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Song structure and repertoire variation in ortolan bunting (*Emberiza hortulana* L.) from isolated Norwegian population

Tomasz S. Osiejuk[1]*, Katarzyna Ratyńska[1], Jakub P. Cygan[2] & Svein Dale[3]

[1]) *Department of Animal Morphology, Institute of Environmental Biology, Adam Mickiewicz University, 28 Czerwca 1956 / 198, PL-61-485 Poznań, Poland (*e-mail: osiejuk@amu.edu.pl)*
[2]) *Department of Population Ecology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, PL-05-092 Łomianki, Poland (e-mail: jpcygan@wp.pl)*
[3]) *Department of Biology and Nature Conservation, Agricultural University of Norway, P.O. Box 5014, N-1432 Ås, Norway (e-mail: svein.dale@ibn.nlh.no)*

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This paper describes song structure and repertoire variation in ortolan buntings (*Emberiza hortulana*) from an isolated and declining Norwegian population, analysed by using the minimal unit of production approach. Males from the studied population sang strophes similar to both dialects found in geographically closest populations in Sweden. We did not observe any simplification of song structure, which is typical for isolated populations of birds. On the contrary, the studied population was characterised by a greater song variation. Song type repertoires were larger both at the individual level and if we considered numbers of different syllables and song types found within the population. This variation seems to reflect the influence of habitat fragmentation and female deficiency at the boundary of the species range on song learning processes and males' dispersion. We also found a remarkable within-song-type variation, which seems to be independent of song type variation level of song production, but its function is unexplained.

Introduction

Songs of passerine birds vary considerably, both between, and within species. The basis of variation is two-fold, and the interaction between genes and the cultural component (learning processes) produce an enormous number of patterns of song organisation, which are still not fully understood (Catchpole & Slater 1995). Considering within-species song variation, we can find examples of acoustically different songs used for different purposes (Catchpole 1983, Kroodsma *et al*. 1989, Byers 1995, Luschi & del Seppia 1996, Nemeth 1996), different strategies of repertoire usage (e.g. song matching, Beecher *et al*. 2000; or repertoire matching, Beecher *et al*. 1996) or distinct temporal organisation of song output (e.g. Alatalo *et al*. 1990, Langmore 1997) depending on the singing context. In some species males considerably differ in repertoire size, which has been recently proved to function as an honest signal in sexual selection (Hasselquist *et al.* 1996, but *see* also Gil & Gahr 2002). Considerable progress has been made also in understanding factors shaping the design of many types of animal signals (Vehrencamp 2000). The next aspect is geographical differentiation of song features. Some species are characterised by the presence of constant characters over large parts of their ranges (so called regiolects or song institutions; review in Martens 1996). Many passerines exhibit a so-called dialect variation, which makes it possible to distinguish groups of males of one species singing their own variant of song on a smaller geographical scale. Although in some species dialect formation and maintenance are well described (e.g. indigo bunting *Passerina cyanea*: *see* Payne 1996), and dialects in some species are known to persist for decades (McGregor & Thompson 1988, Conrads 1992), the mechanisms of their maintenance are unknown and even their functionality is still questionable (Catchpole & Slater 1995). Several different hypotheses have been put forward to explain the rich and diversified geographical patterns of song variation, e.g. habitat matching, genetic adaptation and social adaptation hypotheses (review in Catchpole & Slater 1995). The one and only thing we can be sure of, is that there is no single explanation of geographic variation.

The ortolan bunting *Emberiza hortulana* is an age limited, discontinuous singer with a relatively simple song and small repertoire size (typically 2–3 song types). Like many other species, ortolan buntings exhibit geographic variation in song structure, usually described as dialects (Cramp & Perrins 1994). Dialects, studied in detail in Central Europe, clearly differ from each other in the structure of one or two end phrases of the song. The structure of the end phrase is extraordinarily consistent within particular dialects, and boundaries between dialects are often sharp, without any transition zones (Conrads & Conrads 1971, Conrads 1976, 1992). On the other hand, it is hard to find any certain pattern of song variation on a macrogeographical scale. For example, Conrads (1992) in his Central European survey of dialect distribution, found that similarly singing populations are sometimes fairly distant (hundreds of kilometres away from one another).

In this paper, we describe, for the first time, song structure and repertoire variation of an isolated ortolan bunting population from Norway (Hedmark County). This gives an opportunity to compare song structure and repertoire variability of this declining Norwegian population with others, of a much more continuous character. Especially, we tried to address the question of the nature of song differences between a continuous and an isolated population of well-studied ecology (Dale & Hagen 1997, Dale 2000, 2000a, 2000b). First, songs and calls of geographically isolated bird populations are often quite distinct (Thielcke 1973, Mirsky 1976, Thielcke & Wüstenberg 1985). So, we wanted to check if differences between a Norwegian population and a geographically close, but anyway isolated Swedish population, are greater than between, for example, local populations from Central Europe. Such differences may be limited to repertoire composition (i.e. particular song types present in a local population), but can be also more essential and concern song syntax, as it happens for example in the case of the blue tit *Parus caeruleus* (Doutrelant *et al.* 2000). Especially, we can expect occurrence of specific isolation effects, such as: (1) song structure simplification (Baptista & Johnson 1982, Miller 1982, Lynch & Baker 1990, Hamao & Ueda 2000, Baker *et al.* 2001) or (2) increased individual song variability (Schottler 1995). We also investigated the relationship between song variation at different levels (syllables, song types and song variants of repertoire size) and proposed a universal method of describing the ortolan bunting song structure, which enabled direct comparisons between different populations.

