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Overlapping and matching in the song contests of black-capped chickadees

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During vocal contests, animals alter both the timing and the patterning of responses to their opponents. Time-specific responses (such as overlapping an opponent's song) and pattern-specific responses (such as matching the type of an opponent's song) may reveal information about interacting animals. Here we explore the consequences of overlapping and frequency matching during song contests of male black-capped chickadees, *Poecile atricapillus*. Using interactive playback, we engaged birds of high and low dominance status in vocal interactions with a simulated territorial intruder. The playback intruder either overlapped or avoided overlapping the subjects' songs and either matched or avoided matching the frequency of the subjects' songs. Individuals who were overlapped by the playback intruder showed higher variability in their song length and song timing than individuals who were not overlapped. Individuals who were frequency-matched by the playback intruder responded with more agitated responses (more flights and passes over the speaker and closer distances of closest approach) and spent more time farther away from the loudspeaker. We argue that the timing of song delivery and the choice of song type are distinct functional components of vocal interactions, where overlapping and matching songs are threatening signals that have separate consequences for opponent behaviour and song performance. High-ranking males responded at greater distances from the loudspeaker in all treatments and responded with lower agitation levels than low-ranking males. We demonstrate that males of different quality show different behavioural responses to territorial intruders, where males of high status appear reluctant to engage an intruder as intensely as males of low status.

During vocal interactions, such as the song contests of territorial male songbirds, animals exchange information by using dynamic communication strategies where both the type of signal and the timing of signal delivery may carry information about the signaller's quality, status, intentions or motivational level (Vehrencamp 2000). Vocal communication strategies vary in two primary dimensions; interacting animals may alter their time-specific responses (e.g. by overlapping an opponent's signal) or their pattern-specific responses (e.g. by matching the type of an opponent's signal) and signal variants in either of these dimensions may carry information (Todt & Naguib 2000).

Vocal matching is a pattern-specific singing response that occurs when an individual produces the same type of vocalization as an opponent. Investigations of many different songbirds (reviewed in Todt & Naguib 2000) provide strong support for the hypothesis that vocal matching is a more threatening singing strategy than is vocal nonmatching (Krebs et al. 1981). Vocal matching is manifested at many levels, including the matching of song types (e.g. Vehrencamp 2001) and shared repertoire elements (e.g. Burt et al. 2001), the matching of strophe length (e.g. McGregor & Horn 1992) and the matching of song frequency (e.g. Shackleton & Ratcliffe 1994). Vocal overlapping, which is less widely studied, is a time-specific singing response that occurs when an individual begins vocalizing before an opponent's vocalization is complete. Support for the hypothesis that an overlapping vocalization is a more threatening singing strategy than is a nonoverlapping vocalization (Todt 1981) comes from several types of investigations, including interactive playback mimicking an overlapping intruder (Brindley 1991; Dabelsteen et al. 1997; Naguib 1999; Langemann et al. 2000), two-speaker playback experiments mimicking an overlapper and an overlapped intruder (Naguib & Todt 1997; Mennill & Ratcliffe, in press), and observation of the singing location

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(Todt 1981) and song performance (Hultsch & Todt 1982) of overlapped singers.

Song contests have immediate importance for the contestants directly involved in the exchange of information, but have additional importance to the audience surrounding the contestants. Recent evidence shows that matching and overlapping during male–male song contests may be of particular interest to females making reproductive choices (Otter et al. 1999; Mennill et al. 2002) and to nearby males making territorial decisions (Naguib & Todt 1997; Peake et al. 2001). Consequently, the dynamics of information exchange during male countersinging interactions are critical to our comprehension of sexual selection through both female choice and male–male competition. Despite an increasingly broad understanding of the separate signal function of matching and overlapping (Todt & Naguib 2000), we know remarkably little about the interplay between time-specific and pattern-specific singing responses and the relative signal function of matching and overlapping. Here we evaluate the signal function of matching and overlapping during the song contests of black-capped chickadees, *Poecile atricapillus*.

Male black-capped chickadees sing a tonal two-note song, ‘fee bee’. Although chickadees have only one song type, they adjust their song by transposing it across a continuous frequency range of approximately 800 Hz (Horn et al. 1992; Kroodsma et al. 1999). Males change their song frequency, shifting by intervals greater than 80 Hz every 41 ± 8.8 songs (Shackleton & Ratcliffe 1994). Song contests often include frequency matching and overlapping between opponents and typically involve territory holders countersinging with neighbours or with nonterritorial individuals (personal observation). Black-capped chickadees live in small flocks structured by stable linear dominance hierarchies where high-ranking males benefit from preferential access to food during the winter (Ficken et al. 1990; Smith 1991). In the early breeding season, chickadees divide their winter-flock home range into all-purpose territories, such that high- and low-ranking males typically occupy neighbouring territories. High-ranking males benefit from preferential choice by females as social partners (Ramsay et al. 2000) and extrapair copulation partners (Otter et al. 1998) during the breeding season. High-ranking males have higher song output during the dawn chorus compared with low-ranking males (Otter et al. 1997) and the performance of high-ranking males in song contests during the breeding season influences female choice (Mennill et al. 2002). Black-capped chickadees provide a unique system to investigate pattern-specific and time-specific variation in singing behaviour because dominance rank serves as a proxy for the quality of males who routinely engage in contests involving both overlapping and frequency matching.

