

Song repertoire and microgeographic variation in song types distribution in the corn bunting *Miliaria calandra* from Poland

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A b s t r a c t. Corn buntings in the Wielkopolska region (W Poland) show a clear local dialect pattern of microgeographic song variation only in relatively dense and stable populations, which inhabited typical farmland landscape. In less preferred habitats, where males were much more dispersed, or in sites that were colonized recently, we found no such a pattern of song type sharing. The between-individual song type variation was higher in such sites and males from such locations did not sing any common dialect. The pattern of full and shortened song variant usage was rather inconsistent. Shortened song variants were used more frequently during counter-singing than solo-singing, but some song types were shortened more often than others regardless of the context.

Key words: song variation, dialect, song variants, passerines

Introduction

Passerine songs undoubtedly play an important role in mate attraction and stimulation as well as male-male competition (C a t c h p o l e & S l a t e r 1995). As a sexually selected trait, songs vary substantially between species with respect to acoustic structure and temporal pattern. Many hypotheses involving intra- and inter-sexual selection and several putative constraints have been presented in an attempt to explain this variation (K r o o d s m a & B y e r s 1991, P o d o s 1997, G i l & G a h r 2002). Comparisons within and between species reveal that our knowledge is limited. In particular, influence of various factors on evolutionary trajectories in song complexity require investigation (K r o o d s m a & B y e r s 1991, K r o o d s m a 1996, V e h r e n c a m p 2000).

Members of the family Emberizidae have been subjects of numerous bioacoustic investigations, which have employed a wide range of methods, from simple observations (A n d r e w 1987, M ø l l e r 1983) to comparative studies (C a t c h p o l e & M c G r e g o r 1985) and advanced playback experiments (S t o d d a r d et al. 1991, B e e c h e r et al. 2000). The corn bunting *M. calandra* (L., 1758), the only representative of the genus *Miliaria* possesses many similarities to its closest relatives (i.e. *Emberiza* spp.) but diverges from them in some traits, such as sexual dimorphism, mating system and song complexity (C a t c h p o l e & M c G r e g o r 1985, G r a p u t t o et al. 2001). The corn bunting thus offer a unique opportunity to compare relationships between song and other traits within the bunting family. The most characteristic features of the corn bunting are: the polygynous mating system and sexual dimorphism expressed only in size (males are ca. 8% larger than females). The majority of well-studied *Emberiza* spp., including yellowhammer *E. citrinella*, ciril bunting *E. cirilus*, ortolan bunting *E. hortulana* and reed bunting

E. schoeniclus, are monogamous (at least socially) and have more or less distinct plumage sexual dimorphism (C a t c h p o l e & M c G r e g o r 1985, C r a m p & P e r r i n s 1994). The corn bunting seems to be clearly different from its relatives also in terms of song. Admittedly, the corn bunting is also a typical discontinuous singer with a small song repertoire (typically 2–3 song types), like many other buntings, but it 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 several song types characteristic of the population. Very few males sing song types of two dialects. Except for those unusual individuals, all song types within a local population of the corn bunting are shared (M c G r e g o r 1980, 1986, H o l l a n d et al. 1996). By contrast, other *Emberiza* buntings typically share only some song types within a local population (C a t c h p o l e & M c G r e g o r 1985, O s i e j u k et al. 2003). Unfortunately, no study has provided an unambiguous answer to the question of whether local dialects are functional (C a t c h p o l e & S l a t e r 1995). Local dialects sometimes persist over a decade, but the mechanism of their maintenance is also unknown (T r a i n e r 1983, C a t c h p o l e & S l a t e r 1995, H o l l a n d et al. 1996). In the case of the corn bunting, C z i k e l i (1982) suggested that usage of different song types is density-dependent and related to habitats occupied by the birds. However, there are no direct proofs of such a mechanism working and there are some disagreements between C z i k e l i (1982) and other authors in understanding the concept of song type and song dialect in the corn bunting (C r a m p & P e r r i n s 1994).

