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Effect of time of season and neighbours on singing activity in the Corn Bunting *Miliaria calandra*

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Abstract. The seasonal pattern of singing activity was studied in the Poznań region, W Poland. Males sang from mid-March till late July with a song rate varying between 3.2 and 11.1 songs/min. Song activity peaked at the beginning of the breeding season, in late March and April. In following months males also sang at quite a high rate, but the probability of finding a singing male within the territory was lower. Males sang mainly from tree tops and power lines at a height between 8 and 10 m. Males with larger numbers of neighbours had a significantly lower mean song rate than those with a single neighbour. Most probably, males with more neighbours had to spend more time on more active and direct territorial defence, and/or listening to the song of other males. The pattern we found suggests that song is mainly used in territorial defence against rivals, and that it is used as a first line of defence. Nevertheless, this does not preclude its usefulness for attracting a mate.

Key words: Corn Bunting, *Miliaria calandra*, song rate, seasonal pattern, territoriality

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INTRODUCTION

The main functions of bird song are to attract females and/or to deter rivals (Catchpole & Slater 1995). These functions are not mutually exclusive and might be accomplished by several patterns of song organisation in time and space (Kroodsma & Byers 1991). One of the simplest but very efficient ways of grading acoustic signals, is a modification of singing activity, which is usually demonstrated as song rate changes (number of song strophes produced per time unit). The seasonal cycle of singing activity was found to be one of the most characteristic features, which clearly differs between species singing mainly to attract females or to deter rivals (e.g., Catchpole 1973, Krebs et al. 1981, Osiejuk & Kuczyński 2000). We may expect that the temporal changes in singing activity may differ also within species, as individuals varying in condition and other traits should put more or less effort into singing, depending on their status and behaviour of other individuals (Vehrencamp 2001).

The Corn Bunting *Miliaria calandra* seems to be an ideal species for studying song rate differentiation. The Corn Bunting is a discontinuous singer with a very small song repertoire (typically 2–3 song types) and is characterized by a mosaic pattern of geographical variation, reflected in the formation of so-called “local dialects”. In such a pattern, each male within a local dialect population sings only few (usually two) song types characteristic of the population (McGregor 1980, 1986, Holland et al. 1996, Latruffe et al. 2000, Osiejuk & Ratyńska 2003). Therefore, the Corn Bunting has a very limited “arsenal” of acoustic tools for male-male interaction. Males may differentiate song output by switching between different song types from their own repertoire, may sing shortened versions of full song phrases, but first of all may change song rate (Ratyńska 2001, Osiejuk & Ratyńska 2003). It has been shown that Corn Bunting males tend to shorten song phrases and inter-song intervals in aggressive contexts, e.g. when counter-singing with a rival or when

a floater approaches (Ratyńska 2001, Osiejuk et al. in press). Such behaviour escalates song rate and highly aroused Corn Buntings may sing very short song phrases almost without breaks (Cramp & Perrins 1994, Ratyńska 2001). Territories in this species are usually clumped and males often hear songs of several neighbours simultaneously, which results in frequent aggressive interaction, like flights, chasing, etc. This is probably intensified also by living in open farmland habitats, where effective territory defence requires perpetual presence (visual or acoustic) of owners (Møller 1986).

The main aim of this study was to describe the seasonal pattern of singing activity of Corn Buntings from a local population singing the same dialect and also to test how the number of conspecific neighbours affects the singing activity.