In this study, we used interactive playback to investigate the responses of high- and low-ranking male black-capped chickadees to a simulated territorial intruder. We engaged males in song contests with a simulated opponent using one of four playback treatments involving a factorial design of frequency matching and overlapping (Fig. 1). Based on Krebs et al.’s (1981) hypothesis that vocal matching is a more threatening signal than is vocal nonmatching, we predicted that males receiving matching playback would show more intense responses than males receiving nonmatching playback. Based on Todt’s (1981) hypothesis that an overlapping vocalization is a more threatening signal than is a nonoverlapping vocalization, we predicted that males receiving overlapping playback would show more intense responses than males receiving nonoverlapping playback. If matching and overlapping convey information independently, we predicted that there would be no interacting effects of playback treatment on male responses. If, however, matching and overlapping work together as graded, aggressive signals, we predicted that male playback responses would show interaction effects. Kroodsma (1979) and Hultsch & Todt (1982) suggested that time-specific and pattern-specific responses of territorial birds to intruders might reflect social dominance. We tested this hypothesis directly by comparing the responses of high-ranking and low-ranking male chickadees across playback treatments.

METHODS

General Methods

We monitored a population of black-capped chickadees at Queen’s University Biological Station (44°34′N,

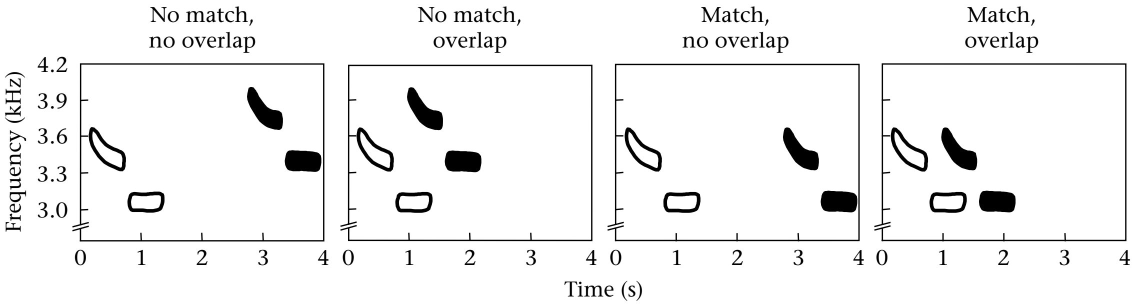

Figure 1. Sound spectrograms depicting vocal interactions between subjects (white) and playback intruders (black) for four interactive playback treatments. To match the subject, the playback intruder produced songs at the same frequency as the subject’s songs. To avoid matching, the playback intruder produced songs at a higher frequency than the subject. To overlap the subject, the playback intruder gave an immediate response, singing before the subject’s songs were complete. To avoid overlapping, the playback intruder gave a delayed response, singing in the silent interval following the subject’s songs.

76°19′W) between January and July of 2000 and 2001. In January of each year we colour-banded all individuals in the 2.0-km^2 study site ($N = 133$ birds in 2000, $N = 183$ birds in 2001). We tabulated pairwise interactions between birds at winter feeding stations to establish each bird's position in its winter flock dominance hierarchy ($N = 2208$ interactions in 2000, $N = 4026$ interactions in 2001). We inferred dominance when an individual (1) supplanted or chased an opponent, (2) resisted a supplanting attack by an opponent, (3) elicited a submissive posture in an opponent, or (4) fed while an opponent waited to approach a feeder (Ficken et al. 1990; Otter et al. 1998). Flock membership was confirmed by following groups as they travelled between feeding stations. Using MatMan software (De Vries 1998; Noldus Information Technology, Leesburg, Virginia, U.S.A.), we reordered dominance interaction matrices to fit a linear hierarchy for the males in each flock. We identify '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 identify 'low-ranking males' as the bottom-ranking males in flocks with two or three males or the bottom two males in flocks with four or five males.

In this study population, flocks break up in mid-April and birds begin defending all-purpose breeding territories against their former flockmates. Playback treatments were conducted between 24 April and 13 May, the period following flock break-up but preceding the end of female egg laying. We determined female reproductive status by observing females and their nests directly. We determined territory boundaries during focal watches of territorial pairs and we placed playback loudspeakers near the centre of subjects' territories to avoid the confounding influence of neighbouring males' responses.

