

Corn bunting (*Miliaria calandra*) males respond differently to alternating and overlapping playback of song

Tomasz S. Osiejuk · Katarzyna Ratyńska ·
Jakub P. Cygan

Received: 25 January 2006 / Accepted: 3 July 2006 / Published online: 29 July 2006
© Japan Ethological Society and Springer-Verlag 2006

Abstract Interactive playback experiments were used to study the signal value to the corn bunting, *Miliaria calandra*, of alternating and overlapping singing. We subjected 15 males to two stimuli that differed in the temporal pattern of song playback (alternating or overlapping). We measured eight characteristics of the males' response in two categories—song output and movements. Overlapping and alternating playback elicited a similar song response, characteristic of highly aroused males. Song response correlated positively with males' singing activity before playback, irrespective of stimulus. There were significant differences between latency of approach to the loudspeaker and number of flights. Birds approached the loudspeaker more quickly and spent more time close to it when playback alternated with their songs. The results suggest overlapping song could be interpreted as a stronger threat but elicits a more cautious, rather than stronger, response than the alternating pattern. Males were found to shorten songs during the playback compared with songs sung before and after stimulation. The only predictor of degree of song shortening was

song activity before the playback began. It should, therefore, be regarded as a signal which is related to escalated, close-distance counter-singing.

Keywords Overlapping singing · Aggressive behaviour · Interactive playback · Corn bunting

Introduction

Territorial neighbours of many songbird species occur within hearing range of others and constitute a communication network, the members of which have numerous possibilities of gaining information (McGregor and Dabelsteen 1996; Otter et al. 1999). Neighbouring males often interact by counter-singing, in which birds sing in response to the singing of neighbours, so that their song sequences are temporally related (Hyman 2003; Mennill and Vehrencamp 2005). Such dyadic interaction may be characterized by a variety of patterns reflecting specific song-type repertoire usage (e.g. song-type matching—Beecher et al. 2000) or specific temporal relationships (e.g. overlapping singing—Naguib 1999), and are affected by such factors as amplitude or signal degradation, which modify song recognition and sender location (Naguib et al. 2000; Todt and Naguib 2000). Temporal patterning of song sequences (overlapping, alternating, etc.) seems to be a relatively simple strategy, because it could be applied even without any repertoire variation. Consequently, such a mutually dependent temporal patterning of song might be particularly important in species with a small repertoire size, for which more sophisticated systems of counter-singing are unavailable. This applies, for example, to the corn bunting

T. S. Osiejuk (✉) · K. Ratyńska · J. P. Cygan
Department of Behavioural Ecology, Adam Mickiewicz
University, Umultowska 89, 61-614 Poznań, Poland
e-mail: t.s.osiejuk@life.pl

K. Ratyńska
e-mail: kasiiek@amu.edu.pl

J. P. Cygan
e-mail: jpcygan@wp.pl

(*Miliaria calandra*). Males of this species have a very small song type repertoire and share song types within local populations. All or most of the males within a so-called local dialect usually sing the same 2–3 song types (McGregor 1980; McGregor and Thompson 1988; Latruffe et al. 2000; Olinkiewicz and Osiejuk 2003; Osiejuk and Ratyńska 2003). There is no evidence that corn buntings use song types in a way resembling song matching, which seems to be logical for species with such a small repertoire (Cramp and Perrins 1994). Corn bunting males may, however, still communicate aggression and grade the signal by changing song rate or shortening song strophes (Ratyńska 2001; Olinkiewicz and Osiejuk 2003). Our observations suggest that males in highly aggressive situations simultaneously increase song rate, shorten song strophes, and fly toward the rival. One of the results of such behaviour is that the songs of the intruder may be overlapped by songs of the territory owner. Such overlapping or alternating of songs of neighbours or trespassers could, at least theoretically, be a strategy of interaction with rivals, useful both in grading and directing signal. Although the possibility of studying dynamic communication in birds by using interactive playback design was suggested more than 10 years ago, surprisingly little research has been conducted on the function of overlapping singing (Dabelsteen and McGregor 1996). Most studies in this field have been concerned with the signal value of alternating and overlapping singing in the great tit (*Parus major*), European robin (*Erithacus rubecula*), and nightingale (*Luscinia megarhynchos*) (Dabelsteen et al. 1996, 1997; Naguib 1999; Otter et al. 1999; Langemann et al. 2000). The results of these studies have revealed that overlapping singing is important in close-range escalated aggressive encounters whereas alternating singing functions better as a long-range signal (Brindley 1991; McGregor et al. 1992). Mennill and Ratcliffe (2004) recently showed that overlapping singing in black-capped chickadees (*Poecile atricapillus*) is a threatening signal with different consequences for opponent behaviour than choice of the song type and time of song delivery. Our experiments with the yellowhammer (*Emberiza citrinella*) have revealed that overlapping singing does not necessarily generate a stronger response, but may delay it (Osiejuk et al. 2004). For this species we found some differences in responses to alternating and overlapping playback, which suggest that overlapping singing may reduce the receiver's ability to detect and locate the source of the signal quickly.