The main aims of this study were (1) to describe song variation of the corn bunting from Poland (no other data on this subject are available from this part of Europe), (2) compare the pattern of microgeographical song types distribution between local populations of different density, and (3) compare these data with other populations studied earlier in Europe.

Material and Methods

Study area and population

The study was carried out in three open areas located south of the city of Poznań – in the Wielkopolska National Park (Plot A) and its vicinity (Plots B and C) - (W Poland, 52°17'N, 16°56'E', Fig. 1). The study area is typical for this region of Poland, dominated by farmland with a mosaic of fields, meadows, rough ground and wasteland. Some parts of Plot A are overgrown with young oak (*Quercus* sp.), beech (*Fagus silvatica*) and birch (*Betula* sp.) trees (< 10 years, 1-3 m high). The area between plots is generally unsuitable for corn buntings (woodlands, wetlands) or for recordings (fields along a major road). Territories of corn buntings are often placed linearly and at the geographical scale chosen for the study birds generally tend to occur in clusters. Therefore, the density estimations for study plots (A - 3 males · 10 km², B - 6 males · 10 km², C - 11 males · 10 km²) are low and did not reflect real differences in distribution. These values much more depend on the size of the study area and how many aggregations were found within it. So we assigned males to one of two simple categories: (1) those with ≤ 1 neighbour, or (2) those with ≥ 2 neighbours within hearing range. Base on this assumption, we can indicate one high density population on Plot A, two on Plot B and one on Plot C (Fig. 1). There was also one crucial difference between study plots. Plot A was know to be relatively unsuitable for corn bunting, which generally avoid