Interactive Playback

We used interactive playback to simulate intrusions by unknown countersinging male chickadees. To create playback stimuli, we digitized six songs recorded from six chickadees in 1987, ensuring that playback songs were unknown to birds in the study population. We created three 'master songs' by pairing the first syllable of three songs with the second syllable of the other three songs to produce songs with between-syllable frequency differences and duration differences that were within the natural range of variation for the population (Horn et al. 1992). We transposed these three master songs across the chickadee singing range (ca. 2960–3500 Hz; Horn et al. 1992) at intervals of 100 Hz to create three 'song libraries'. With each of these song libraries, we could simulate a different territorial intruder capable of frequency matching any playback subject's song to within 50 Hz. We randomly chose one song library for each playback session, with the concession that each library would be used in each treatment and for an equal number of times in playbacks to high- and low-ranking males. During interactive playback trials, we ran Syrinx-PC sound analysis software (J. Burt, University of Washington, Seattle, U.S.A.; Mennill & Ratcliffe 2000) on a Panasonic Toughbook CF-45 portable computer connected to a Sony SRS-77G loudspeaker and an Audiotechnica 815b directional microphone amplified by a Saul-Mineroff preamplifier. Volume of the playback speaker was standardized in the field to an amplitude of 90 dB at 1 m using a Realistic sound level meter (model 33-2050) on slow setting.

Each playback session consisted of a lure phase and an interactive phase. The lure phase involved loop playback of unfamiliar 'chick-a-dee' calls to incite singing by the territorial male. As soon as the territorial male responded with song, we began the interactive phase of playback. If the lure call attracted the territorial male to the speaker location but failed to incite singing, we broadcast a noninteractive playback of synthetic song up to a maximum of 10 times. The synthetic song lure was created in Cool Edit 2000 (Syntrillium Software, Phoenix, Arizona, U.S.A.) by modifying two pure tones to mimic the frequency characteristics of chickadee song without conveying any individually distinctive characteristics. During the interactive phase, we used the Syrinx-PC on-screen scrolling spectrographic display to assess the timing and absolute frequency of every song given by the subject. We gave exactly one playback song for each subject song according to the appropriate treatment (see below). The interactive phase of playback trials lasted 360 s or until the focal male stopped singing (average trial length: 327 ± 14 s).

Subjects received one of four playback treatments, which involved all possible combinations of frequency matching versus nonmatching and overlapping versus nonoverlapping (Fig. 1). In overlapping trials, we played a song as soon as we detected the subject's song on the real-time scrolling spectrograph, with the effect that the subject's bee note was overlapped by the playback intruder's fee note (delay between key press and broadcast of stimulus was approximately 250 ms). In nonoverlapping trials, we waited for 1.5 s after the subject's song had terminated to play a response, so that the playback response fell in the space between consecutive subject songs. In matching trials, we evaluated the frequency of the subject's song on the real-time scrolling spectrograph and chose the closest matching playback response. In nonmatching trials, we chose a playback response that was 300–400 Hz higher than the subject's song, so that the pitch of the response was considerably higher than that of the subject without being outside of the chickadee's normal singing range. We held the frequency of the playback songs constant unless the subject shifted the frequency of his song. If the subject shifted his singing frequency during a matching trial (12 of 42 matching trials), we shifted frequencies to match the subject. If the subject shifted his singing frequency during a nonmatching trial (six of 39 nonmatching trials), we did not change the frequency of the playback song unless the subject matched the original playback frequency (which occurred twice), in which case we shifted playback frequency to remain 300–400 Hz higher than the subject's new frequency.

Subjects' Responses to Playback

To evaluate male singing responses to playback intruders, we recorded all subject–playback interactions using an Audiotechnica 815b directional microphone, a Saul-Mineroff preamplifier and a Sony Professional tape recorder. We digitized these recordings using Syrinx-PC and extracted two singing response variables: (1) the total number of songs sung by the subject, and (2) the number of times the subject shifted the frequency of his song (frequency shift reported as a change in frequency greater than 80 Hz; Horn et al. 1992). Based on the first 30 exchanges between the subject and playback in each trial, we made six measurements using Cool Edit 2000: the start time and end time of the subject's songs, the start time and end time of the playback songs, the frequency of the subject's bee note (frequency of maximum amplitude) and the frequency of the playback's bee note (effective resolution of 1 Hz for all frequency measures and 1 ms for all temporal measures). From these measurements we extracted four additional singing response variables: (3) average length of subjects' songs, (4) the coefficient of variation in the length of subjects' songs, (5) average length of the interval between consecutive subjects' songs and (6) the coefficient of variation in the length of the interval between subjects' songs. Subjects occasionally stopped singing for brief periods during trials; we did not measure between-song intervals greater than 10.0 s to avoid including these extended breaks in variables (5) and (6).

To evaluate male behavioural responses to playback intruders, an observer naïve to the subject's rank and the design of the experiment described the subject's activities into a dictaphone, providing a running commentary of the subject's location relative to the speaker, and the direction and distance of the subject's movements. The observer followed the subject throughout the lure phase and interactive phase as well as a postplayback observation period, where each subject was followed for at least 5 min after the end of playback, until the subject began foraging in silence. We extracted the following behavioural response variables from the observer's dictaphone tapes using the event recorder J-Watcher (Blumstein et al. 2000): (1) proportion of the playback period spent less than 5 m from the speaker, (2) proportion of playback period spent greater than 10 m from the speaker, (3) proportion of postplayback period spent less than 5 m from the speaker, (4) proportion of postplayback period spent greater than 10 m from the speaker, (5) subject's closest approach distance, (6) number of flights exceeding 1 m during playback, (7) number of passes over the speaker during playback.