The purpose of this study was to investigate the effect of experimental overlapping and alternating of the

songs of the corn bunting males in a simulated situation of close-range territory intrusion. We focussed on such overall measures of males' response to playback as song rate, flight, and staying close to the loudspeaker. We also looked for changes in the duration of songs sung by the birds tested. Although corn buntings are known to shorten length of strophes, the context and possible functions of this behaviour is poorly understood (Ratyńska 2001; Osiejuk and Ratyńska 2003). The study is part of wider research with the objective of comparing song overlapping in closely related bunting species.

Methods

Study area and subjects

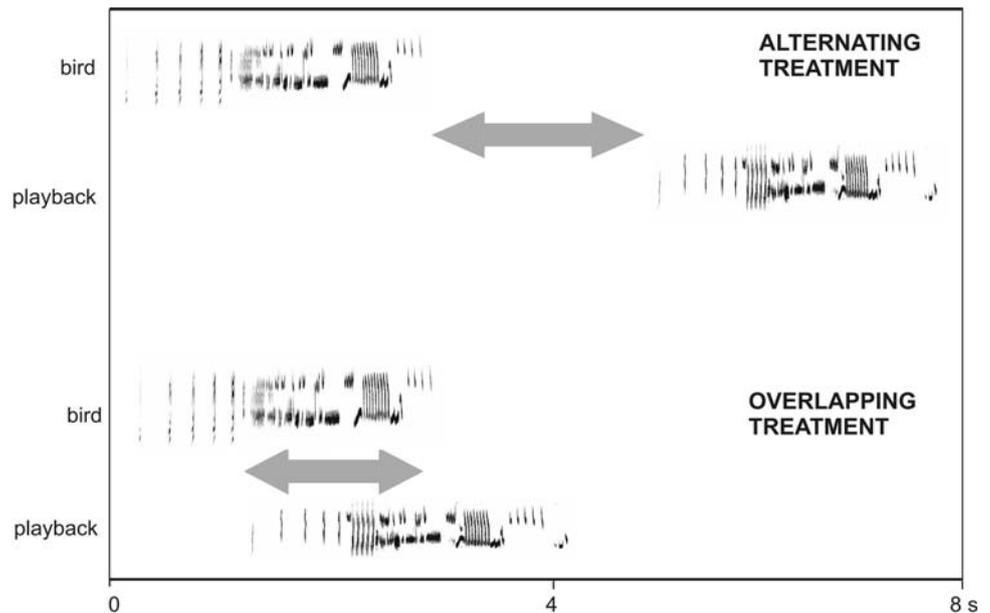
The study was conducted in open habitats located south of the city of Poznań in the Wielkopolska National Park and its vicinity (W Poland, coordinates of the centre of the study area: 52°17'N, 16°56'E). The study area is typical of this region of Poland, dominated by farmland with a mosaic of fields, meadows, and wasteland. Corn buntings are common, breeding preferentially along roads, power lines, or alleys surrounded by mosaic farmland; they tend to occur in clusters (Osiejuk and Ratyńska 2003). For the experiments we randomly selected 15 males with two dominant song-types, A and B, from a local dialect area (Fig. 1). The population studied and its song are described in more detail elsewhere (Osiejuk and Ratyńska 2003).

Playback equipment and test songs

For the playback experiments we used a Toshiba Tecra 8000 notebook computer with a 16-bit sound card and wireless HAMA SP433 loudspeaker (frequency range 20–20,000 Hz). Playback songs were digitized in 16 bits at a 48 kHz sampling rate. We used the Syrinx 1.1 sound-analysis program (developed by John Burt, University of Washington, Seattle, <http://www.syrinxpc.com>) to play songs interactively.

For each stimulus we used two different song-types (A and B) of a randomly chosen non-neighbour of the subject males. All the songs used were of good quality and were digitally prepared (1 kHz high-pass filter, amplified or attenuated) to match 90 dB signal pressure level (SPL) 1 m from the loudspeaker (measured with a CHY 650 sound-level meter, C-settings, fast response). The SPL value was set on the basis of the normal amplitude of corn bunting song, which had previously been measured in the field. Amplitude

Fig. 1 Schematic representation of timing of playback, in relation to the song of the tested males, for alternating and overlapping stimuli. The sonograms represent the two song-types (A and B) characteristic of the population studied



manipulation never exceeded ± 5 dB and never affected song structure. Avisoft SAS-Lab Pro 4.1 software was used to prepare playback sound samples (Specht 2002).

Playback procedure

We conducted the experiments between 25 April and 5 May in 2001 (between 05:30 and 09:30 h local time). The period of the experiment was chosen on the basis of behavioural observations, which lasted from March to July. The experiments were conducted at the time when males vigorously defended territories and were involved in the first breeding attempt. All subject males were recorded before experiments and their territories were mapped a few days before the experimental period. Before each stimulus the loudspeaker was placed in a tree or bush approximately 2.5–3 m above the ground. The place was always within the subject male's territory and at a distance of 20–30 m from his preferred song post observed during equipment settlement.

Each stimulus consisted of three stages: a 3-min baseline period (PRE), when the male's behaviour was recorded (including his vocalizations), followed by 5 min of playback (PLAY) and then 3 min of recording after playback (POST). Timing of the PRE, PLAY, and POST stages were determined on the basis of earlier preliminary experiments. The PRE stage was shorter than the PLAY stage, to reduce the risk of males leaving or stopping singing before playback started. The POST stage was only 3 min long to avoid including in the analysis any behaviour caused by non-playback factors which might occur after we

stopped playback. We had a single instance (ALT stimulus for male no. 5) in which a male stopped singing just before we started the PRE stage. As the male was observed sitting on a perch within 20 m of the loudspeaker during the whole PRE stage and then started to react to a playback like the other males, we did not remove these data from the analysis. Because we do not have song-duration data for the PRE stage and ALT stimulus for this particular male, however, we did not take him into account when testing how stimuli affected song duration.