Material and methods

Study area and population

The study was done in May 2001 in County Hedmark, south-eastern Norway. The study area covered the main part of the ortolan bunting distribution range in Norway. Ortolan buntings occurred on 25 sites within an area of about

500 km^2. We recorded males on 11 of those sites, which encompassed all habitats used by this species in Norway (raised bogs, forest clear-cuts on poor sandy soils, land being cleared for cultivation, and burnt forest). It was not always possible to record all birds at a particular site, but the number of birds recorded was proportional to the total number of territorial males at a particular site ($r_s = 0.95$, $N = 11$, $P < 0.001$). The total number of males in the population was about 150, of which 115 were colour-ringed. For a more detailed description of the study area and population, *see* Dale (2000, 2001a).

Recording

Birds were recorded between 04:00 and 11:00, by using a HHB PDR 1000 Professional DAT recorder with a Telinga V Pro Science parabola, a Sony TCD-D8 DAT recorder with a Sennheiser ME 67 shotgun microphone or an Aiwa HS-200 DAT recorder with a Sennheiser ME 67 shotgun microphone. Study sites with a higher number of males were visited by three researchers simultaneously, of which one (with a telescope) mainly helped the others in individual recognition of colour-ringed males. Sites inhabited by 1–3 males were visited by a single person, which in such a situation spent more time to individually recognise males. Generally, the recording person used current data gathered in the previous 1–2 days by the other team members and were aware of the location of particular males, their status (paired, unpaired) or any special behaviour that could make recognition or recording easier (e.g. preferred song posts, characteristic features of vocalisation, etc.). Positions of all recorded males were marked on sketch maps of sub-plots (based on aerial photos) and in most cases the geographic coordinates were also measured by using a Garmin 12CX GPS receiver with at least ± 10 m accuracy. Beside the location of the subject male, each recording was given an unrepeatable number and the following notes: time, behaviour of the subject (song, calls etc.), context status (counter-singing, solo singing), song post characteristics (sitting place, height of sitting place, distance to an open area), and colour-ring code. In the case of unmarked males, their identity was determined on the basis of location of their territory, location of singing posts within the territory and, if necessary, repertoire analysis. In sites with a higher density of males, neighbours were recorded simultaneously by two or three observers, which also ensured that identification of different males was unequivocal.

Song analysis and bioacoustic terminology used

All recordings were digitally transferred from Technics SV-DA10 recorder via a SPDIF cable to a PC workstation with SoundBlaster Live! 5.1 (full version) using 48 kHz/16 bit sampling. Recordings were analysed with Avisoft SASLab Pro 4.1 software within the following set of parameters: 1024 FFT-length, Frame (%) = 25, Window = Hamming and Temporal Overlap = 87.5%. This gave a 244 Hz bandwidth with 42 Hz frequency and 2.9 ms time resolution (Specht 2002).

Songs of ortolan buntings were described usually on the basis of phrase definition, which was understood as a part of a song consisting of a number of repeated, fairly identical syllables. For example, Helb (1996) distinguished A-phrase, B-phrase, M-phrase and E-phrase on the basis of the position of phrase within the song (i.e. first, second, middle or end position, respectively). Songs were assigned to particular types depending on a certain kind of syllables present in phrases. There is some inconsistency in such a procedure. For example, shortened songs were usually assigned to the same type as long versions (e.g. Conrads 1986). Preliminary analysis of Norwegian ortolan bunting songs reveals that such a description system is unsatisfactory. We found that it is not a rule that series of syllables (phrases) occupy always the same position within songs. Simply, some syllables tend to occur at different positions in songs, and such variation is observed both within and between individuals. Second, the use of shortened songs was too common to assume that this is only a production error and it should be somehow included in a song description system. Therefore, we decided to describe songs by using single syllables as