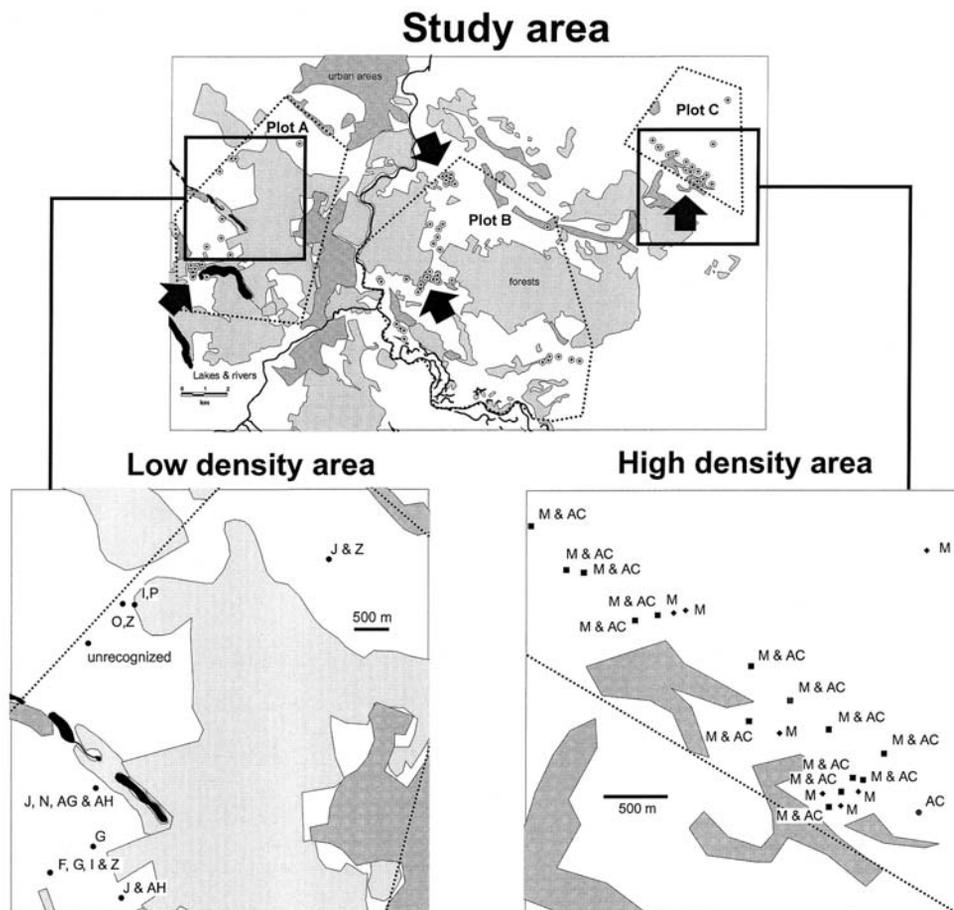


Fig. 1. Map of the study area, showing Plots A, B, C and location of male corn bunting \odot , Wielkopolska Region, Poland. Black arrows indicate area of high corn bunting density. A two examples of low and high density area are enlarged for detailed comparison of song types distribution.

forest vicinity (K u Ź n i a k 2000). Detailed census in the entire Wielkopolska NP in 1992 revealed occurrence of only five males, but subsequently the number increased to 16 in 1995 (B e d n o r z 1997). Birds from the only high density group on Plot A inhabited an area, which was overgrown by small trees and became suitable for them a few years ago (area accessible since 1991). More than five males was observed here firstly in 2000. On the other hand, local populations on Plot B and C were connected with stable agricultural or wasteland habitat, which remained unchanged for at least 20 years. These population were known to be rich and stable at least since 1996, when we started recording of other buntings in this area (O s i e j u k unpublished).

Basic methods

The study was conducted between March and June 2001. Birds were recorded in the morning (between 0500 and 1100) using a HHB PDR 1000 Professional DAT recorder with a Telinga

V Pro Science parabola, and a SONY TCD-D8 recorder with a Sennheiser ME 67 shotgun microphone. All recorded males were positioned on a map with the use of Garmin 12CX GPS with at least ± 10 m accuracy. We estimate that we recorded over 90% of males present in the field. For identification we also used recordings from playback experiments, which were conducted simultaneously and will be a subject of another paper. In sites of higher density of males, neighbours were recorded simultaneously by two observers, which also ensured that identification of different males was unequivocal. Although the birds were not marked individually, it was usually easy to identify males because each had a few permanent song posts within the territory.

Sonogram analysis and bioacoustic terminology used

All recordings were digitally transferred from the above-mentioned HHB DAT recorder via a SPDIF cable to a PC workstation with SoundBlaster Live! 5.1 (full version) using 48 kHz / 16 bit sampling and analysed using Avisoft SASLab Pro 3.9 software (S p e c h t 2002). All sonogram measurements were calculated using the following settings of SASLab: 1024 FFT-length, Frame [%] = 25, Window = Hamming and Temporal Overlap = 87.5%. This gave 244 Hz bandwidth with 42 Hz frequency and 2.9 ms time resolution.

We used the same terminology as in previous studies of corn bunting vocalisation and tried to identify each strophe according to a level of its completeness (henceforth called variant), song type and finally a dialect (e.g. M c G r e g o r 1980, H o l l a n d et al. 1996 or L a t r u f f e et al. 2000). First, regardless of belonging to a particular song type and dialect, each song represented a full or incomplete strophe. Detailed comparison of sonograms revealed that predominantly males shorten strophes in fixed positions, which enabled categorization into different song lengths variants: (a) full song phrase, (b) song phrase lacking a portion of the final part, (c) song phrase lacking the final part and a portion of the middle part, and (d) only the initial part of song phrase (Fig. 2). Second, each male had a finite repertoire of strophes similar in structure, which were called song types (Fig. 3). Third, we hypothesized that neighbouring males (within so called local dialect) would share the same song repertoire types and that in their song types the back part of a strophe-end would be similar (M c G r e g o r 1980, M c G r e g o r & T h o m p s o n 1988, H o l l a n d et al. 1996). Song types that shared the same strophe end were assigned to the same dialect (Fig. 3). However, many song types identified, even within a repertoire of particular male, did not share any part of a strophe. Therefore, we were unable to assign such a song types to any dialect. Different song type strophes (regardless of their completeness) were named with a capital letter (e.g. A, B, etc.) or letters (AA, AB, AC, etc.). If two or more song types shared strophe ends, their were designated as belonging to the same dialect named by Arabic numerals (1, 2 and so on).

