tubing mounted on top of 3 m wooden poles. Microphone poles were elevated off the ground and attached to trees with bungee cords. Input from all microphones was digitized using a multichannel data acquisition card (National Instruments DAQ-6260) and stored as 16-channel AIF files (16-bit sampling, 22 050 Hz sampling rate). This design was an extension of the eight microphone system used by Mennill et al. (2006).

Each 16-channel microphone array recorded an area of approximately 160 000 m^2, encompassing the territories of 7–10 male chickadees. We used this ALS to record 10 different neighbourhoods of territorial chickadees between 27 April and 15 May 2005 and 2006. At this time of year, females are fertile and male–male song contests are common (Mennill & Otter 2007). We define a neighbourhood as a cluster of breeding territories with multiple males defending adjacent territories against one another. The neighbourhoods we recorded were often bounded by natural boundaries (e.g. lake shoreline, large fields). Neighbourhoods consisted of birds familiar with one another from the previous winter, either from the same winter flock or adjacent winter flocks. We recorded each neighbourhood continuously between 0425 hours (prior to first light) and 1130 hours for two or three consecutive days. Chickadees sing in two primary contexts: (1) they sing extended bouts of song at dawn and (2) they engage in countersinging interactions after dawn (Mennill & Otter 2007). Here we limit our analysis to postchorus countersinging behaviour (after 0600 hours).

Array Analysis

We used Syrinx-PC (J. Burt, Seattle, WA, U.S.A.) to browse 16-channel spectrograms of array recordings. Our recordings consisted of periods of silence, solo singing and interactive countersinging. We define a contest as occurring when males sing two or more songs each in a back-and-forth exchange at a distance less than 200 m apart. We chose countersinging interactions that were isolated from other singing events by at least 1 min before and after each contest, and that were recorded in three or more microphones to allow triangulation of singing males. We attempted to analyse 10 contests from each of the 10 neighbourhoods, although for two neighbourhoods it was difficult to find contests to match all of the above criteria, resulting in an average of 10.0 ± 0.5 contests per neighbourhood. These contests involved 34 males from 16 flocks in 2005 (17 high-ranking, five mid-ranking, 12 low-ranking) and 30 males from 19 flocks in 2006 (14 high-ranking, 10 mid-ranking, six low-ranking). The 100 contests derived from a total of 28 days of recording (three to five contests analysed per day). We selected contests arbitrarily with respect to male identity; consequently, a few contests within years involved the same pair of males. We ensured that no pair of males was represented in more than two contests. We observed the same patterns when only one contest per pair of males was used; we therefore present analyses of all 100 contests.

For each contest, we annotated every song using the frequency and time cursors in Syrinx-PC. For frequency analysis, we used a focal window with 1024 Blackman FFT, and measured song frequency one-quarter of the way into the bee note (following Christie et al. 2004b), which was repeatable to 2 Hz. For each song contest, we quantified the number of times that a male sang a song that was frequency matched within 50 Hz of his opponent's previous song (difference based on frequency of the bee note) and the number of times that a male sang a song that was overlapped with his opponent's song. We used a combination of focal recordings, field notes, fine structural characteristics and location information to confirm the suspected identities of singing males.

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

Statistical Analyses

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

We compared the observed levels of matching and overlapping to those expected by chance. To establish chance levels of matching and overlapping during chickadee contests, we generated 100 randomized contests by pairing the frequency and timing of songs contributed by two males recorded in different contests. To create these randomized contests, we equated the start time of the first song in all 100 of our recorded contests, defining the contest start time as the beginning of the first song in the first exchange of each contest. We then paired the songs contributed by each of the 100 males who were the first bird to sing in a contest with the songs contributed by one of the 100 males who were the second bird to sing in a different contest, selecting the second bird randomly without replacement. We then calculated how often the songs of the two randomly paired males were matched and overlapped, in the same manner as we did for real contests. Techniques for developing appropriate null models of matching and overlapping signals during animal contests is an important topic for future studies.