Each subject was given two stimuli, and the time between the first and the second stimuli ranged from 1 to 3 days. During alternating playback stimuli (ALT) a song was played 2–3 s after the male finished a strophe. During overlapping playback stimuli (OVR) a song was played immediately after the male started a strophe (Fig. 1). For both stimuli the two song types (A and B) used in playback were switched in the same way: ten repetitions of song A, ten repetitions of song B, etc., which simulated the natural pattern of song-type switching. In each experiment and stimulus a different set of two song-types was used. Consequently, playback songs always belong to the same dialect as songs of the subject male.

The males' song performance was recorded into one channel on a HHb PDR1000 Professional DAT Recorder with a Telinga V Pro Science DAT parabolic microphone, while the songs played from the loudspeaker were recorded on the second channel with a Sennheiser Me 67 shotgun microphone. Data from both channels were used to test the correctness of the alternating and overlapping playback for all stimuli.

The behaviour of the males was recorded with Noldus Observer Mobile software by using a PSION Workabout logger. Responses recorded with the logger were: numbers of flights over a distance >1 m and time spent by the male at a distance <5, 5–10, 10–20 and >20 m from the loudspeaker. The start of each stimulus was synchronized on the recorder and logger by saying “start” to the microphone and simultaneous pressing the key starting the stimulus session on the logger. All experiments were performed by three people:

- 1 recording person,
- 2 logger operator, and
- 3 Syrinx software operator.

The loudspeaker was placed in a way which enabled the focal male to move toward the loudspeaker and to land on a tree, bush, rock or elevated ground at a distance less than or equal to 5 m from it. The loudspeaker was always placed in such a position that the bird did not move toward the observers, who were located approximately 20–30 m perpendicular to the straight line between the loudspeaker and the focal male at the beginning of the trial.

Preparing data for analysis

Recordings of the experiments were digitally converted into WAV files via a SPDIF cable from the HHb PDR1000 recorder to SoundBlaster Live! Platinum with 16 bit quality and 48 kHz sampling rate. Each channel was separately analysed by Avisoft SASLab Pro 4.1 software with the following settings: 1,024 FFT-length, frame (%)=25, window=hamming, and temporal overlap=87.5%. This gave a 244 Hz bandwidth with 46 Hz frequency and 2.7 ms time resolution of sonograms used for measuring song time properties (Specht 2002). Song timing was automatically transferred to MS Excel (DDE option) then linked with data on bird locomotion saved, in the field, on the PSION logger. Finally, all behaviour categories were counted by use of Noldus Observer 3.0.

Measures of response

We extracted eight basic behavioural response variables describing the males’ response to playback (Table 1). These measures describe their response along two axes: song output and mobility (distance and flights). Each response measure was analysed separately for PLAY and POST stages. Latency of the first flight over a distance of >1 m and latency of approach

Table 1 Measures of corn bunting males’ response to playback

Abbreviation	Description
SONGS-PLAY	Number of strophes sung during the playback stage
SONGS-POST	Number of strophes sung during the post-playback stage
DIST5M-PLAY	Time spent at a distance of less than 5 m from the loudspeaker during the playback stage (s)
DIST5M-POST	Time spent in at a distance of less than 5 m from the loudspeaker during the post-playback stage (s)
FLIGHTS-PLAY	Number of flights over 1 m during playback stage
FLIGHTS-POST	Number of flights over 1 m during post-playback stage
FLIGHTS-LAT	Latency of first flight over 1 m after playback start (s)
DIST5M-LAT	Latency of male approach less than 5 m to loudspeaker (s)

to a distance of <5 m could not be assigned to the PLAY or POST stage in advance, because, at least theoretically, the male may delay such a reaction over the PLAY period. We assumed that males may also respond with calls, as was found for yellowhammers (Osiejuk and Ratyńska 2003), but this was not observed. Sonogram analysis of vocalizations performed by males during stimuli revealed that they uttered songs almost exclusively.

We have excluded from this analysis all occasions when corn buntings moved over a distance >10 m in the PRE stage. The only measure of males’ engagement in territory defence and/or self-advertisement was, therefore, the number of songs sung by males during the 3 min before playback was started (variable called later SONG-PRE).

In some analyses we used song output as song rate (SR, i.e. number of songs sung per minute) to enable easier comparison of song output before and after the stimuli. We also extracted the duration of all songs sung (SL) by each male. These data were used to test how playback affects song duration and whether different stimuli affect this differently.

Statistical approach

Because measures of reaction to playback (i.e. song and movements) are not independent of each other, principal component analysis (PCA), using a correlation matrix of $\log(x+1)$ -transformed reaction measures (Table 1), was performed to obtain a few independent compound variables describing the birds’ response more simply (McGregor 1992). We report all principal components with eigenvalues greater than 1.0. They

were subjected to varimax rotation to create interpretable combinations of the original variables. We then used repeated measures general linear models (GLM) to estimate different effects of alternating and overlapping stimuli on subject response measured as principal components. GLMs applied usually followed Grafen and Hails (2002) suggestions; we also used model notation based on this handbook.