The sonograms were categorized through a three-step process. First, the second author assigned song strophes to different types and variants within each type by visual inspection. At this stage, each new type and variant for each male was printed and described. In the second step, the first author checked the coherence of categorization at random examples of each song category for each male. In cases of any doubt, more examples were compared visually and with respect to the measured parameters: frequency range, frequency of maximal amplitude and cross-correlation coefficients. In the third step, song types sharing strophe-ends were grouped into dialects.

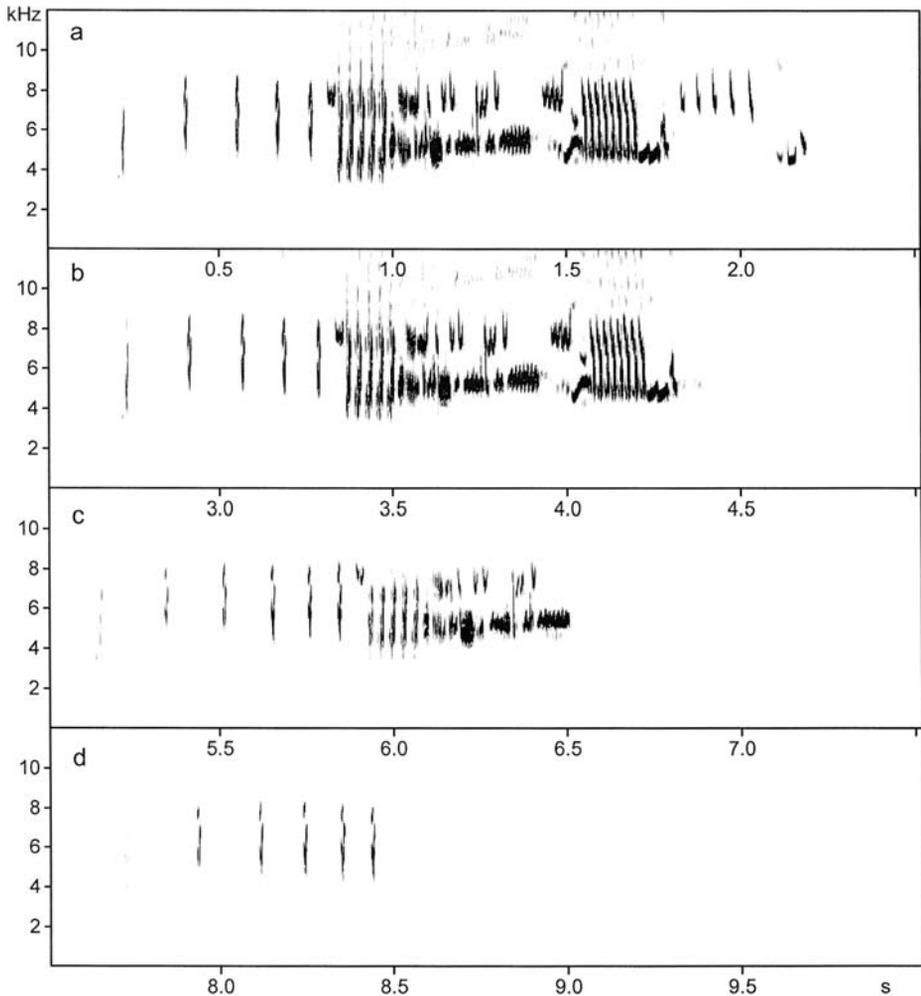


Fig. 2. Sonograms of examples of the four song variants (a, b, c, d) of song type A, in corn bunting of the Wielkopolska Region, Poland. The following sonograms illustrate the method of distinguishing complete and incomplete song versions.

We also tested geographical pattern of song type sharing. Within the studied group of 86 males we randomly generated 43 pairs and repeated such drawing 10 000 times (Manly 1991). Then we tested the relation between male to male distance and the probability that randomly paired males had at least one common song type in their repertoires.