STUDY AREA AND METHODS

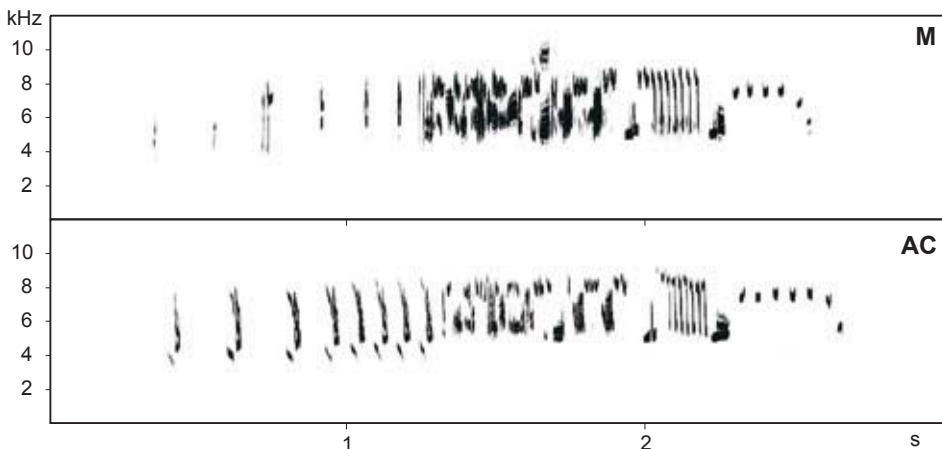
Study area and population

The study was carried out in typical farmland habitats (fields and wastelands) located west of the city of Poznań, between Tulce and Dachowa villages (W Poland, coordinates of the centre of the study area: 52°18'N, 17°13'E). The studied birds belong to one local dialect, so all males sang the same two song types (M and AC) with different structure of the first part of strophes and with similar end parts (Fig. 1). A detailed analysis of song variation of this and neighbouring populations was presented elsewhere (Osiejuk & Ratyńska 2003).

Observations and data analysis

From mid-March till end of July 2001, we made regular censuses in 10-day intervals (in total, 14 times), by walking through all territories in early morning after sunrise. We did censuses as regularly as possible, but exceptionally in case of rain or strong wind we were forced to do censuses on the following day with good weather. Birds were monitored before the first census, which date was fixed based on changes in males behaviour (cease of flocking and onset of singing within territories). Also the end of censusing was connected with end of territorial behaviour within studied population. During a 10-min period spent in each territory, we recorded: 1) whether the male sang, 2) number of songs uttered, 3) song post details (place, height), 4) other behaviour of the subject male (flights, dangling legs flights, etc.), and 5) behaviour of its nearest neighbours. We gathered data for randomly selected 23 males. The total number of males in the studied population was about 40. Censuses were started randomly from different part of the study area to avoid any systematic bias in gathering data. All observed males were recorded at least once on a tape-recorder to check their song repertoire and dialect membership (Osiejuk & Ratyńska 2003).

We used three basic variables for describing the song activity of Corn Bunting males: 1) the fraction of males singing during each census; 2) the mean song rate SR1 (songs/min) during a census based on songs counting for males, which were found to sing during the census; 3) the mean song rate SR2 (songs/min) for all males. In the case of variable SR2, for males that were not sing-



ing during the 10-min census, we assigned song rate zero. Thus SR2 depended not only on how intensively the observed males sang, but also on how many males were found to sing. All means are presented with standard error (\pm SE).

RESULTS

Corn Bunting males started singing regularly in mid-March. Before that time, singing males were also observed, but they formed small flocks, and did not behave territorially. The fraction of singing males was the highest throughout April. In that month, up to 70% (maximum $n = 16$) of all males were found to sing during a census (Fig. 2). The fraction of males singing was also quite high in March and May, but decreased markedly in June and, especially, in July. During the last census only two males were found to sing.

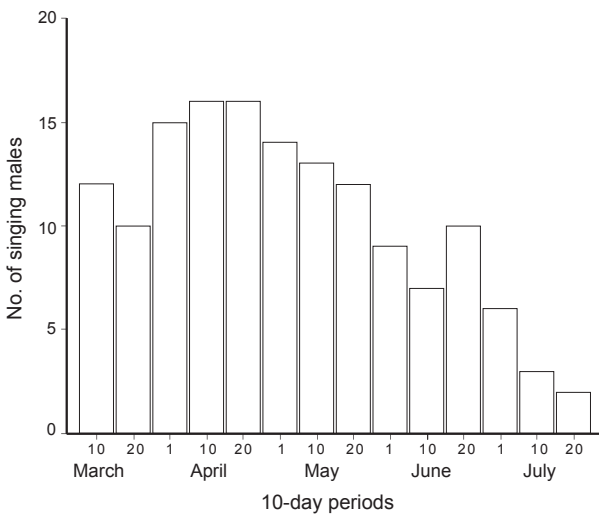


Fig. 2. Seasonal song activity of Corn Bunting measured as the number of males singing in the study area.