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

To test the effects of dominance rank on measures of contest intensity (number of exchanges, proportion of songs that were frequency matched and overlapped, direction of movement and distance moved between songs), we conducted analyses of variance (ANOVA). For our non-normal data, we used Mann–Whitney *U* tests and Kruskal–Wallis tests to compare rank disparity and minimum, average and maximum distances between birds, as well as dominance rank and the number of songs during a contest. We performed chi-square tests to investigate whether interactions containing matching or overlapping were more likely to occur between former flockmates or nonflockmates. We performed all statistical analyses in JMP 5.1 (SAS Institute, Cary, NC, U.S.A.). Descriptive statistics are given as mean ± SE. All tests are two tailed.

RESULTS

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

Overlapping exchanges were commonplace. Eighty per cent of contests had at least one instance of song overlap. Exchanges involving frequency matching were less common. Thirty-seven per cent of contests included males countersinging with songs that were frequency matched within 50 Hz. Thirty-five per cent of contests included both frequency matching and song overlap. Of the average 30.7 exchanges between contestants, 7.9 ± 1.6% of songs were matched and 15.9 ± 1.2% were overlapped. These frequencies did not differ significantly from chance (chi-square test: matching: $\chi^2_1 = 2.3$, $P = 0.13$; overlapping: $\chi^2_1 = 2.4$, $P = 0.12$). There were also no differences in the number of songs sung by males of different rank (Mann–Whitney *U* test: $U = -1.12$, $N_1 = 106$, $N_2 = 39$, $P = 0.29$) or in the number of exchanges between males of different rank (ANOVA: $F_{2,97} = 1.95$, $P = 0.15$) during a contest.

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

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

Contestants moved often during countersinging exchanges (Fig. 3). Males moved on average 22.3 ± 1.3 m between songs. In 51 contests, the males approached

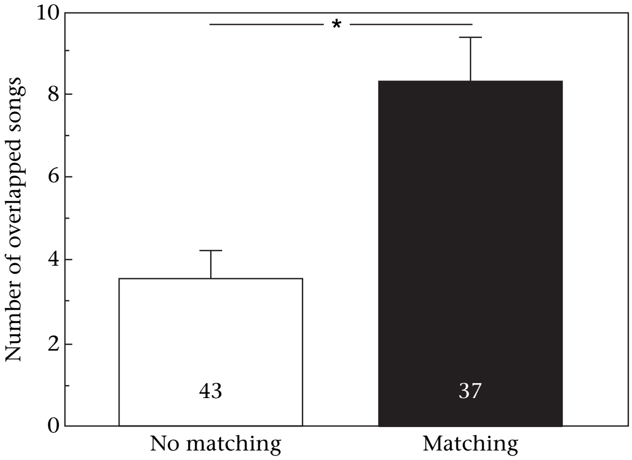

Figure 1. Mean + SE number of overlapped songs in song contests with and without instances of frequency matching. Numbers of contests are shown at the base of each bar. Asterisk shows significant difference between groups at $P < 0.05$.

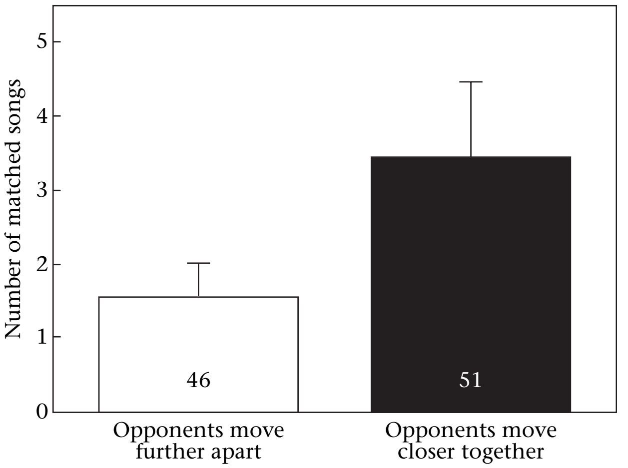

Figure 2. Mean + SE number of frequency matched songs during contests in which males either moved further apart or closer together. Numbers of contests are shown at the base of each bar.