Results

A total of 145 recordings of 86 male corn buntings (Plot A – 15 males, Plot B – 49 males, Plot C – 22 males) were made, containing 4,149 song phrases and last over 10 h. Most males were recorded only once, but some males were recorded twice or more times, also in different contexts (e.g. solo- or counter-singing).

Repertoire composition

The visual inspection of sonograms enabled us to distinguish 32 song types. The most common song types were: A (25 males; 29.1%), M (20 males; 23.3%), B (19 males; 22.1%), I (19 males; 22.1%), H (18 males; 21.0%) and AC (13 males; 15.1%). The next 10 popular song types were sung by 2 to 6 males (i.e. 2.3–7.0%) and the other 16 types were sung only by single males from the studied population. Altogether we found 36 combinations of one or more song types building individual repertoires. Only 4 of them were common: H + I (13 males), A + B (12 males), M (8 males) and M + AC (7 males), and another 4 occurred in 2-4 males: A (4 males), H (3 males), F + G and G (2 males). The remaining 28 repertoire combinations were specific to a single male.

We were able to distinguish only four clear dialects: dialect 1 with five song types (A, B, C, D, Q); dialect 2 with two song types (S, T), dialect 3 with two song types (M, AC) and dialect 4 with two song types (H, I) (Fig. 3). In all cases, song types within dialect shared a large portion of the end strophe. All of the other 21 song types were much more different from each other and did not share either of the initial or final parts of a strophe.

We also found three examples of evident mixing of song types within a repertoire. Male 23, which sang types B and C from dialect 1, occasionally (3 times per 92 strophes

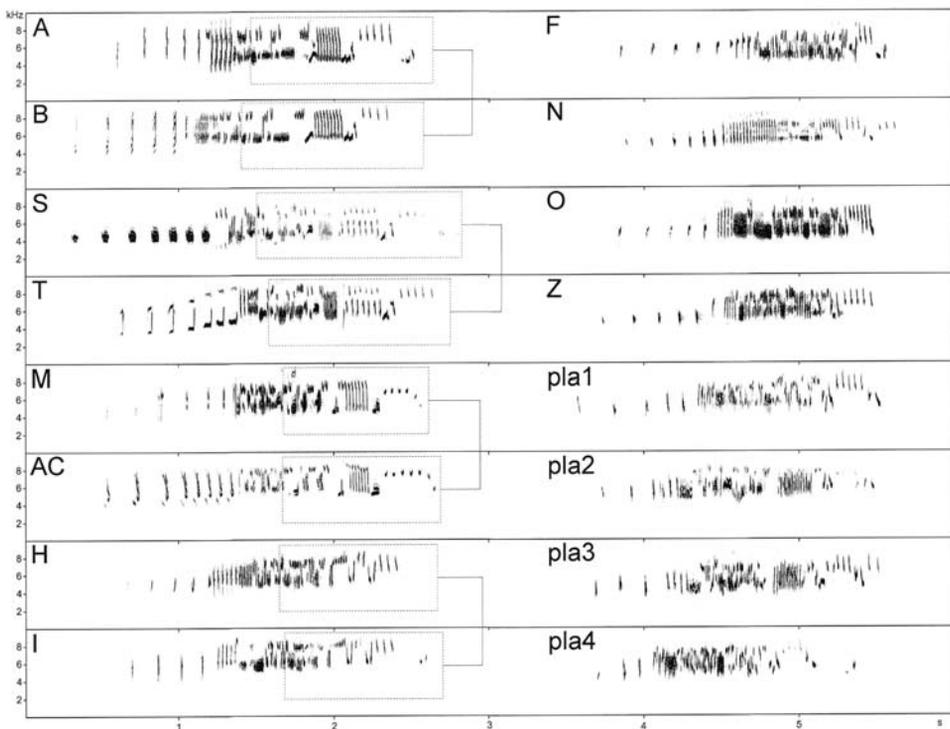


Fig. 3. Sonograms of song types from dialects in corn bunting of the Wielkopolska Region, Poland: 1 (A, B), 2 (S, T), 3 (M, AC) and 4 (H, I). Joined rectangles indicate parts of song strophes, which are common for a particular dialects. Sonograms of strophes F, N, O and Z are examples of song types, which were not find to share final part with any other type. Sonograms marked as pla1 – pla4 are examples of plastic strophes sung successively by one male early in the season.