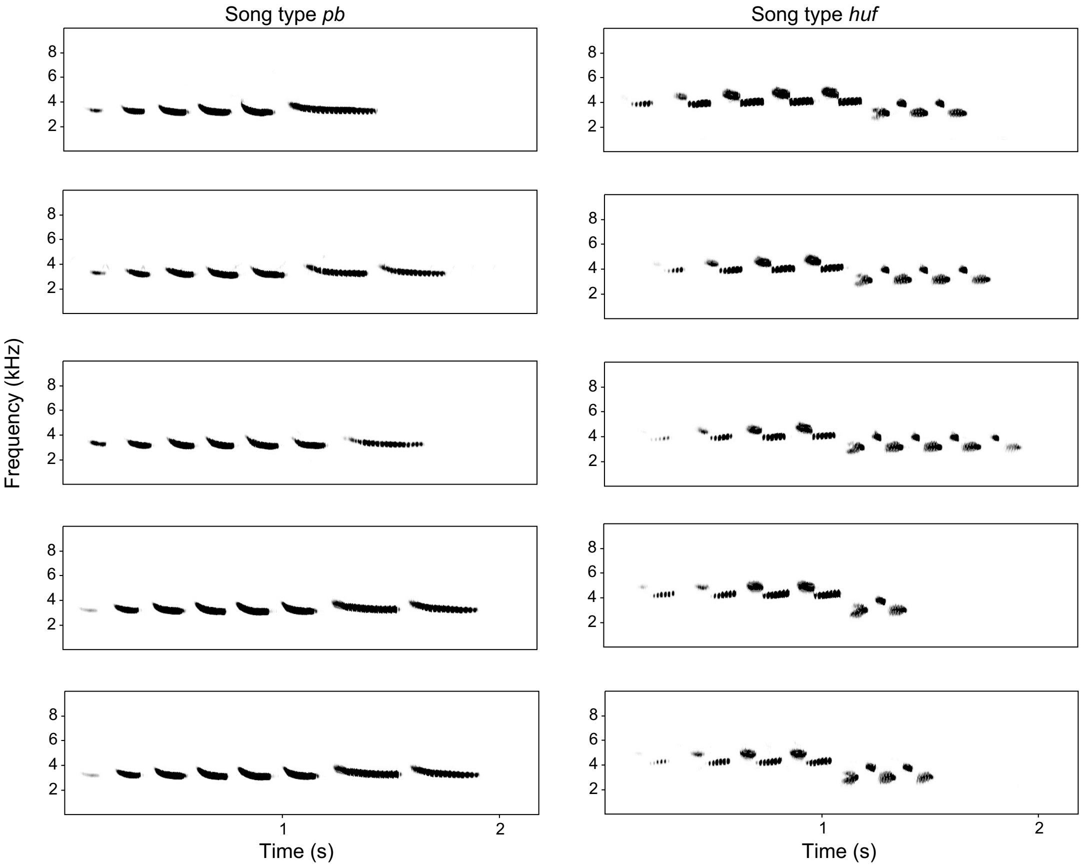

Fig. 1. Within-song-type variation in Norwegian ortolan bunting. Exemplary variants of the *pb*-song type and *huf*-song type are presented. Starting from the top these are described by the following letter notations: *pppppb*, *pppppbb*, *ppppppb*, *ppppppbb*, *ppppppbb* and *hhhhhuff*, *hhhhufff*, *hhhhuffff*, *hhhhuf* and *hhhhuff*. The *pb*-type was uttered by one male only, and we found totally four different variants of it. The two sonograms of *pb*-type at the bottom present two renditions of the same variant. Type *huf* was much more common, sung altogether by 26 males and in 13 variants, five of which are presented. Note that the first syllable has usually lower amplitude and is less visible on sonogram.

minimal units of song production (defined as the smallest invariant units in a male's repertoire; compare the definition by Podos *et al.* 1992). We first divided each song into syllables, and described them by using letter notation, e.g. *aaaabb* or *eeeeehff*, where letters denoted particular syllables. Syllables of the same category had the same shape on sonograms but they might, to some extent, differ in length and frequency between individuals and/or between performances (but within-syllable variation will be the subject of a different paper). In this paper we used the term 'song type' to indicate a group of songs that consist of the same syllables arranged in the same order. For example, according to our classification system, songs *aaccbbbb* and *aacbbb* belong to the same *acb*-type, while song *bbbcccca* should be classified as a different, *bca*-type. In our nomenclature song types are unequivocal, which is especially important when a male, in his repertoire, has such songs as for example *ab*, *ad* and *a*. In the former method the last one could be regarded as a shortened version of both *ab* and *ad* types. Songs of the same type, which differed only in the number of syllables, were termed 'song variants'. For example, within the *pb*-type, many song variants might exist, e.g. *pppppb, pppppbb, ppppppb,* and so on (*see* Fig. 1). The method applied is time-consuming and differs from those used in previous studies, but it has many advantages: (1) songs are described more accurately, as it is possible to detect within-song-type variation, (2) it allows analysis of song syntax rules, (3) it allows direct comparison between different populations, and (4) results obtained can be easily transcribed to fit any other method of song description used in the past. A similar method of scoring song repertoire variation has previously been used in *Acrocephalus* warblers (e.g. Catchpole *et al.* 1984, Catchpole 1986, Hasselquist 1986).

Syllables, song types and variants were assigned to a particular class by visual inspection of sonograms. Classification was done independently by two persons. To explore rules of song syntax we also analysed basic acoustic parameters (minimal frequency, maximal frequency, frequency range, frequency of maximal amplitude and length) of particular syllable types. We calculated acoustic parameters on the basis of a random sample taken from recordings of all males, with the exception that we never took for measurements the initial syllable in a song. We knew from our earlier analyses and literature (Åstrom & Stolt 1993) that the initial syllable in the song of ortolan buntings is slightly lower in amplitude and frequency, which is probably caused by the mechanism of song production.

Material

This study is based on 196 recordings of 59 ortolan bunting males (including 37 recognised by colour rings), containing 5451 songs. We succeeded in recording on average (± SE) 92 ± 10.0 songs per male. As sometimes measurements of all song parameters were not possible, e.g. because of recording quality or background noise, the sample sizes (*N*) are given, and may differ between analyses.