each other; in 46 contests, the males moved apart; in the remaining three contests, the males did not move relative to each other (estimated distance between birds changed by less than 1.0 m from the beginning to the end of the contest). The distance moved between songs did not differ by rank (ANOVA: $F_{1,142} = 1.93$, $P = 0.17$). The minimum, maximum and average distances between birds did not vary with the rank disparity of the contestants (Kruskal–Wallis test: minimum distance: $H_2 = 0.11$, $P = 0.94$; maximum distance: $H_2 = 1.99$, $P = 0.37$; average distance: $H_2 = 2.41$, $P = 0.30$).

DISCUSSION

Our evaluation of naturally occurring diurnal countersinging exchanges between territorial male black-capped chickadees in 10 different neighbourhoods reveals that song contests are commonplace and dynamic exchanges that feature both time-specific and pattern-specific variation. Our analysis of 100 countersinging interactions reveals that overlapping is more common than frequency matching, occurring in 80% and 37% of song contests, respectively. On average, 16% of male's responses were song overlaps, whereas only 8% were frequency matches to their opponent's songs. Surprisingly, observed levels of both matching and overlapping were not significantly different from those expected by chance. Contests in which males were frequency matched contained more instances of song overlap. Our predictions about singing strategies and male dominance rank, as well as the distance between opponents, were not supported by our results. There were no rank-related differences in the proportion of opponents' songs that were frequency matched or overlapped, or in the distance that males moved between songs. Song contests in which the birds

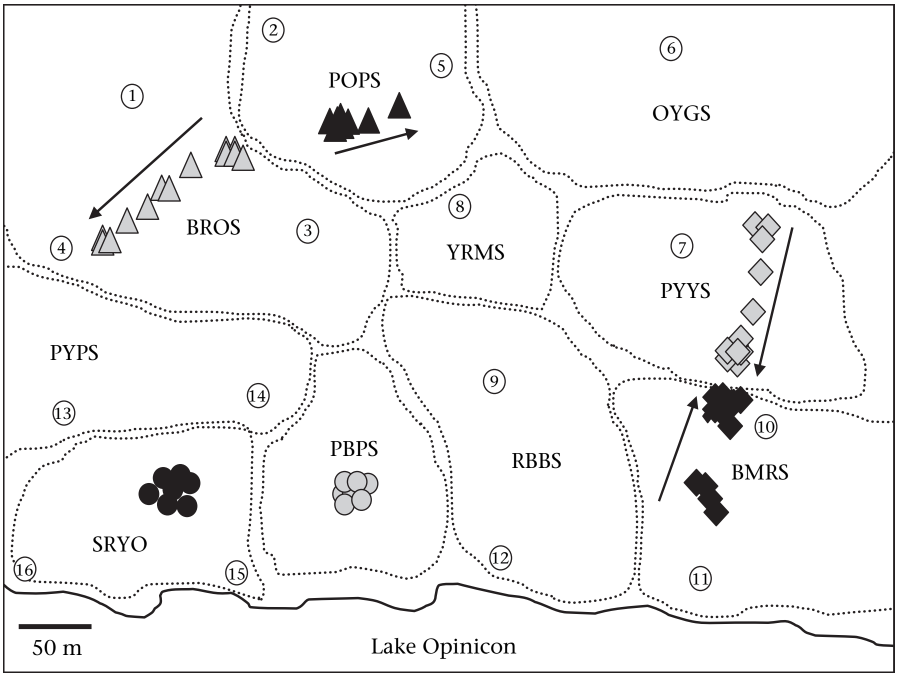

Figure 3. A neighbourhood of singing males recorded with a 16-microphone Acoustic Location System (numbers indicate microphone locations). Three examples of countersinging contests are shown; male identity is indicated by four-letter abbreviations, and arrows indicate direction of male movement. The contest between a high-ranking male and mid-ranking male (locations shown with triangles) begins with the contestants at their territory boundary; the males move apart as the contest progresses. This movement pattern was observed in 46% of contests. The contest between two high-ranking males (locations shown with diamonds) escalates and the birds approach each other, facing off at their territory boundary. Contesting males approached each other in 51% of contests. A high-ranking male and a low-ranking male (locations shown with circles) are engaged in a long-distance contest. There is no approach or retreat in this contest, which was observed in 3% of naturally occurring chickadee contests.