We also tried to assess how alternating and overlapping playback affect song structure, especially song duration, which, for this species, is known to vary according to behavioural factors (Ratyńska 2001; Osiejuk and Ratyńska 2003). Effects of playback stimuli and effects of the order of playback stimuli on the subject’s song duration were therefore tested using mean song length in a repeated measure ANOVA. Similarly to Naguib (1999), we used the means for each male to avoid pseudoreplication by entering multiple measures from the same individuals in the analysis.

Statistics were calculated use of by SPSS 10 software (Norusis 2000) and Minitab 13 (Ryan and Joiner 2001). To keep type I error constant ($\alpha=0.05$) we used the Bonferroni correction if multiple tests of similar null hypotheses were conducted. *P* values are two-tailed, unless stated otherwise.

Results

Response to playback

Corn buntings respond to playback of both types. This was manifested in slightly increasing song rates calculated as songs (\pm SE) sung per minute (PRE: 5.3 \pm 0.39, PLAY: 6.1 \pm 0.34, POST: 7.3 \pm 0.46) and, especially, by flying toward and over the loudspeaker. Response to a rival (and to playback) is complex behaviour involving a variety of mutually dependent actions, for example singing, calling, flying, and chasing. We used PCA to reduce the number of variables involved in the analysis and emphasize mutual dependencies between them. PCA helps to explain how birds combine song output and mobility into one complex behaviour. Three principal components were derived by PCA from the correlation matrix of eight original variables (Table 2). All these compound variables were highly correlated with some response measures included in the analysis (Table 2). PC1 (approach latency) was strongly correlated with latency of coming close (<5 m) to the loudspeaker and with latency of the first flight toward the loudspeaker. PC1 was also negatively correlated with time spent close to the loudspeaker (especially during playback). The higher was the value of PC2

Table 2 Eigenvalues, variance explained, and weightings of the original variables in the first three principal components extracted from the eight original variables (Table 1) of the response to the playback

	Principal component		
	PC1 (response latency)	PC2 (flights and proximity)	PC3 (song output)
Eigenvalue	2.29	1.99	1.31
Percentage of variance	28.57	24.91	16.39
Cumulative %	28.57	53.49	69.88
SONG-PLAY	0.10	0.14	0.76
SONG-POST	- 0.13	- 0.36	0.68
FLIGHT-LAT	0.67	- 0.20	- 0.30
FLIGHTS-PLAY	- 0.47	0.60	0.23
FLIGHTS-POST	0.21	0.87	0.01
DIST5M-LAT	0.90	0.15	0.02
DIST5M-PLAY	- 0.80	0.14	- 0.29
DIST5M-POST	- 0.28	0.79	- 0.19

(flights and proximity), the more males flew during and after playback, and the more time they spent close to the loudspeaker after playback. PC3 (song output) correlated highly with song output both during and after playback. We expected response to playback to be affected not only by the stimulus (ALT or OVR) but also by the birds activity before the playback. The only measure of such activity was number of songs sung during the PRE stage of experiments (SONGS-PRE). In the PRE stage, males sang 16.0 \pm 1.17 strophes on average. A paired *t*-test revealed no statistically significant differences between ALT and OVR stimuli ($t_{14}=-1.932$, $P=0.074$). As the number of songs sung before the experiment (controlled for the stimulus) correlated significantly with some reaction measures (e.g. SONG-POST, $r=0.51$, $P=0.0005$) we used SONG-PRE as a covariate. Finally, we used the model: PC1+PC2+PC3=TREATMENT+MALE+SONG-PRE, with TREATMENT as a fixed factor, male as a random factor and SONG-PRE as covariate (Fig. 2). TREATMENT significantly affected PC2 only ($F_{1,14}=5.93$, $P=0.030$) whereas SONG-PRE was found to affect response of PC3, i.e. overall song output after the PRE stage ($F_{1,14}=4.83$, $P=0.047$). To summarize, when birds were subjected to the alternating stimulus they approached quickly and made more flights whereas when they were subjected to the overlapping stimulus they approached slowly and made fewer flights.

Song duration changes

We compared song duration before, during, and after playback of song with different temporal patterns

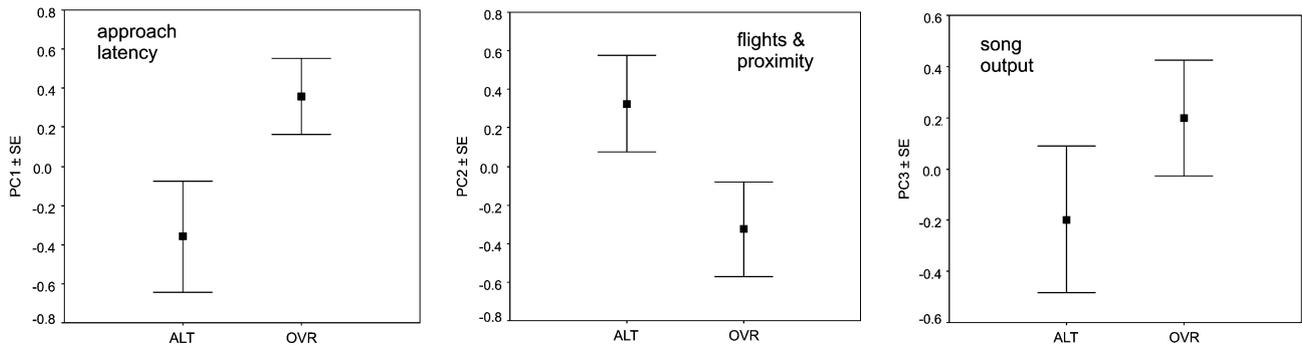


Fig. 2 Responses (mean±SE) of corn bunting males to alternating and overlapping stimuli measured by three principal components: PC1 (approach latency), PC2 (flights and proximity), and PC3 (song response)