Results

Song structure and syntax

Ortolan bunting males sang with a mean rate of 4.9 ± 1.61 (SD) strophes per minute. The mean song rate varied between recordings from 1.4 to 10.4 strophes per minute. Average inter-song intervals varied between 2.6 and 27.8 s, with a mean (± SD) of 9.0 ± 3.9 s. Songs were combinations of 2–12 syllables of 1–5 different syllable types (Fig. 2, and Tables 1 and 2). This resulted in quite a high song length variation: the longest strophe recorded was over six times as long as the shortest one (Table 2). On average, the song consisted of six syllables and lasted about 1.5 s. The internal (within-song) delivery rate of syllables varied between about 3 and 6 notes per second. Only in songs of one male, which included a phrase copied from the Yellowhammer *Emberiza citrinella*, the modulation rate was significantly higher (Table 2; T. S. Osiejuk *et al.* unpubl.). Song frequencies varied between 1.9 and 6.7 kHz, with a typical frequency of about 2.85 kHz. The minimal values of frequency range were found in the *p*-type song, which was sang by only one male. Interestingly, the *p* syllable was probably mimicked, or at least acoustically highly similar, to initial notes from the local dialect of redwing *Turdus iliacus* (Fig. 1). The most variable parameter was inter-song interval, which describes the pattern of song delivery rather than song structure (Table 2).

In total, we found 63 different song types and 234 different song variants, composed of 20 different syllables (Table 3 and Fig. 3). The distribution of syllables within songs was not random. Some syllables showed a tendency to appear at certain positions. We found typical initial and final syllables. Some syllables occurred in many, sometimes even all possible positions (i.e. initial, middle and final position).

While analysing all syllable types it seems, at first glance, that there is no clear relationship between syllable position within a song and its acoustic parameters (Fig. 4). Furthermore, because of low representation of some syllable types (we found only two syllables, *b* and *i*, which occurred only at the final position in a song), it is hard to test such differences. However, looking at the structure of particular song types, the evident feature of non-single-syllable song types is that syllables in the initial position usually have a higher frequency than those in the middle and final positions. In most non-single-syllable song types it is easy to detect the

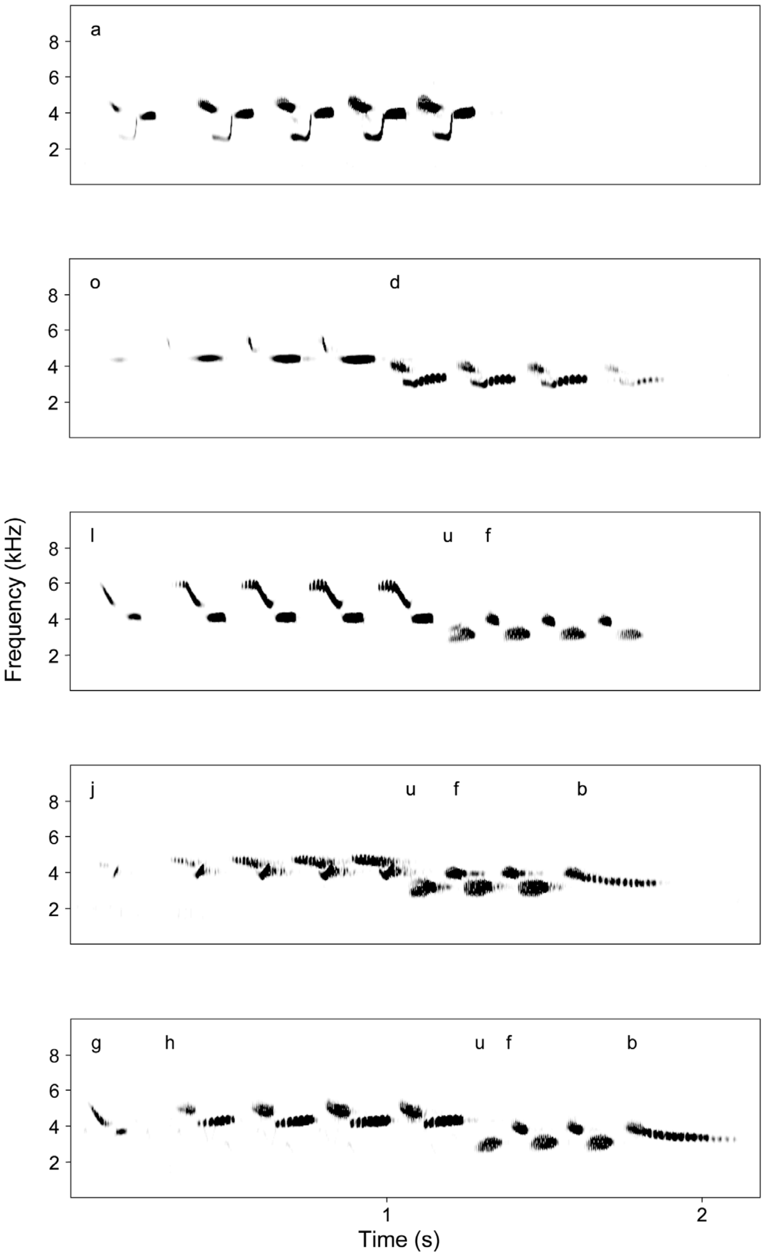

Fig. 2. Sonograms of Norwegian ortolan bunting song illustrating all found levels of strophe complexity. Starting from the top, presented strophes are build by one to five different syllables: *a*-, *od*-, *luf*-, *lufb*- and *ghufb*-type.