recorded) uttered phrases with mixed B–C initial part of song. Such mixed versions were always preceded by song type B and followed by song type C. The second example, male 153, was similar. Only once in the 64 strophes recorded for this individual was a mixed D-A song version recognized; thus still matched dialect 1 characteristics. In the third example, male 137 mixed song phrases that did not belong to one dialect, i.e. AC and AI, and this behaviour was sporadic (2 times per 130 strophes recorded).

Two males sang a number of variable strophes, which differed slightly in consecutive performance (Fig. 3), in addition to songs that could be assigned to particular types. However, in both cases the recordings were made rather early in the season and the reason for this variation was probably an unfinished process of repertoire crystallization, rather than exceptional repertoire size. Therefore, we did not analyse these recordings in the context of repertoire size.

Repertoire size

Reliable data on individual repertoire size depends upon a sufficiently large sample of recorded phrases with which to estimate full repertoire size. The situation of the corn bunting is ambiguous, as we found that some males switched song types very rarely. In an extreme example, a male switched to the second song type after 120 phrases in a bout. If we consider only bouts of at least 50 song phrases, then the second song type appeared on average (\pm SE) after 24 ± 3.7 phrases (min-max: 2–121, $n = 37$). The third type appeared after 25 ± 5.5 phrases (min-max: 4–45, $n = 8$) and the fourth type after 55 ± 13.0 phrases (min-max: 39–81, $n = 3$). As we had recordings varying from 1 to 200 phrases in a bout, the possibility of underestimating repertoire size for some males was high. Therefore, we present data on repertoire size just as they are (Table 1), and note that the proportion of males having more than one song type in their repertoire is probably higher. On the other hand, there is no doubt that repertoires composed of two song types predominated in the studied population.

Table 1. Song type repertoire size of corn bunting males from Wielkopolska. (*Including one male with two typical song types and one mixed song type and one male with two typical song types and several plastic song phrases; **Including two males singing three typical song types and one mixed song type; ***Including one individual singing 4 typical song types and several plastic song phrases).

Repertoire size	n	%
1	24	27.9
2	48*	55.8
3	10**	11.6
4	4***	4.7
Total	86	100.0

Microgeographical distribution of song types and dialects

The distribution of males in the study area was not even (Fig. 1). In some locations, several males had territories close to each other, but in other locations territories were separated by hundreds of meters. We also found some males that were acoustically isolated from other individuals. The large gaps between aggregations of males are natural to a large extent,

because the gaps are dominated by forest stands, wetlands or urban areas, which are unsuitable for the corn bunting. On the other hand, even in some seemingly suitable habitats we found no singing males. In places of highest male density, we found a high within-population homogeneity of repertoires.

In Plot C, all males sang one or both song types from dialect 3 (i.e. M and AC) We found only one male singing song type M outside this area (ca. 10 km away). Song type AC was exclusive to this population (Fig. 1). In Plot B, we found two high-density populations separated by a distance of a few kilometers. In the northern plot, we found only males singing song types from dialect 4 (H, I), whereas the southern plot was dominated by males singing song types A and B from dialect 1. Along the road linking the two plots, we found males inhabiting roadside fields and rough lands but in a much lower density; this distribution resembled the shape of hourglass, with a few linearly distributed males linking the two plots. In the southern plot, we found a few males singing the northern dialect as well as males singing songs from both the northern and the southern dialect.

A completely different situation was observed in areas where territories were distributed in small groups of one or a few males (northern part of Plot A and the southern part of Plot B). In such cases, the repertoire of the population was much more variable, but still neighbouring males shared some song types (Fig. 1). Males did not exhibit local dialect pattern on relatively recently inhabited area in SW part of the Plot A, where birds were local density was at similar level to that of Plots B and C.