moved closer together had no more instances of frequency matching than contests in which the birds moved apart. Contrary to our expectation, there were no rank-related differences in the number of exchanges between opponents.

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

Higher levels of song overlap were associated with higher levels of frequency matching, but overlapping itself was not related to subsequent approach in escalated contests. This result stands in contrast to Mennill & Ratcliffe (2004b), who found that overlapping was related to how closely chickadees approached the playback apparatus. Our results based on natural interactions are more difficult to tease apart than controlled playback studies, because many of our contests that involved song overlap also contained frequency matching. Similarly, Otter et al. (2002) found that males who received just overlapping playback treatment often began frequency matching, thereby escalating contests themselves. Overlapping in chickadees appears to serve as a signal of arousal or willingness to escalate a contest, as has been found, for example, in European robins, *Erithacus rubecula* (Dabelsteen et al. 1997) and nightingales, *Luscinia megarhynchos* (Naguib & Kipper 2006). In addition to matching and approach responses, other behaviours might act in concert with overlapping to convey information during song contests. In blue tits, *Cyanistes caeruleus*, intruder location influences the effect of overlapping on territorial males' responses to a challenge (Poesel & Dabelsteen 2005). Thus, since overlapping is a common aggressive singing strategy, often associated with frequency matching, it is difficult to distinguish its distinct functional role in natural chickadee song contests.

Many territorial animals display lower levels of aggression towards familiar neighbours than towards unfamiliar strangers (reviewed in Temeles 1994). Playback experiments at territory boundaries in numerous songbirds have shown that males perceive the songs of established neighbours as less threatening than the songs of strangers (reviewed in Stoddard 1996). We might expect black-capped chickadees to respond differently in countersinging interactions with established neighbours, the focus of the present study, and strangers, the focus of previous playback experiments. In such experiments, researchers have simulated unknown intruders broadcasting highly aggressive singing strategies (Mennill et al. 2002; Otter et al. 2002; Mennill & Ratcliffe 2004b). Using interactive playback, Mennill & Ratcliffe (2004b) were able to simulate intruder males whose frequency matched 100% of focal males' songs and overlapped up to 96.8% of focal males' songs. Broadcasting highly aggressive playback elicited strong approach responses (Otter et al. 2002; Mennill & Ratcliffe 2004b) and incited eavesdropping females to seek extrapair copulations after hearing their mates dominated by the simulated aggressive males (Mennill et al. 2002). However, our results indicate that when neighbours engage in natural song contests, they use aggressive singing strategies much more sparingly. The highest levels of matching and overlapping that we observed in natural contests between neighbours were 75.0% and 55.0%, respectively, and the mean levels were 7.9% and 15.9%, respectively. The observed levels of matching and overlapping were not significantly different from the levels expected by chance, suggesting that territorial males are not using abnormally intense signalling strategies during their day-to-day interactions with territorial neighbours. Our analyses were limited to post-chorus singing; a separate study is currently investigating whether chickadees engage in more intense interactions during the dawn chorus.