first part of a song (higher in frequency) and the second part (lower in frequency). Such a position dependence was typical for both double-syllable song types, such as *ab* or *sb*, and song types with a higher number of different syllables. Finally we tested significance of differences between two groups of syllables: (1) initial or middle and (2) final or middle. Syllables from the first group had a significantly higher maximum frequency, a higher frequency of maximal amplitude and a wider frequency range (Table 4). In the field, the most easily detectable effect of such song syntax is the falling melody line, except the songs that consist of only one syllable type, whose melody line is flat. The common rule was: the more different syllables formed a song type, the lower was their minimum frequency ($r_s = -0.43$, $N = 63$, $P < 0.001$) and the wider was the frequency range ($r_s = 0.42$, $N = 63$, $P < 0.001$) (Fig. 5). Such a correlation was not found for maximum song frequency and number of different syllables in song type ($r_s = 0.22$, $N = 63$, $P = 0.078$). Song types that did not fit the syntax pattern described above, were rarely recorded. The exceptions were *mluf*- and *ml*-type, where a single *m* syllable at the beginning had lower frequency parameters than syllables following it.

It was impossible to classify all songs recorded in Norway to the same dialect using the definition by Conrads (1992). Songs differed strongly in the structure of the end and middle phrases, and we found altogether nine different syllables building the end phrase and 12 different combinations of middle phrases, which contained up to three different syllables. Despite this high variety we found syllable and song types that dominated in the studied ortolan bunting population. Most often, end phrases consisted of a single syllable or a short series of *b* syllables, and we found males singing such songs at each of the 11 sites. Almost half of all recorded males sang *ab*-type, while a few other types (*gb*-, *a*-, *cb*-, *cd*-, *c*- and *h*-type) were sang by more than 10 males (Fig. 6). The most popular were syllables *u*, *f* and *b*, found in over 30% of all described song types (Table 5). The high song type variation within the population was an effect of a large number of rare song types: 29

Table 1. Frequency of song types built with different number of syllable types.

No. of different syllables in a song type	No. of types	% of population repertoire	No. of songs recorded	Percentage of songs recorded
1	10	15.9	346	6.3
2	28	44.4	4703	86.3
3	15	23.8	309	5.7
4	9	14.3	52	0.9
5	1	1.6	41	0.8
Total	63	100.0	5451	100.0

Table 2. Basic parameters of Norwegian ortolan bunting song.

Variable	Minimum	Maximum	Mean±SD	*N*
Minimum frequency (kHz)	1.87	4.12	2.70±0.314	5451
Maximum frequency (kHz)	3.98	6.66	5.55±0.450	5450
Freqency range (kHz)	1.12	4.12 (4.36)[1]	2.85±0.482	5450
Song length (s)	0.36	2.32	1.56±0.234	5450
Inter-song interval (s)	0.80	143.38	8.79±7.356	5257
Number of syllables in a song	2	12	6.7±1.07	5451
Number of different syllables in a song	1	5	2.0±0.47	5451
Modulation rate (syllables/s)	2.89	5.95 (8.25)[1]	(4.30±0.465)	5450

[1] The values in brackets show the exceptional high values of modulation rate and frequency range, which were found only in song phrases copied by one ortolan bunting male from Yellowhammer (T. S. Osiejuk *et al.* unpubl. data).

Table 3. Mean ± SD (minimum, maximum) repertoire size of ortolan bunting males from Norway.

Variable	All males included (*N* = 59)	Only males with at least 50 songs recorded included (*N* = 36)
Syllables repertoire	3.9±1.65 (1, 8)	4.2±1.73 (2, 8)
Song type repertoire	3.7±2.20 (1, 11)	4.2±2.43 (1, 11)
Song variant repertoire	9.9±5.40 (1, 26)	12.5±4.90 (5, 26)

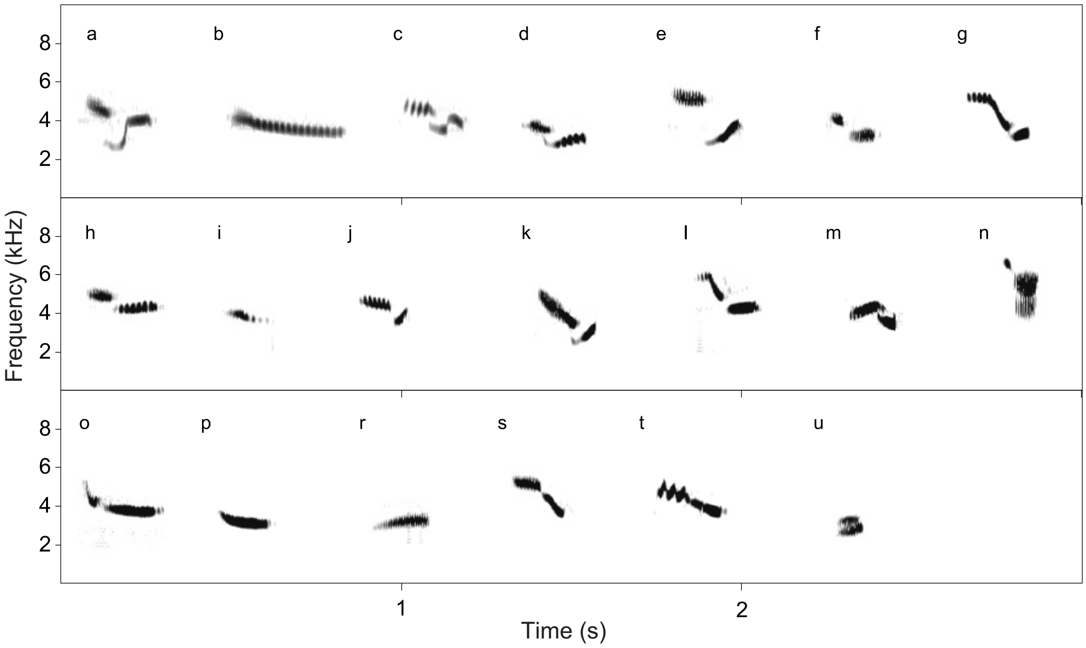

Fig. 3. The complete set of syllables found in a Norwegian population of ortolan buntings in 2001.