In 2000 and 2001 we gave 81 playback trials to 61 male chickadees. Forty-one males received only one playback trial. Of 20 males who received two playback trials, none received the same treatment twice and none received more than one playback per year. The playback responses of these 20 males in separate years were treated as independent data points. To assess any effects of including multiple trials for these males, we conducted all analyses twice, first using only the first trial from each male ($N = 61$), and then using all trials ($N = 81$). There were no differences in the results and therefore the analyses using the entire data set are presented. Owing to a tape malfunction in one trial, we obtained a singing response but no behavioural response.

Statistical Approach

We conducted two principal components (PCs) analyses to summarize male playback responses, one for subjects' singing responses and one for subjects' behavioural responses. We report all PCs with eigenvalues greater than 1.0 (Bryant & Yarnold 1995). PCs were subjected to varimax rotation to create interpretable combinations of the original variables.

Analysis of singing response measures generated three PCs that explained 73.8% of the variation in subjects' singing performance during playback (Table 1). PC1 is an indicator of 'rapid singing and switching', where males with high PC1 scores sang many songs at short intersong intervals, and showed an increased propensity to change their singing frequency. PC2 is an indicator of 'shortened songs', where males with high PC2 scores sang shorter songs and showed greater variation in song length. PC3 is an indicator of 'variable song timing', where males with high PC3 scores sang with more variable intersong intervals. Hereafter, we use these three PCs to describe subjects' singing responses.

Analysis of behavioural response measures generated two PCs that explained 73.2% of the variation in subjects' behaviour during playback (Table 2). PC1 is an indicator of 'close proximity to speaker', where high PC1 scores reflect a greater proportion of the playback and postplayback period spent near the simulated intruder. PC2 is an

Table 1. Principal components analysis of male singing responses during interactive playback; three principal component factors summarized the variation in male song performance during playback trials

Singing response variable	PC1 (rapid singing and switching)	PC2 (shortened songs)	PC3 (variable song timing)
Number of songs sung by subject	**0.87**	−0.12	−0.05
Number of times subject frequency-shifted his song	**0.64**	−0.36	0.44
Song length average (s)	−0.08	**−0.82**	0.01
Song length coefficient of variation (%)	−0.08	**0.76**	0.20
Intersong interval length average (s)	**−0.81**	−0.28	0.05
Intersong interval length coefficient of variation (%)	−0.03	0.19	**0.92**
Eigenvalue	1.88	1.55	1.00
Percentage of variation explained	31.3	25.8	16.7
Cumulative variation explained	31.3	57.1	73.8

Components were subjected to varimax rotation. Bold face indicates variables that contributed strongly to each principal component factor.

Table 2. Principal components analysis of male behavioural responses during interactive playback; two principal component factors summarize the variation in male behaviour during playback trials

Behavioural response variable	PC1 (close proximity to speaker)	PC2 (agitation level)
Proportion of playback <5 m of speaker (%)	**0.77**	0.42
Proportion of playback >10 m from speaker (%)	**−0.76**	−0.39
Proportion of postplayback <5 m from speaker (%)	**0.86**	−0.06
Proportion of postplayback >10 m from speaker (%)	**−0.87**	0.04
Closest approach distance (m)	−0.20	**−0.81**
Number of flights during playback	−0.11	**0.81**
Number of passes over speaker during playback	0.21	**0.84**
Eigenvalue	3.38	1.75
Percentage of variation explained	48.2	25.0
Cumulative variation explained	48.2	73.2

Components were subjected to varimax rotation. Bold face indicates variables that contributed strongly to each principal component factor.

indicator of subjects' 'agitation level', where high PC2 scores reflect closer approach to the loudspeaker, greater numbers of flights, and greater numbers of passes over the loudspeaker. Hereafter, we use these two PCs to describe subjects' behavioural responses.

To test the effects of playback treatment and subject rank on male playback responses, we conducted three-factor analysis of variance (ANOVA), where the variables were subjects' response scores and the effects were playback overlapping strategy (overlapping versus nonoverlapping), playback matching strategy (frequency matching versus nonmatching), subject rank (high versus low) and four interaction terms (Table 3). All statistical analyses were conducted in JMP 4.0. All values are reported as mean ± SE.

RESULTS

Accuracy of Interactive Playback

The interactive playback intruder accurately overlapped or avoided overlapping the subjects' songs. The average latency from the start of the subject's song to the start of the playback song was 2.43 ± 0.03 s in nonoverlapping trials, significantly longer than 0.57 ± 0.03 s in overlapping trials (ANOVA: $F_{1,80} = 2264.3$, $P < 0.0001$). Because subjects occasionally altered the timing of their songs in subtle ways, our overlapping consistency was not perfect; however, in overlapping trials, we successfully overlapped 82.5 ± 1.3% of subjects' songs, significantly more than in nonoverlapping trials where we accidentally overlapped only 0.9 ± 1.3% of subjects' songs (ANOVA: $F_{1,80} = 2048.8$, $P < 0.0001$).