This distribution of song types reflects to some extent the mosaic pattern of local dialects. The randomization procedure showed that the probability of sharing song types decreases with growing distance between males (Fig. 4). However, boundaries between males singing different dialects were not always sharp.

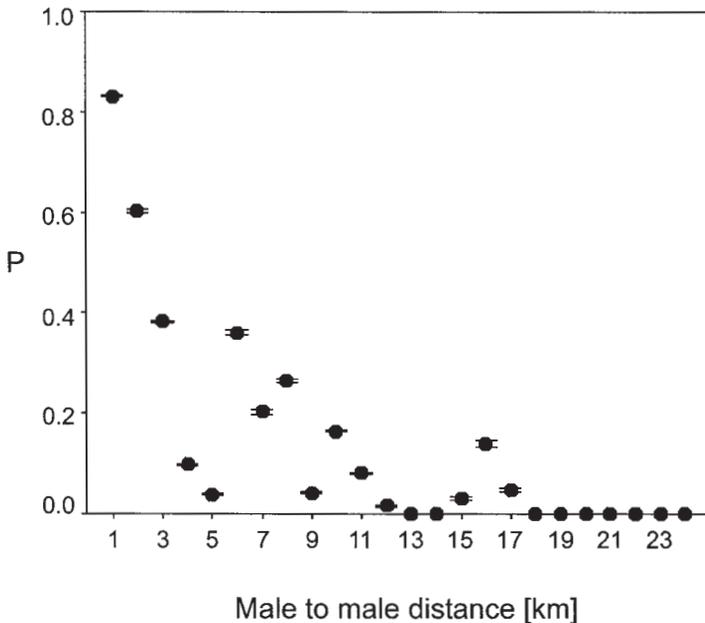


Fig. 4. Probability (mean \pm SE) of sharing at least one song type (P) for randomly chosen pairs of male corn bunting in the Wielkopolska Region, Poland. The procedure of choosing 43 pairs was repeated 10 000 times.

Song versions

Most males sang a few versions of each song type from their own repertoires, but full and slightly shortened versions predominated (Table 2). Males sang shorter versions more frequently when counter-singing (31.9% of strophes) than when singing solo (25.6%). To avoid pseudo-replication, we randomly chosen one recording per male. The differences in proportion of shortened strophes sung during solo and counter-singing context were not significant (Mann-Whitney *U*-test, $Z = -0.043$, $n = 86$, $P = 0.966$). We also tested differences in proportion of singing incomplete strophes sung by the same male recorded during solo (median = 0.17, 95% CI = 0.02 – 0.53) and counter-singing (median = 0.33, 95% CI = 0.09 – 0.75) context (Wilcoxon matched pairs test $Z = -1.572$, $n = 8$, $P = 0.156$). The last test indicate that males may shorten song strophes in aggressive context but we had to small sample size of “paired” recordings to reach significance level. The last method of testing seems to be the most valuable as it eliminates an influence of between males differences in song type repertoires. On the other hand, our results indicate also that shortening of strophes may be connected with a character of a particular song type. Among most popular song types (i.e. A, B, H, I, M and AC) for which we have a representative number of recordings (i.e. both recordings of different males and in different context), all types except AC where shortened in ca. 30% of cases. Song type AC was shortened in about 75% of all recorded performances and simultaneously had one of the longest complete variant, lasting over 3 seconds. We also found that there was a general positive relationship between strophe duration (complete song) and the frequency of shortening in particular song types ($r = 0.49$, $n = 15$, $P = 0.066$; for the most common 15 song types).

Table 2. Length (sec) and frequency singing complete (a) and incomplete (b-d) variants of song strophes in corn bunting from Wielkopolska Region, Poland.