The mean song rate SR1 was the highest in March and early April (nearly or over 7 songs/min, Fig. 3). Later on, SR1 fluctuated around 5–6 songs/min, except for the last census, when it decreased below 4 songs/min. We found that SR1 varied significantly between males ($F_{22,109} = 2.91$, $p < 0.001$) and 10-day periods ($F_{13,109} = 7.94$, $p < 0.001$). SR1 ranged from 3.2 to 11.1 songs/min, and the average was 6.2 ± 0.15 ($n = 145$). It significantly decreased during the breeding season ($\beta = -0.474$, $r^2 = 0.22$, $t = -6.436$, $p < 0.001$).

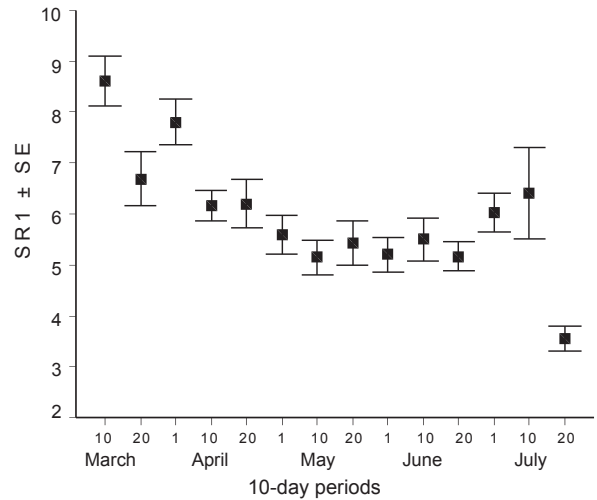


Fig. 3. Seasonal song rate changes of Corn Buntings studied. SR1 — song rate (songs/min) of singing during censuses.

The mean song rate (SR2) varied between 0 and 11.1 songs/min, and the average was 2.8 ± 0.18 ($n = 322$). We can extract more information if we take together data on males' presence and their song rate (Figs 3 and 4). The highest values of SR2 were found in April, although the mean SR1 was at that time slightly lower. This was a consequence of increased presence of singing males within territories in April. In each 10-day period of that month we found at least 15 singing males. Starting from early May, SR2 was continuously decreasing and this was mainly an effect of males' absence than of a reducing song rate.

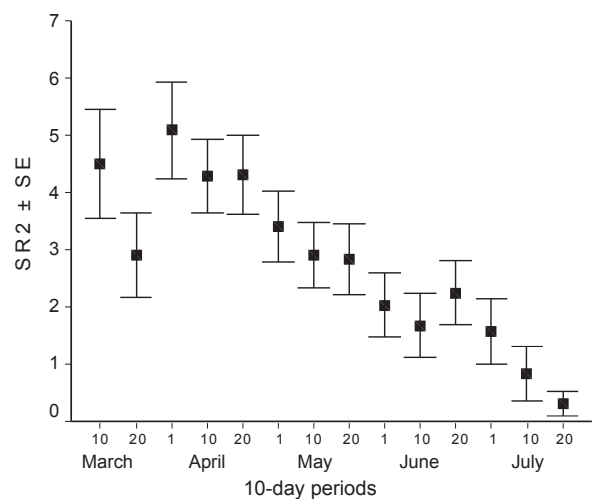


Fig. 4. Seasonal song rate changes of Corn Buntings studied. SR2 — song rate (songs/min) of all (singing and non-singing) males.

We found that males with a single neighbour had a higher song rate SR1 (6.4 ± 0.21) than males with two or more neighbours (5.8 ± 0.20). The number of neighbours significantly affected SR1 ($F_{1,145} = 5.77$, $p = 0.018$; time of the season was included in the model). If we compare song rate measured as SR2, the differences between males with a single and at least two neighbours became even more conspicuous (3.7 ± 0.29 vs. 2.1 ± 0.22). This resulted from the fact that males with a smaller number of neighbours were more frequently found to sing.

We found a very small variation in song post localisation ($n = 150$). Corn Buntings sang mainly from trees (49%) and power lines (32%). Singing from the ground (7%), bushes (6%) and other (1%) places was relatively rare. When singing from trees, birds preferred tops (72%). Song post height varied between 0 and 12 m, with an average at 7 ± 0.2 m ($n = 138$). We found that 62.4% of song posts were localised between 8 and 10 m. We found no relationships between time of season and height of song post selected by males (Kruskal-Wallis ANOVA, $\chi^2 = 8.82$, $df = 13$, $p = 0.786$).