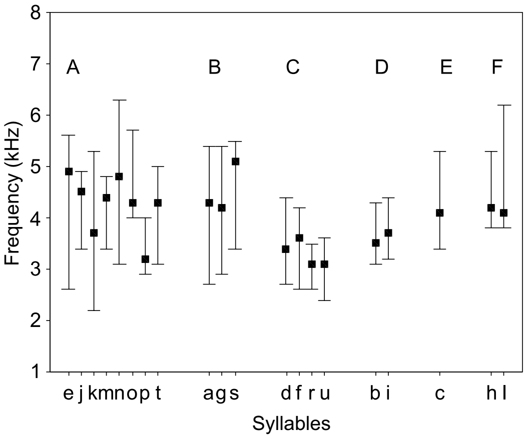

Fig. 4. Mean frequency range and frequency of maximal amplitude of syllables occurring at particular positions within a song: A = initial (including single-syllable types); B = initial or middle; C = middle or final; D = final; E = initial or final; F = all positions.

sang by single males and 15 sang by only two males. We found no clear pattern of between-site song differences, e.g. males from different sites always shared some song types or at least syllables.

Repertoire size variation

We made efforts to estimate male repertoires at three levels: syllable, song type and song variant. In each case we calculated the number of different units (i.e. syllables, types or variants) for particular males. The detected repertoire size is usually only an estimator of actual repertoire size, depending on the number of songs recorded (Garamszegi *et al.* 2002). In our case, only the repertoire size of song variants was significantly

Table 4. Acoustic differences between syllables occurring at different locations within songs.

Variable	First or middle	Final or middle	Mann-Whitney *U*-test
Min freq. (kHz)	3.0 ±0.49	2.8± 0.31	$U = 18$, $N = 17$, $P = 0.149$
Max freq. (kHz)	5.3 ±0.59	4.1± 0.41	$U = 4$, $N = 17$, $P = 0.002$
Freq range (kHz)	2.2 ±0.74	1.3± 0.33	$U = 9$, $N = 17$, $P = 0.015$
Freq of max ampl. (kHz)	4.3 ±0.53	3.4± 0.25	$U = 4$, $N = 17$, $P = 0.002$
Length (ms)	164 ±32	173± 70	$U = 27$, $N = 17$, $P = 0.591$

correlated with the number of songs recorded ($r = 0.58$, $N = 59$, $P < 0.001$). Syllable repertoire size ($r = 0.13$, $N = 59$, $P = 0.340$) and song type repertoire size ($r = 0.18$, $N = 59$, $P = 0.171$) did not show such a relation. Plotting the number of new repertoire units in a recorded sample against the total number of songs recorded, we found that with ≥ 50 songs recorded we can safely estimate the actual syllable and song type repertoire size (Table 3). We also found that new song variants appeared frequently after the 50th recorded song, and the more songs were recorded, the more new song variants were detected. Although mean syllable and song type repertoire sizes were similar for more extensively recorded males (ca. 4.2), song type repertoire varied slightly more than syllable repertoire (Table 3). Syllable repertoire size and song type repertoire sizes were strongly correlated, both when all males were analysed ($r_s = 0.79$, $N = 59$, $P < 0.001$) and when only those with ≥ 50 songs recorded were considered ($r_s = 0.78$, $N = 36$, $P < 0.001$). If, to be comparable with other authors, we regarded single-syllable songs only as shortened versions of full songs (not separate types), the average repertoire size decreased to 2.75 ± 1.85 (SD) for all males in general, and 3.1 ± 2.03 for males with ≥ 50 songs recorded. After rejecting single-syllable song types, the repertoire still shows a high value of up to nine different song types per male. We found only one male that sang single-syllable songs.

To sum up, ortolan bunting males had 2–8 different syllables in their repertoire, which were uttered to compose up to 11 different song types (Table 3). The size of variant repertoire correlated with syllable repertoire and song type repertoire, both when we analysed all males ($r_s = 0.56$, $N = 59$, $P < 0.001$; $r_s = 0.79$, $N = 59$, $P < 0.001$) and when only those with ≥ 50 songs recorded were considered ($r_s = 0.58$, $N = 36$, $P < 0.001$; $r_s = 0.78$, $N = 36$, $P < 0.001$).

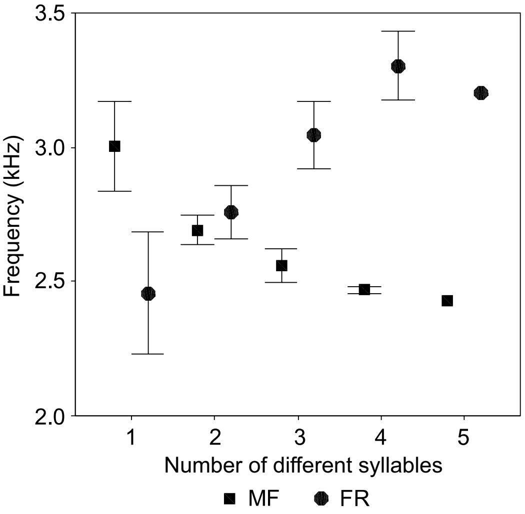

Fig. 5. Relationships between the number of different syllables building a song type and its mean (± SE) minimal frequency (MF) and frequency range (FR) (*N* as in Table 1).