The interactive playback intruder accurately matched or avoided matching the frequency of the subjects' songs. In nonmatching trials, the playback intruder sang at a frequency 346 ± 16 Hz higher than the subject's singing frequency, significantly higher than in matching trials where the playback intruder sang at a frequency 7 ± 15 Hz lower than the subject's singing frequency (ANOVA: $F_{1,80} = 267.9$, $P < 0.0001$). In matching trials, the difference between the subject's frequency and playback frequency was not significantly different from zero (*t* test: $t_{40} = -0.8$, $P = 0.45$). There were no significant differences in total playback song output associated with playback treatment (two-factor ANOVA: playback overlapping

Table 3. Comparison of male singing responses and behavioural responses against the playback intruder's overlapping and matching strategy and the subject's rank

	ANOVA			
	Playback overlapping strategy	Playback matching strategy	Subject's rank	Interaction terms
Male singing responses				
PC1: Rapid singing and switching	$F_{1,73} = 0.2$ NS	$F_{1,73} = 2.3$ NS	$F_{1,73} = 0.0$ NS	$F_{1,73} < 1.3$ NS
PC2: Shortened songs	$F_{1,73} = 9.1$ ***	$F_{1,73} = 0.8$ NS	$F_{1,73} = 1.1$ NS	$F_{1,73} < 2.8$ NS
PC3: Variable song timing	$F_{1,73} = 7.5$ **	$F_{1,73} = 9.3$ ***	$F_{1,73} = 1.8$ NS	$F_{1,73} < 1.4$ NS
Male behavioural responses				
PC1: Close proximity to speaker	$F_{1,72} = 1.0$ NS	$F_{1,72} = 19$ ***	$F_{1,72} = 3.9$ *	$F_{1,72} < 0.3$ NS
PC2: Agitation level	$F_{1,72} = 0.1$ NS	$F_{1,72} = 1.5$ NS	$F_{1,72} = 8.7$ ***	$F_{1,72} < 4.8$ *†

*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$.

†The overlapping * matching interaction term was significant ($F_{1,72} = 4.7$, $P = 0.03$), but the other three interaction terms were not ($F_{1,72} < 2.3$).

strategy: $F_{1,77} = 0.1$, $P = 0.75$; playback matching strategy: $F_{1,77} = 2.5$, $P = 0.12$; interaction term: $F_{1,77} = 0.0$, $P = 0.90$) nor were there differences in the length of playback trials (two-factor ANOVA: playback overlapping strategy: $F_{1,77} = 1.1$, $P = 0.30$; playback matching strategy: $F_{1,77} = 2.0$, $P = 0.16$; interaction term: $F_{1,77} = 0.0$, $P = 0.97$).

Male Singing Responses

Two of three measures of male singing response varied with playback treatment. Variation in subjects' rapid singing and shifting was not related to playback treatment (Fig. 2a, Table 3). Subjects who received overlapping treatments gave significantly more shortened songs during playback (Fig. 2b, Table 3). Overlapped males were more likely to drop the terminal syllable of their song (the bee syllable), resulting in an increased number of truncated, one-note songs. In overlapping treatments, one-note songs comprised 7.3 ± 1.6% of all songs given by the subject, whereas in nonoverlapping treatments one-note songs comprised only 4.1 ± 1.5% of all songs given by the subject (ANOVA: $F_{1,80} = 3.9$, $P = 0.05$). By producing one-note songs, subjects significantly reduced the time between the onset of consecutive songs (average delay between the start of a one-note song and onset of subject's next song: 3.55 ± 0.13 s; average delay between the start of a full song and onset of subject's next song: 4.15 ± 0.06 s; paired *t* test: $t_{40} = 4.1$, $P < 0.0005$). The silent interval between consecutive subject songs showed significantly higher variability when the intruder overlapped and matched the subject (Fig. 2c, Table 3). In summary, the subjects' singing responses were influenced by intruder overlapping, where subjects shortened their songs and increased the variability of their song timing when the intruder overlapped.

Male Behavioural Responses

Subjects began singing after 3.05 ± 0.33 min of noninteractive playback of lure calls. Subjects typically gave their first song as they approached the speaker, although in 36% of playback sessions the subject approached the speaker in silence and we broadcast synthetic song to incite singing. During the interactive phase of playback trials, all subjects responded aggressively to the playback speaker, with average closest approach distances of less than 1.5 m in all playback treatments (nonmatching, nonoverlapping: 1.3 ± 0.6 m; nonmatching, overlapping: 1.5 ± 0.6 m; matching, nonoverlapping: 1.2 ± 0.6 m; matching, overlapping: 0.6 ± 0.6 m; two-factor ANOVA: $F_{1,77} < 0.8$, NS).