Why is overlapping a more common response than frequency matching? Time-specific variation (i.e. overlapping) appears to be a more dynamic singing strategy than pattern-specific variation (i.e. matching) in black-capped chickadees. Birds may be capable of altering their time-specific responses with each successive song, whereas frequency shifting may be more constrained. For instance, at dawn, male chickadees sing bouts of approximately 41 songs before shifting frequencies by more than 80 Hz (Horn et al. 1992). Black-capped chickadees may be unable to shift song frequency as often as they can shift song timing, perhaps because of motor or neurological constraints on song production, contributing to an asymmetry in their use of pattern- and time-specific responses during countersinging interactions. Similarly, western meadowlarks, *Sturnella neglecta*, are less likely to match playback when they have just begun a bout of another song type than when they are further into a bout (Falls & d'Agincourt 1982). Alternatively, overlapping may be more common because it serves as the first aggressive response in graded contest escalation (Otter et al. 2002), beginning with overlapping and escalating to matching if necessary. Graded aggressive displays are widespread in an array of animal taxa and sensory systems (Searcy & Andersson 1986). In vocalizing fish, most sounds are produced in concert with other aggressive behaviours (Ladich 1997). A similar pattern of stereotyped levels of aggression during agonistic interactions is seen in a mormyrid electric fish, *Gnathonemus petersii* (Terleph 2004) as well as a cichlid fish, *Nannacara anomala* (Enquist et al. 1990). African painted reed frogs, *Hyperolius marmoratus*, use a graded system of aggressive calls to escalate contests in a continuous fashion (Grafe 1995). Graded aggressive displays are seen in several bird species; the nonmatching/repertoire matching/type matching system in song sparrows, *Melospiza melodia*, is a well-studied example (e.g. Burt et al. 2001).

We predicted that male rank would be related to singing behaviour, such that high-ranking males would use more aggressive signalling strategies during song contests. However, we found no rank-related differences in the use of frequency matching or overlapping. Mennill & Ratcliffe (2004b) found rank-related differences in behavioural responses to these singing strategies, whereby high-ranking males responded with lower agitation levels and spent more time further away from playback-simulated opponents. This finding, taken in concert with the present study, provides insight into the complexities of chickadee countersinging strategies. In natural contests between neighbours (present study), both high- and low-ranking males use similar degrees of aggressive vocal signals, and rank appears to have little influence on male singing behaviour. In contrast, playback experiments (Mennill & Ratcliffe 2004b) reveal rank-related differences during interactions with unknown intruders. High-ranking males may suffer considerable loss of paternity as a consequence of aggressive song contests (Mennill et al. 2002); an aggressive, well-matched opponent poses more of a threat to high-ranking males, and the benefits of escalating contests at close range may outweigh the costs.

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

Using an Acoustic Location System to passively record naturally occurring interactions allowed us to investigate song contests in a unique way. To date, all studies of countersinging interactions have used playback, simulating an intruder, to engage territorial males and record their subsequent responses. Our natural, observation-based approach reveals the sophistication of the seemingly simple chickadee communication system, and the complex interplay between pattern- and time-specific responses as directed signals of aggression. Importantly, our analyses reveal that the commonplace interactive exchanges between neighbouring territorial songbirds are quite different from the interactive exchanges that may occur during highly escalated encounters between territorial birds and rival intruding males (Mennill & Ratcliffe 2004b). In addition, our study suggests that an ALS is a promising new tool for the study of communication networks, in which several individuals are within signalling range of one another (McGregor & Peake 2000), providing the opportunity to examine the wider social context of interactions and the potential selective effects of eavesdroppers on animal communication systems.

In summary, our results reveal that song contests containing frequency matching contain more instances of song overlap. Song matching has been shown to serve as a conventional signal of aggressive intentions in several species (Vehrencamp 2001), and our results support the evidence for this function in chickadees (Shackleton & Ratcliffe 1994; Otter et al. 2002; Mennill & Ratcliffe 2004b; Mennill & Otter 2007). Contrary to the sequential assessment model and findings in other systems (Foster 1981; Enquist et al. 1990; Grafe 1995; Terleph 2004), contests between evenly matched chickadees were not more escalated or lengthier than contests between males of disparate dominance ranks. Further research into naturally occurring contests is needed in a variety of systems in order to formulate accurate models and predictions of dynamic signalling behaviours during social interactions.

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