Discussion

Syntax and structure of song of Norwegian ortolan buntings

Even for inexperienced listeners, songs of ortolan buntings from Norway sound different from songs of the same species from many other populations, e.g. from Poland or Germany. This is not surprising, as songs of this species vary both individually and regionally (Cramp & Perrins 1994). A comparison of basic acoustic parameters shows no striking differences in song structure between Norwegian and other populations of ortolan buntings. This similarity concerns frequency range, number of syllables building the song, number of different syllables building the song, and the tonal character of syllables (Conrads 1992, Cramp & Perrins 1994, Helb 1997). It also seems that there is at least one common rule of song syntax in this species, shared by the studied population: the end phrases have a lower frequency and narrower frequency range than first ones. This rule is observed in all types of dialects: with buzz, tremolo or single syllables in the end phrase (Conrads 1992, Helb 1997). Looking closer at the syllable repertoire, the songs of ortolan buntings from Norway undoubtedly resemble those of birds from Sweden (Stolt & Åstrom 1975, Åstrom & Stolt 1993, and Glutz von Blotzheim & Bauer 1997). Some syllables recorded in our study seem to be identical to those recorded by J. R. Roché in Finland (Cramp & Perrins 1994). Similarly to birds from Sweden and Finland, end phrases of Norwegian ortolan

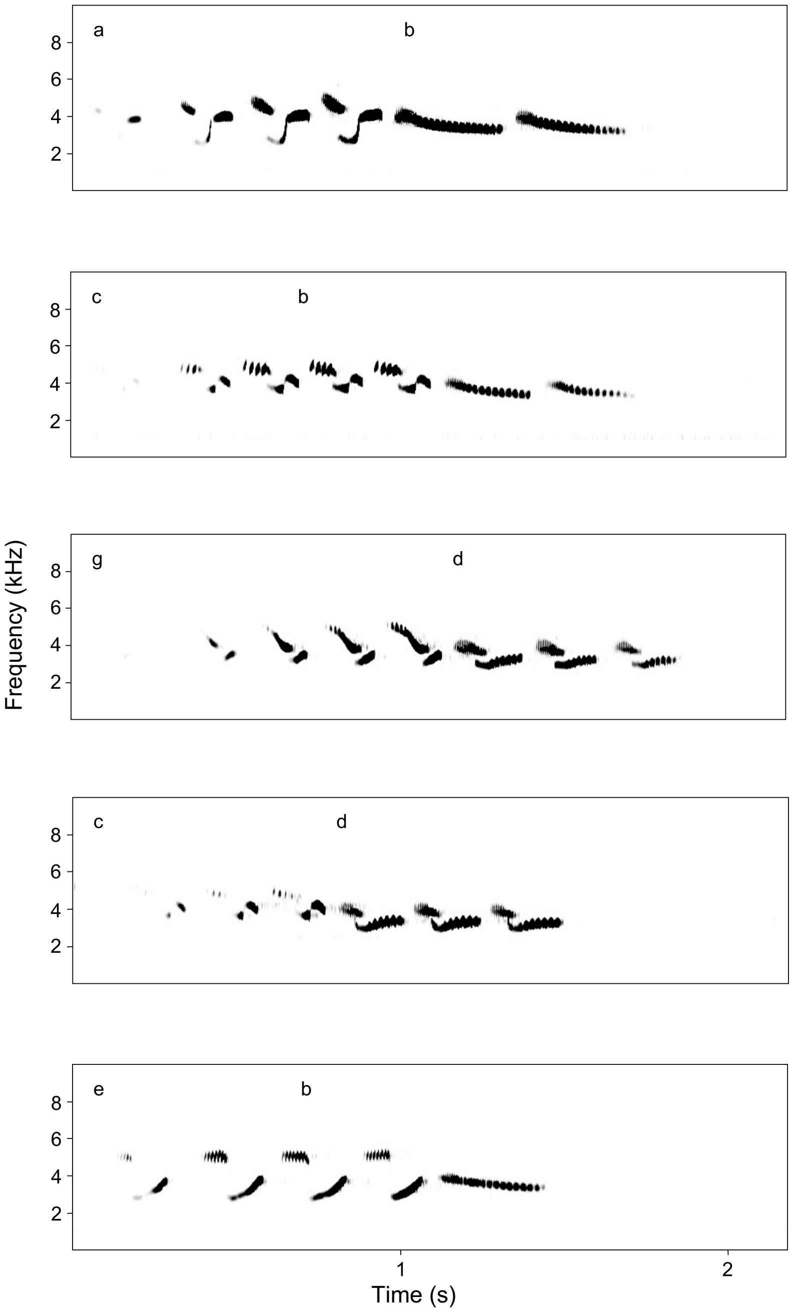

Fig. 6. Sonograms of the most common song types found in Norwegian population of ortolan bunting: *ab*-, *cb*-, *gd*-, *cd*- and *eb*-type.

buntings consisted of syllable/syllables lower in pitch, not tremolo or whistles like in other European countries (Conrads 1992, Helb 1997). The Norwegian population demonstrates song characters typical for both dialects found in Sweden (Åstrom & Stolt 1993). A similar situation was found in a local population from central Sweden (Åstrom & Stolt 1993). Therefore, despite a distinct spatial isolation from other Fennoscandian populations, the Norwegian population of ortolan buntings seems to be very similar with respect to song syntax, dialect affiliation and even syllable repertoire. It seems that 50 years of population decline and fragmentation did not affect the song structure significantly (Väisänen 1992, Dale 2001a). We did not observe the most typical isolation effect of song structure simplification (Baptista & Johnson 1982, Lynch & Baker 1990, Hamao & Ueda 2000).