Both measures of male behaviour varied with playback treatment. Subjects who received matching treatments spent significantly more time farther away from the speaker than subjects who received nonmatching treatments (Fig. 3a, Table 3). The agitation level of subjects showed an interactive influence of matching and overlapping treatments (Fig. 3b, Table 3). Males who received both overlapping and matching treatment showed the highest levels of agitation, reflecting increased numbers of

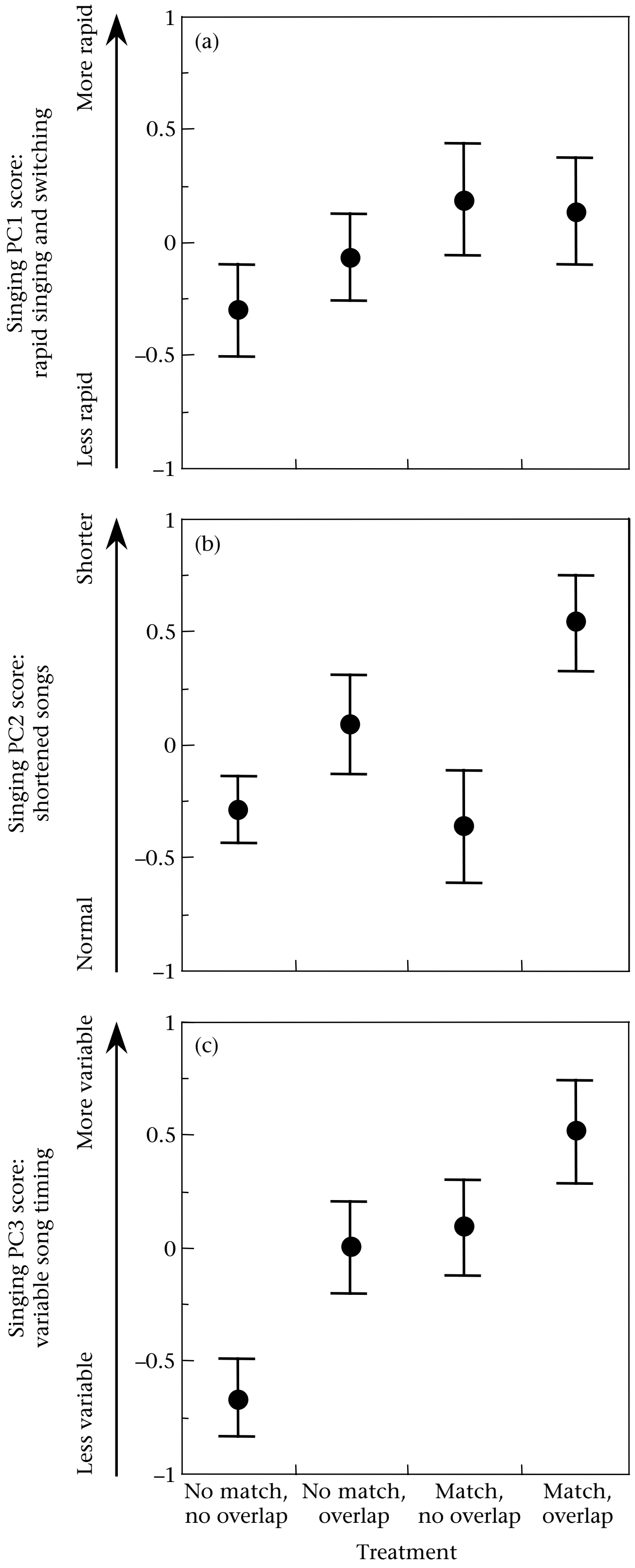

Figure 2. The influence of four interactive playback treatments on the singing responses of male black-capped chickadees: (a) rapid singing and switching; (b) shortened songs and (c) variable song timing. Error bars show standard errors.

flights and passes over the speaker as well as closer distances of closest approach.

Male Rank

High- and low-ranking males showed different behavioural responses to playback. High-ranking males spent significantly more time farther away from the speaker in all playback treatments (Fig. 3a, Table 3). Furthermore, high-ranking males showed significantly lower agitation levels than low-ranking males (Fig. 3b, Table 3), making more distant closest approaches and fewer flights and passes over the speaker than low-ranking males in all playback treatments. Separating subjects by rank revealed that the interactive effect of matching and overlapping on subject's agitation level (Table 3) was driven by strong responses from low-ranking males to nonmatching nonoverlapping treatments (Fig. 3b). Subjects showed no significant rank-related differences in singing responses (Table 3). None of the differences in male singing responses or behavioural responses associated with playback overlapping strategy, playback matching strategy, or subject's rank (Table 3) showed a relationship with the specific song library that was used in interactive playback (ANOVA: $F_{1,80} < 1.7$, NS), suggesting that the three song libraries were functionally equivalent.