(ALT or OVR). We found that males sang shortened songs during playback of the overlapping stimulus (Fig. 3). The repeated-measures ANOVA revealed a close to significant effect of playback stimuli ($F_{1,13}=4.29, P=0.059$), and insignificant effects of the order of stimuli ($F_{1,13}=0.28, P=0.607$) or the interaction between playback stimulus and order of stimulus ($F_{1,13}=0.82, P=0.383$) on the duration of subjects' songs during the PLAY stage of experiments.

We calculated an index of relative song duration (RSD) by dividing mean song duration during the PLAY stage by mean duration of songs during the PRE stage. Values of this index <1 indicate that male shorten their songs during response to playback, in comparison with the songs sung before playback. In general, the more a male sang before the experiment, the shorter were his songs during a playback (Fig. 4). RSD was clearly related to the singing activity before the playback. The correlation between RSD and SONG-PRE was significant only for the OVR stimulus

($r=-0.62, N=15, P=0.013$), not for the ALT stimulus ($r=-0.43, N=14, P=0.125$). The linear stepwise regression model ($RSD=SONG-PRE+PC1+PC2+PC3+TREATMENT$) revealed that the only good predictor of relative song length is SONG-PRE ($\beta=-0.572, t=-3.621, P=0.001$). We did not find significant differences between RSD for ALT and OVR stimuli (paired t -test, $t_{14}=1.22, P=0.243$).

Discussion

We found significant differences between responses of territorial corn bunting males to overlapping and alternating playback. When songs of subject males were alternated in playback, birds approached the

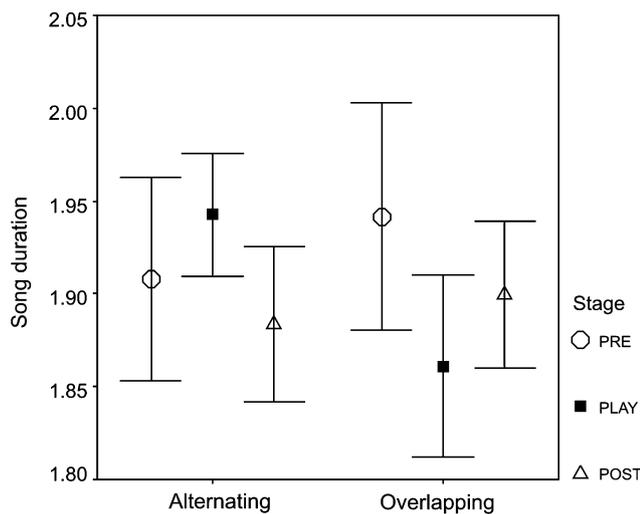


Fig. 3 Mean (±SE) duration (s) of corn bunting males' song at different stages (PRE, PLAY, POST) of experiments with alternating and overlapping playback pattern

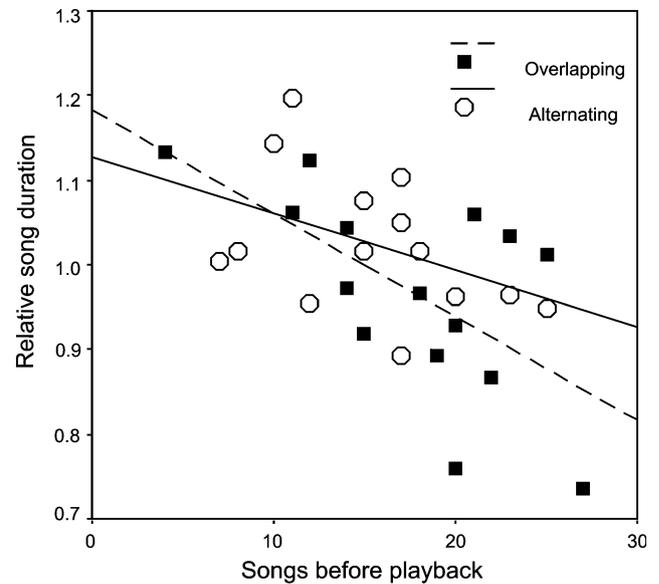


Fig. 4 Scatter plot of relationships between the number of songs sung before the playback (SONGS-PRE) and relative song duration ($Y=1$ indicates no change in mean song duration between PRE and PLAY stage of the experiment). Different symbols indicate points (and regression lines) for overlapping and alternating stimuli

loudspeaker faster, spent more time close to it, and flew more frequently. We found no significant difference between song output after the two stimuli. After both the males increased song rate in PLAY and POST in comparison with the PRE stage. So, the essential differences between reaction to alternating and overlapping playback was apparent from movements rather than the song output. Song output during and after playback also correlated positively and significantly with song activity before trials, irrespective of stimulus. The song response of males should therefore linked with their initial state before each trial. Consequently, males' song activity should be regarded as a signal of their motivation, and possibly quality. We also found that playback affected song length and that shortening songs was more emphasized during overlapping stimulus.