Variant	Mean	SE	n	%
a	2.02	0.004	2884	69.5
b	1.73	0.006	953	23.0
c	1.47	0.012	301	7.2
d	0.61	0.055	11	0.3
Total	1.91	0.004	4149	100

Discussion

Song type repertoire and local dialects

If we consider only areas with high density of corn buntings, then the pattern of song type variation and the system of local dialects found in Wielkopolska corresponds in general with results obtained in Britain (McGregor 1980,1986, Holland et al. 1996, McGregor et al. 1997). However, when all studied sites in Wielkopolska are considered, song variation is higher in Poland than in the UK (McGregor 1980, 1986, McGregor et al. 1988). First, the UK populations studied by those authors were dominated by males singing exactly the same number and combination of song types, with the rare exception of mixed dialect singers. Although our study area was also dominated by males with 2 song

types in their repertoire, over 16% of individuals had 3 or 4 song types. Furthermore, many males inhabiting less preferred sites sang strophes typical for more than one dialect, or song types, which did not share final parts (i.e. could not be assigned to the same dialect). The term local song dialects is typically used to refer to clear microgeographic song variation with a mosaic of different dialects occurring within the species' dispersal capacities (McGregor 1980). Our findings and those of some earlier studies indicate that local dialects may have slightly different character if viewed from a larger geographical perspective. For example in Portugal, song types were found to be restricted to sub-groups of males within local dialect rather than all males singing all song types as in Britain (Latruffe et al. 2000). Whereas no local dialects have been reported for Azerbaydzhan (Sultanov & Gumbatova 1989). The local dialect pattern also seems to be a density-dependent phenomenon, in which formation and maintenance depend on habitat changes, duration and stability of local population. In Poland, clear local dialects were typical only for three high-density populations inhabiting Plots B and C (Fig. 1). Outside these high-density areas, the pattern of song type distribution was much more random, and neighbouring males often did not share any song type. We also found that borders between dialects were not sharp under some conditions. For example, males were observed singing songs typical for one dialect in an area dominated by another dialect. Moreover, some males had song types of different dialects in their repertoires or they even mixed song types from two dialects in one song phrase. McGregor & Thompson (1988) reported similar results. Similar to Holland et al. (1996), we found males singing a song characteristic of a dialect population several km away from the centre of that population, which indicates that birds can disperse to recolonise.

Furthermore, in this study we found an evident example of a disturbance of a local dialect pattern and this disturbance was found on less preferred or relatively new sites (Bednorz 1997, own unpubl. data). Thus, it might be an effect of, for example, offspring overproduction, increased winter survival, or other reasons that caused some males to fail to settle within the local dialect area. Such males try to recolonise or colonise less suitable areas, which is manifested in a higher song variation in such areas (multiple founder effect, see Holland et al. 1996). Formation of a new local dialect in such less suitable areas is rather unlikely. First, corn bunting males in less suitable areas have larger territories, often separated by unoccupied areas (Crampton & Perrins 1994, this paper), which due to reduced social interaction lower the chance of creating a common dialect. Second, in corn buntings, females tend to be mated to males singing the same local dialect as their father (McGregor et al. 1997), which should act as a stabilizing factor for the existing local dialect population and at the same time negatively affects mating success on recolonised areas outside (see McGregor & Thompson 1988, Holland et al. 1996).

Song variants

The usage of full and shortened song versions gives ambiguous results. Generally, males sang shorter versions during counter-singing, but some song types were shortened more frequently regardless of the context. Constable (1989) and Shepherd (1992) (both after Crampton & Perrins 1994) showed similar results, namely some song types in populations studied by them were more likely to be sung as incomplete versions. Shepherd (1992) found that mated males sang more incomplete phrases of one song type from their two-type

repertoire. The pattern found in Wielkopolska indicates that longer complete versions of a song type are more likely to be abbreviated during song performance. It is difficult to determine now whether shortening songs should be considered as an independent level of within-song type variation, which may serve as, for example, an aggressive signal. A few other explanations are still possible, e.g. variant switching might be a signal of submissiveness, tendency to shortening may be culturally transmitted or even represent only a production error, and should be tested experimentally (Searcy & Nowicki 1999, Searcy et al. 2000).

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