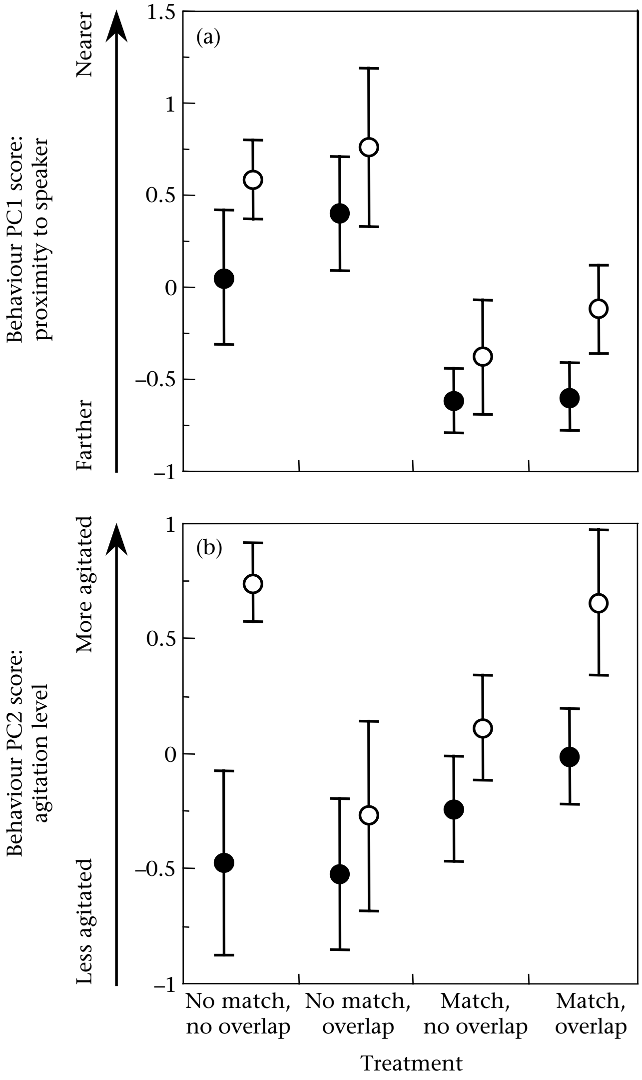

Figure 3. The influence of four interactive playback treatments on the behavioural responses of high-ranking (●) and low-ranking (○) male black-capped chickadees: (a) proximity to the loudspeaker and (b) agitation level. Error bars show standard errors.

DISCUSSION

The response of male black-capped chickadees to countersinging territorial intruders varied with the overlapping and matching strategy of the intruder. Males gave more variable song performances during song contests with overlapping versus nonoverlapping intruders, singing more shortened songs with more variable song timing in contests with an overlapping opponent. Males behaved differently towards frequency matching versus nonmatching intruders, showing more highly agitated behavioural responses to matching opponents and spending more time closer to nonmatching opponents. Males of high and low dominance rank showed status-related differences in behavioural responses to intruders, where high-ranking males responded with lower agitation levels and by spending more time farther away from opponents. In total, male responses to interactive playback treatments demonstrate that both time-specific and pattern-specific elements of song contests convey information and that behavioural responses to these elements change with the quality of the territorial singer.

Our results support the prediction that overlapping playback elicits more highly aroused responses than nonoverlapping playback. Arousal from overlapping was manifested most obviously in subjects' truncated songs and variable song rate. Vocal overlapping produces similar levels of arousal in other animals. Nightingales, *Luscinia megarhynchos*, shorten their songs and increase the variation in their song timing during overlapping playback (Hultsch & Todt 1982; Naguib 1999). Great tits, *Parus major*, increase variation in their song timing (Dabelsteen et al. 1996) and often stop singing altogether when overlapped (Langemann et al. 2000). Both blackbirds, *Turdus merula*, and European robins, *Erithacus rubecula*, decrease their song output when overlapped by an opponent (Todt 1981; Brindley 1991). Although the social context of avian song contests differs from the choruses of insects and anurans, there is evidence that males in other taxa will also adjust their vocalizations to avoid overlap (e.g. Greenfield 1994; Grafe 1996).

Mechanistically, overlapping an opponent's signal is a more aggressive tactic than alternating with an opponent's signal for two reasons. First, the transmission of the overlapped individual's signal is unexpectedly impaired by the masking effects of the overlapper's signal (Todt 1981). The cost of being masked increases in close-range encounters (Todt & Naguib 2000), such as song contests during territorial intrusions. The cost of being masked also increases in song contests where third-party eavesdroppers are assessing the contestants (McGregor & Peake 2000), such as male–male contests taking place during periods of female mate choice. Second, overlapping may signal a refusal to continue receiving information from the overlapped opponent (Dabelsteen et al. 1996), although the idea that birds cannot sing and listen to others simultaneously (Hultsch & Todt 1982) remains an untested assumption.

In animals that sing with predictable rhythm between consecutive songs, overlapping creates a predicament; an opponent who overlaps one song is likely to overlap consecutive songs, unless the overlapped individual alters its singing rhythm. What advantage do chickadees find in producing shortened, variably timed songs when countersinging with an overlapping opponent? When playback subjects truncated their songs by dropping the second syllable, the time interval between consecutive songs was not significantly reduced (average length of break following one-note songs: 3.07 ± 0.13 s; average length of break following full songs: 3.17 ± 0.07 s); in fact, black-capped chickadees seem to be incapable of reducing their intersong silent interval below 2.5 s (personal observation). However, by truncating songs, subjects significantly reduced the time between the onset of their truncated song and the onset of their next song. That is, an overlapped singer who truncates his song may start his next song earlier than if he sang a full song and thereby avoid consecutive overlaps by a rhythmically singing opponent. Increasing variability in song timing may achieve a similar effect by making song onset more difficult for an opponent to anticipate.