DISCUSSION

Corn Bunting males showed a clear pattern of singing activity during the breeding season. Singing activity started in mid-March with an eruption of high-rate singing, but initially only a half of controlled males were found to sing. A high singing activity was noted in April, which coincided with the highest probability of finding a male singing. After that time, males spent less time on singing, but if they were singing, the song rate was usually quite high. This pattern is slightly different from that described by Møller (1983), who found only small seasonal changes in song activity during the period from mid-April till late July. However, he also found the highest peak of singing activity in April. Corn Buntings in the studied population have only one distinct peak of seasonal singing activity, which corresponds with the time of territory establishment and mating. On the other hand, quite a high song activity was observed till the end of June. This pattern suggests that singing in the Corn Bunting is especially important during territory establishment and is used mainly as a defence tool against rivals. However, this does not exclude using song for mate attraction. The pattern is different than that found in the Yellowhammer *Emberiza citrinella* and Ortolan Bunting *E. hortulana*, which are closely related to the Corn Bunting and live in similar habitats. Catchpole (1982) found that Yellowhammers have a peak of song production in summer (June–August), although territorial behaviour and pairing occur earlier, in spring (March–May). In general, Møller (1988) confirmed this finding and found a correlation between mate guarding and song activity within the fertile period. The pattern of song production within the breeding season is different in Ortolan Buntings. Males of this species usually cease singing after mating, but may have a second, smaller peak of singing before the second breeding attempt (T. S. Osiejuk unpubl. data.).

If the song of Corn Buntings functions as a rival deterrent, we might expect that males with a larger number of neighbours spend more time singing. By contrast, we found that males with a single neighbour were singing more actively than those with a larger number of neighbours. Males from patches with a higher density were also less frequently found to sing. The explanation of this discrepancy is quite simple. Singing in the territory with many neighbours provokes frequent aggressive interactions. Therefore, males from high-density patches more often had to cease singing, and threaten rivals more actively. This interpretation is supported by Shepherd et al. (1996), who found that Corn Bunting territories are mostly invaded by the closest neighbours. Similar results were presented by Møller (1988), showing that Yellowhammer males sang less in territories where intrusions occurred than in territories without intrusions. Also Osiejuk et al. (in press) found that simulated intrusions may not increase song rate in the Yellowhammer. An alternative explanation of the pattern we found is that males with many neighbours spend less time singing in order to listen to the singing of other males. Both suggested mechanisms may in fact work simultaneously.

Corn Bunting males are singing from exposed places (Møller 1986, Tryjanowski 2001). Usually the male has only a few main song posts within the territory, from which it sings predominantly (Osiejuk & Ratyńska 2003). Therefore, singing in this species resembles acoustic marking of a territorial space. If this space is disturbed by a rival, males may counter-sing, which is usually connected with a higher song rate and shortening of song phrases, and finally with direct aggressive behaviour (Ratyńska 2001). Hence, song in this species is only the first requirement of effective

territory defence, which must be supported by other kinds of aggressive behaviour. Effective defence against many neighbours involves especially intensive visual and acoustic observations, movements, flights and other tactile behaviour (Møller 1986).

Corn Buntings did not cease singing after territory establishment and after pairing. This suggests that song is useful throughout the breeding season. The Corn Bunting is a polygynous species, as males may pair with more than one female (Hartley et al. 1992, 1995, Hartley & Shepherd 1995, Shepherd et al. 1996). Attracting and maintaining mates may require a relatively high song output during a prolonged period. However, we cannot preclude that song is used only to protect the territory, which is a prerequisite to attract females. In polygynous species, the size and quality of territory may be especially important for female choice (Searcy & Yasukawa 1989, Hartley et al. 1995, but see also Hartley & Shepherd 1995). Importance of territory quality is supported by behaviour of Corn Bunting males in winter. High-quality territories are frequently visited by males even in January, and males try to occupy them very early (Harper 1995). Shepherd et al. (1996) suggested that living in an open habitat coincides with a high detectability of intrusions and, consequently, males may benefit more from maintaining territory in the hope of attracting more females, rather than seeking extra-pair copulations. This suggestion also supports singing primarily for territory defence.