These findings seem to refute the hypothesis that overlapping singing is a stronger threat than alternating singing (Naguib 1999; Todt and Naguib 2000). If overlapping pattern is regarded as a stronger threat signal than alternating pattern, one may expect overlapping playback to elicit a stronger response. This is only one possibility, however, because a stronger threat signal may elicit a more cautious response, or a response which depends more strongly on the motivation of a particular male (Langemann et al. 2000; McGregor and Peake 2000). The results we obtained suggest that males interacted vocally with playback irrespective of stimulus (ALT or OVR) but that the stimulus affected their willingness to approach and locate a rival. After the ALT stimulus, males were observed flying toward the loudspeaker relatively quickly, staying there for a longer time and continuously responding to the songs played back. This pattern, in general, typifies cautious (or aversive) response to an apparently aggressive intruder and may also reflect variation of males' willingness to escalate. The results obtained suggest that it is easier for the bird to make the decision where to fly when song broadcast from the loudspeaker did not overlap the subject male's strophes. This is supported by observations of faster approach, staying longer close to the loudspeaker, and an increased number of flights toward or over the loudspeaker, frequently starting just after a song was played back. When subjected to the overlapping stimulus the birds delayed movement reaction but still sang a lot. These results are consistent with our earlier experiments on the yellowhammer (Osiejuk et al. 2004), and suggest that in a dyadic interaction simulating territorial intrusion males try to locate the sender, and that overlapping singing may hinder rapid location. This significantly longer latency in response

could be regarded as a result of difficulties in detecting and/or locating the rival (Naguib 1996; Todt and Naguib 2000). Consequently, the overlapping singing could be a signal that delays or hinders the response of the receiver, rather than a signal of a stronger threat in the sense of generating a stronger response (measured as song output or number of flights). Brumm and Todt (2003) recently showed that nightingale males adjusted their vocal response to playback depending on awareness of the position of the emitted signal.

It is possible there is no disagreement between the "cautious response" and "detection/localization difficulty" hypotheses. Difficulties in detection or/and localization (or, more generally, assessment of the signal) may be a mechanism and "cautious response" an outcome. The crucial question is: are males more cautious when their song is overlapped because they attempt to adjust to the hard-to-manage signal or because they are simply misled by this signal and their reaction is malfunctioning? Although only being cautious is advantageous to the receiver, one may imagine a range of reactions to overlapping song pattern from being unable to chase the rival to managing to hold him off. Placing a rival in a situation which reduces the probability of a stronger response may be advantageous to the sender (Vehrencamp 2000), especially if vocal interactions can be heard by potential mates or other rivals (Otter et al. 1999; Mennill et al. 2002; Peake et al. 2001, 2002).

This interpretation agrees well with the assessment/management approach of Owings and Morton (1998), because overlapping singing enables the sender to manage the behaviour of the receiver in a way which is potentially disadvantageous for the receiver. In other words, corn buntings seem to be able to adjust their response more rapidly when their song is not overlapped by playback (rival).

We also considered the possibility that response strength depends not only on the intruder's behaviour but also on the receiver's current status. Møller (1988, 1991) found that singing activity might be an honest measure of the male's quality or territory/female defence capability. One may, therefore, expect a correlation between the male's singing activity and strength of repelling intruders. We found a significant relationship between song activity of corn buntings before playback and response strength measured as song output after playback. Our results suggest that song rate in corn buntings may be an honest demonstration of aggressive motivation or willingness to defend a territory (Vehrencamp 2000). Corn buntings sing for a very long time during the season (February to August in W. Poland) but the singing activity peaks

in late March and early April—the time of strongest territorial contest (Cramp and Perrins 1994; Olinkiewicz and Osiejuk 2003). If singing activity is an honest advertisement of the male's willingness to fight, then intensively singing males should be more successful at defending resources. The probable cost of honest signalling here is vulnerability to receiver attack or rival retaliation (Vehrencamp 2000). Corn bunting males often attack conspecific intruders throughout the territorial period whereas in the peak period most attacks are directed at intruding neighbours (Cramp and Perrins 1994) and number of neighbours affects song output throughout the season (Olinkiewicz and Osiejuk 2003). Elevated song output may be useful in discouraging a neighbour from fighting physically. This result contradicts our findings for the yellowhammer, which was found to behave otherwise. Males of this bunting species strongly responded to playback, irrespective of prior singing activity (Osiejuk et al. 2004). This difference could be explained by different proximate functions of singing. Corn buntings sing mainly to defend their territories, do not have any particular mate-guarding behaviour, and extra-pair copulations are rarely successful (Cramp and Perrins 1994; Osiejuk and Ratyńska 2003; Olinkiewicz and Osiejuk 2003). Yellowhammers sing to repel rivals, especially when the female is fertile (Møller 1988, 1991; Osiejuk et al. 2004). In the last circumstance there is no time for negotiation and the response should be strong and immediate.