Krebs et al. (1981) hypothesized that vocal matching is a threat, and predicted that matching would be correlated with measures of strong response. Experiments involving birds with a repertoire of song types support this view, demonstrating that type-matching playback elicits closer approaches to the loudspeaker than nonmatching playback (reviewed in Vehrencamp 2001). We found a seemingly contrary relationship between frequency matching and the subject's proximity to the loudspeaker; chickadees spent more time farther away from a frequency-matching intruder. However, it is revealing to compare the distance of closest approach values in the present study with those from other investigations of black-capped chickadees. Nonmatching, noninteractive playback in other studies elicited an average distance of closest approach of greater than 10.0 m ($N = 20$ subjects in Fotheringham & Ratcliffe 1995; $N = 8$ subjects in K. Otter, unpublished data), whereas the distances of closest approach observed in our interactive treatments ranged from just 0.6 to 1.5 m. Therefore, although subjects in our playback study spent more time farther away from a frequency-matching intruder, they retaliated against the intruder with very close approaches. The subjects' propensity to spend more time farther away from a frequency-matching intruder (Fig. 3a) may indicate an aversive response strategy, consistent with the idea that matching is a threatening signal. We suggest that the tool of interactive playback has allowed researchers to test more threatening playback stimuli, and that the four singing strategies in our playback design represent a small scale of variation at the very aggressive end of the continuum. Future playback studies may clarify the relationship between signal threat, aversive response and the distance between vocal contestants.

Male black-capped chickadees have only a single song type, which they vary by transposing across a continuous frequency range (Horn et al. 1992). Despite the unusual nature of this song system, frequency matching appears to be an important feature in other species' song systems. Like black-capped chickadees, stripe-breasted wrens, *Thryothorus thoracicus*, appear to have a continuous frequency range of tonal songs that they frequency-match with neighbours during aggressive contests, although they also have a repertoire of formalized song types that they use in vocal duets with sexual partners (D. J. Mennill, personal observation). Male Kentucky warblers, *Oporornis formosus*, adjust the energy within their single-song repertoire in order to match the frequency of playback songs (Morton & Young 1986). Male Harris' sparrows, *Zonotrichia querula*, have small repertoires, but will match the frequency of playback songs with the song type that matches the playback frequency most closely (Shackleton et al. 1991). Nightingales have enormous repertoires, yet frequency matching using the whistled portion of the nightingale repertoire appears to have special signal value (Naguib et al. 2002). Interactive playback involving matching and nonmatching treatments in these and other systems is an important tool for testing the generality of the patterns we describe here.

Taken together, male responses to all four interactive playback treatments suggest that overlapping and frequency matching convey information independently, where overlapping and matching produce separate effects on male song performance and male behaviour, respectively. Otter et al. (2001) suggested that frequency matching and temporal matching represent a hierarchy of aggressive signals akin to the nonmatching/repertoire matching/type matching system seen in song sparrows, *Melospiza melodia*, and banded wrens, *Thryothorus pleurostictus* (Burt et al. 2001; Molles & Vehrencamp 2001). Alternatively, the degree of temporal matching may constitute one graded system of directed aggression, whereas the degree of frequency matching may constitute another system of directed aggression (particularly in light of the information on distances of closest approach highlighted above; Shackleton & Ratcliffe 1994). Our data suggest that pattern-specific and time-specific signals are distinct functional components of vocal interactions.

Remarkably few playback investigations control for variation in subject quality. In black-capped chickadees, winter dominance rank serves as a proxy for male quality; although both high- and low-ranking males often attract partners and defend breeding territories, females prefer dominant males as social partners (Ramsay et al. 2000) and extrapair copulation partners (Smith 1988; Otter et al. 1998). By involving males of both high and low social status in each playback treatment, we found support for the prediction that dominance and subordinance roles influence male responses to territorial intruders. High-ranking males engaged in song contests at greater distances from the simulated intruder and showed less agitated responses than low-ranking males, regardless of the intruder's singing strategy. High-ranking males may be provoked less by a simulated intruder, or they may try to minimize the costs associated with intense response. Alternatively, we suggest that the individuals listening to male song contests form an audience that has different expectations for the performance of high-ranking and low-ranking males. For black-capped chickadees, low-ranking males are more likely to be divorced by females (Ramsay et al. 2000) and more likely to be cuckolded (Smith 1988; Otter et al. 1998) in favour of high-ranking males. Therefore, it may benefit low-ranking males to engage all territorial intruders to protect their territory tenure and their partnership. High-ranking male chickadees, on the other hand, are unlikely to be cuckolded except when they are dominated in countersinging interactions with territorial intruders (Mennill et al. 2002). Therefore, high-ranking males, who suffer a more dramatic loss as a consequence of intense song contests, may be more reluctant to engage an intruder in an intense song contest, particularly when the intruder's relative quality is unknown. More generally, individual males may differ in the prospective cost of losing a signalling interaction, which may variously influence the performance of males of different quality. Future investigations should attempt to account for variation in male quality and address the question of whether dominant individuals are identified by a propensity to engage opponents closely or to avoid engagement. Furthermore, although our experimental design is useful for testing the function of multiple interactive signals on the effect of males of various qualities, incorporation of a repeated measures design would permit separating the effects of male age or experience from the effects of male dominance or quality.

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