The observed pattern of song post selection was similar to those found by Møller (1986) and Tryjanowski (2001). Corn Buntings preferred well-exposed song posts located high above ground, as they sang mainly from tree tops and power lines. Such behaviour maximizes sound transmission (Wiley & Richards 1978). Thus we do not agree with Møller (1986) that such behaviour could be linked only with female attraction. Moreover, singing from highly exposed places may be also advantageous for rival detection.

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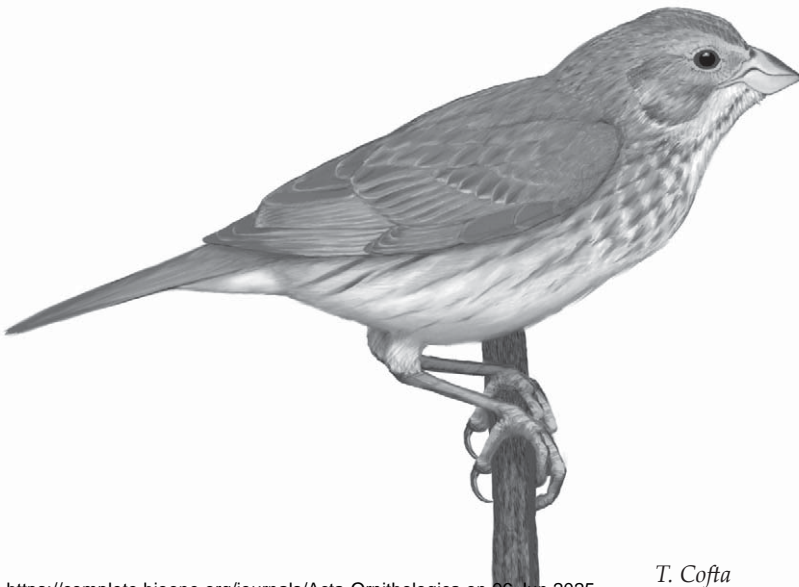
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STRESZCZENIE

[Wpływ terminu w ciągu sezonu i sąsiadujących samców na intensywność śpiewu potrzęsacza]

Badano śpiew (Fig. 1) lokalnej wielkopolskiej (okol. Poznania) populacji potrzęsacza. W okresie od marca do lipca 2001 wykonano 14 jedno- lub dwu-dniowych liczeń, w trakcie których spędzano po 10 minut w terytoriach 23 osobników. Podczas cenzusów rejestrowano intensywność śpiewu wybranego samca (liczba piosenek/min.), notowano również miejsce śpiewu i inne cechy związane z zachowaniem tego samca i jego sąsiadów. Samce śpiewały w terytoriach od poło-

wy marca do końca lipca (Fig. 2), średnia intensywność śpiewu wahała się w poszczególnych dekadach od 3.2 do 11.1 piosenek/min. (Fig. 3). Stwierdzono występowanie jednego szczytu aktywności wokalne, który miał miejsce na początku sezonu. Najwyższą intensywność śpiewu odnotowano w marcu, choć wtedy jedynie ok. połowa z wszystkich osobników była obserwowana w terytoriach. Przez cały kwiecień intensywność śpiewu była tylko nieznacznie niższa, za to ok. 70% samców śpiewało w terytoriach podczas kontroli. Po tym czasie średnia intensywność śpiewu malała sukcesywnie aż do końca sezonu (Fig. 4), choć był to w dużej mierze efekt zmniejszającej się frakcji samców śpiewających a nie spadek intensywności ich śpiewu. Stwierdzono, że samce z więcej niż jednym sąsiadem miały niższą średnią intensywność śpiewu, co jest najprawdopodobniej efektem częstszego angażowania się w bardziej bezpośrednie metody obrony terytorium (wypędzanie, przeloty demonstracyjne itp.) i/lub koniecznością spędzania relatywnie większej ilości czasu na słuchaniu potencjalnych rywali. Niniejsze wyniki wskazują, iż śpiew potrzęsacza używany jest głównie do obrony terytorium przed rywalami, ale stanowi jedynie pierwszą linię obrony, która musi być poparta innymi agresywnymi zachowaniami, szczególnie w warunkach większego zagęszczenia. Jednocześnie, nie wyklucza się, iż śpiew może odgrywać rolę w wabieniu samic, choć wydaje się, iż jest to funkcja drugorzędna.



T. Cofta