Song rate is only one of the possible song variables which could be affected by a rival during counter-singing. In many bird species with short songs, including corn buntings, song rate is mainly an effect of how long inter-song intervals are, because song duration is relatively invariant when compared with inter-song intervals. On the other hand, changes of song duration per se may have informative value. Corn bunting, yellowhammer and ortolan bunting (*Emberiza hortulana*) males may change song length according to the actual context of singing (Hansen 1981; Osiejuk 2001; Osiejuk and Ratyńska 2003; Rutkowska-Guz and Osiejuk 2004). In this study we observed a quite clear pattern of song duration changes. Males shorten their song during the playback, in comparison with the PRE and POST stage. More actively singing birds, i.e. highly motivated before the playback, tended to shorten their songs more after the playback began. Shortening was also more conspicuous when overlapping playback was conducted. Our results indicate that shortening of song in the corn bunting is related to the more aggressive context of counter-singing which, in general, confirms our earlier suggestion that varying song length is

informative in this species and that shortening song is an aggressive signal (Ratyńska 2001; Osiejuk and Ratyńska 2003). Similar results were recently obtained for the banded wren (*Thryothorus pleurostictus*) (Hall et al. 2006), i.e. males shortened song duration when their songs were overlapped by playback. The results we obtained suggest also that an overlapping pattern may be regarded as some kind of disruptive signal. We found that although shortening was more emphasized in an overlapping context, the extent of shortening depends principally on birds' singing activity before playback. Song shortening was apparent only during the PLAY stage whereas increased male song rate and flight activity was still observed after the playback. This suggests that singing of shortened songs by the corn bunting is a signal which should be regarded as partly independent of song rate and related to escalated, close-distance counter-singing.

Our experiment sheds more light on the signal value of overlapping compared with alternating song pattern. Especially, we want to point out that some earlier studies also contradict the common opinion that overlapping singing has a higher threat signal value, which generates a stronger response in the sense of eliciting more songs or flights. Dabelsteen et al. (1996) in experiments with great tits found that only males reply to overlapping playback with significantly greater variation of response measures. Yellowhammers respond with similar strength to both alternating and overlapping stimuli (Osiejuk et al. 2004). Males of the banded wren tended to approach the speaker more closely and to stay closer for longer during alternating stimuli if they experienced it first than if they had been overlapped first (Hall et al. 2006). Studies on more continuous singers gave more unequivocal results. For example, European robin males alternate or overlap songs depending on the distance between counter-singing males (Brindley 1991). In that species, both alternating and overlapping singing is a way of deterring the intended receiver, but the last pattern elicits a stronger response, characteristic of highly aroused males (Dabelsteen et al. 1997). Experiments with nightingales revealed that males exposed to an overlapping song respond stronger to playback (Naguib 1999; Naguib et al. 1999).

We are, certainly, still far away from generalization about the function(s) of alternating/overlapping singing in birds. One reason is the insufficient number of experimental studies conducted on this topic (Dabelsteen et al. 1996, 1997; Naguib 1999; Osiejuk et al. 2004; Mennill and Ratcliffe 2004; Hall et al. 2006). In our opinion, studies on following species may not resolve the problem quickly but then show that response to

alternate and overlapped songs may be even more variable among species than we expect. We need a more general approach to analyse the time patterning of song output; this requires knowledge not only about signaller and receiver, but also on:

- 1 the other individuals (both males and females) within the communication network, and
- 2 effects of being overlapped on the receiver auditory system (including at brain level) and relationships between own song output and perception of rival's song.

Acknowledgments We are grateful to Michelle Hall, Piotr Tryjanowski, and anonymous reviewers for critical remarks on the manuscript. TSO is truly indebted to Sandra Vehrencamp, Michelle Hall, and Thorsten Balsby for their invaluable help during his stay at Cornell Lab of Ornithology. We thank John Burt for allowing us to use his software Syrinx to perform interactive playback experiments. The scholarship to TSO was funded by the Foundation for Polish Science. This research was funded by the Polish State Committee for Scientific Research (KBN grant no. 6 P04C 038 17 to TSO).

References

- Beecher MD, Campbell SE, Burt JM, Hill CE, Nordby JC (2000) Song-type matching between neighbouring song sparrows. *Anim Behav* 59:21–27
- Brindley EL (1991) Response of European robins to playback of song: neighbour recognition and overlapping. *Anim Behav* 41:503–512
- Brumm H, Todt D (2003) Facing the rival: directional singing behaviour in nightingales. *Behaviour* 140:43–53
- Cramp S, Perrins CM (1994) Handbook of the birds of Europe, the Middle East and North Africa. Vol. IX buntings and New World Warblers. Oxford University Press, Oxford
- Dabelsteen T, McGregor PK (1996) Dynamic acoustic communication and interactive playback. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication. Cornell University Press, Ithaca and London, pp 398–408
- Dabelsteen T, McGregor PK, Shepherd M, Whittaker X, Pedersen SB (1996) Is the signal value of overlapping different from that of alternating during matched singing in Great Tits? *J Avian Biol* 27:189–194
- Dabelsteen T, McGregor PK, Holland J, Tobias JA, Pedersen SB (1997) The signal function of overlapping singing in male robins. *Anim Behav* 53:249–256
- Grafen A, Hails R (2002) Modern statistics for the life sciences. Oxford University Press, Oxford
- Hall ML, Illes A, Vehrencamp SL (2006) Overlapping signals in banded wrens: long-term effects of prior experience on males and females. *Behav Ecol* 17:260–269
- Hansen P (1981) Coordinated singing in neighbouring yellowhammers (*Emberiza citrinella*). *Natura Jutlandica* 19:121–138
- Hyman J (2003) Countersinging as a signal of aggression in a territorial songbird. *Anim Behav* 65:1179–1185
- Langemann U, Tavares JP, Peake TM, McGregor PK (2000) Response of great tits to escalating patterns of playback. *Behaviour* 137:451–471
- Latruffe C, McGregor PK, Tavares JP, Mota PG (2000) Microgeographic variation in corn bunting (*Miliaria calandra*) song: quantitative and discrimination aspects. *Behaviour* 137:1241–1255
- McGregor PK (1980) Song dialects in the corn bunting (*Emberiza calandra*). *Z Tierpsychol* 54:285–297
- McGregor PK (1992) Quantifying response to playback: one, many, or composite multivariate measures? In: McGregor PK (eds) Playback and studies of animal communication. Plenum, New York, pp. 79–96
- McGregor PK, Dabelsteen T (1996) Communication networks. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication. Cornell University Press, Ithaca and London, pp. 409–425
- McGregor PK, Peake TM (2000) Communication networks: social environments for receiving and signalling behaviour. *Acta Ethol* 2:71–81
- McGregor PK, Thompson DBA (1988) Constancy and change in local dialects of the corn bunting. *Ornis Scand* 19:153–159
- McGregor PK, Dabelsteen T, Shepherd M, Pedersen SB (1992) The signal value of matched singing in great tits: evidence from interactive playback experiments. *Anim Behav* 43:987–998
- Mennill DJ, Ratcliffe L (2004) Overlapping and matching in the song contests of black-capped chickadees. *Anim Behav* 67:441–450
- Mennill DJ, Vehrencamp SL (2005) Sex differences in singing and duetting behavior of neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). *Auk* 122:175–186
- Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in songbirds. *Science* 296:873
- Møller AP (1988) Spatial and temporal distribution of song in the Yellowhammer *Emberiza citrinella*. *Ethology* 78:321–331
- Møller AP (1991) Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *Am Nat* 138:994–1014
- Naguib M (1996) Auditory distance estimation in song birds: implications, methodologies, and perspectives. *Behav Process* 38:163–168
- Naguib M (1999) Effects of song overlapping and alternating on nocturnally singing nightingales. *Anim Behav* 58:1061–1067
- Naguib M, Fichtel C, Todt D (1999) Nightingales respond more strongly to vocal leaders of stimulated dyadic interactions. *Proc R Soc Lond B Biol Sci* 266:537–542
- Naguib M, Klump G, Hillmann H, Griebmann B, Teige T (2000) Assessment of auditory distance in a territorial song bird: accurate feat or rule of thumb? *Anim Behav* 59:715–721
- Norušis MJ (2000) SPSS 10.0 guide to data analysis. Prentice-Hall, Englewood Cliffs, NJ
- Olinkiewicz A, Osiejuk T S (2003) Effect of season time and neighbours on singing activity of corn bunting *Miliaria calandra*. *Acta Ornithol* 38:117–122
- Osiejuk TS (2001) Repertoire and temporal organization of song bouts in the Yellowhammer (*Emberiza citrinella*) from Western Poland. In: Tryjanowski P, Osiejuk TS, Kupczyk M (eds) Bunting studies in Europe. Bogucki Wydawnictwo Naukowe, Poznan, pp 71–79
- Osiejuk TS, Ratyńska K (2003) Song repertoire and microgeographic variation in song types distribution in the corn bunting *Miliaria calandra* from Poland. *Folia Zool* 52:275–286
- Osiejuk TS, Ratyńska K, Cygan JP (2004) Signal value of alternating and overlapping singing in Yellowhammer *Emberiza citrinella*. *J Ethol* 22:55–61
- Otter K, McGregor PK, Terry AMR, Burford FRL, Dabelsteen T (1999) Do female great tits (*Parus major*) assess males by

- eavesdropping? A field study using interactive song playback. *Proc R Soc Lond B Biol Sci* 266:1305–1309
- Owings DH, Morton ES (1998) *Animal vocal communication: a new approach*. Cambridge University Press, Cambridge
- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2001) Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proc R Soc Lond B Biol Sci* 268:1183–1187
- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2002) Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proc R Soc Lond B Biol Sci* 269:1925–1929
- Ratyńska K (2001) Temporal variation and song structure in corn bunting (*Miliaria calandra*). M.Sc. thesis, Adam Mickiewicz University
- Rutkowska-Guz JM, Osiejuk TS (2004) Song structure and variation in yellowhammers *Emberiza citrinella* from western Poland. *Pol J Ecol* 52:327–339
- Ryan BF, Joiner BL (2001) *Minitab handbook*, 4th edn. Pacific Grove, Duxbury
- Specht R (2002) *Avisoft-SASLab Pro Sound Analysis and Synthesis Laboratory*. A PC-software for MS-Windows 95/98/ME/NT/2000/XP. Berlin
- Todt D, Naguib M (2000) Vocal interactions in birds: the use of song as a model in communication. *Adv Stud Behav* 29:247–295
- Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (eds) *Animal signals: signalling and signal design in animal communication*. Tapir Academic Press, Trondheim, pp 277–300