Repertoire size and variation

Different populations of the same species may differ not only in song structure but also in repertoire size, pattern of song type sharing, etc. (Byers 1996, Matessi *et al.* 2000). Data published on ortolan bunting song variation suggest that this species manifests a rather low repertoire variation. Males typically utter 2–3 (sometimes 1–5) different song types and within-dialect neighbours usually share the final part of the song (Conrads 1969, Conrads & Conrads 1971, Conrads 1976, 1992). Furthermore, there is also a tendency for similar beginning phrases within particular dialects, specific for the locality, so song type repertoires of particular dialect populations are also rather small, usually between 5 and 12 (Conrads 1976, 1992). In Norway, in a relatively small area with only about 150 males, of which 40% were recorded, we distinguished 63 different song types composed of 20 different syllables. Even if we, similarly to other authors, recognise single-syllable song types as shortened versions of full song types (e.g. Conrads 1986), there are still 53 different song types in a relatively small population. Although the mean song type repertoire size was not very large, as compared with other populations, we found quite many males with large, unreported earlier, repertoire sizes (Cramp & Perrins 1994). Unique for the studied population was the high variation in composition of end and middle phrases of songs, found to be invariant within other populations (Conrads & Conrads 1971, Conrads 1992, Osiejuk 2000) and probably occurring also in some small populations in Sweden (Åstrom & Stolt 1993). It is noteworthy that such a greater individual variability sometimes accompanies simplification of song structure in island populations (Schottler 1995). If we compare our results with a long-monitored German population, where song variation is low and dialects have been stable for many years (e.g. no changes during 18 and 27 years; Conrads 1992), it appears obvious that there must be a relationship between population size, its longevity and space continuity as well as song variation. The Norwegian population in fact consists of about 30 subpopulations with the number of males varying from 1 to over 50 (Dale & Hagen 1997, Dale 2000, 2001a). Thanks to a long-lasting ringing program there is no doubt that males move both within and between sites, sometimes even during one season. There is also no doubt that particular sites are to some extent isolated but isolation is probably never absolute (S. Dale unpubl. data). Within-population song variation can be also described in terms of sharing repertoires between males. This may appear when young birds settle for the first time in their territories, and learn songs from their neighbours. It is also possible that young males learn their songs earlier and seek out breeding sites where other males sing in a similar way (Catchpole & Slater 1995). Ortolan bunting males are known to learn their songs during the first 10 months of their life, and later the song type repertoire remains stable (Conrads 1986). This should explain the persistence of dialects in relatively large Central European populations (Conrads 1992). Consequently, explanations of larger repertoires and greater between-individual song variation in Norway, should be sought among factors that affect (1) learning processes and/or (2) dispersion pattern and settlement

Table 5. Frequency of syllables occurrence among 63 different song types recognised within Norwegian population of ortolan bunting.

Syllable(s)	No. of song types with syllable(s)	Percentage
u	23	35.5
f	22	34.9
b	21	33.3
h	16	25.4
g	13	20.6
c	10	15.9
d	7	11.1
l	6	9.5
j	5	7.9
a, m, s, t	4	6.3
e, n	3	4.8
k, p, r	2	3.2
i, o	1	1.6

of males. We think that both factors might be involved. First, in a fragmented population larger repertoires might be a result of males changing subpopulations in different years, and making use of song templates from more than one site. Even slight isolation of sites within the Norwegian population may also increase the possibility of inventing and maintaining new syllables and song types or even maintaining new elements brought by incidental immigrants from another population. The most striking are examples of males singing notes from other species, such as redwing or yellowhammer (T. S. Osiejuk *et al.* unpubl. data). It is also known that ortolan buntings may move and settle in fairly distant areas. For example, in 1977 a few males colonized a moor in Westphalia in NW Germany, and were found to be bioacoustically similar to a population from northern Sweden (Conrads & Kipp 1980). In fact it is not a new idea that fragmentation of habitats into discontinuous patches not only disrupts reproduction and survivorship but also stimulates movement of animals (Smith & Hellmann 2002).

The second factor that can favour an increase in song variation, is female-biased dispersal, with its easily predicted result: a large proportion of unpaired males (25%–35%; Dale 2001a, 2001b). Mating problems may additionally foster males to move between different sites, which can increase song variation in two ways. First, this increases heterogeneity of song templates available within a particular site. Second, the probability of listening to different song templates is greater if the male moves to another site. Furthermore, in ortolan buntings the probability of mating increases with age (Conrads & Quelle 1986). We can expect that younger males are more willing to learn and are more mobile. On the other hand, a large percentage of unpaired males was also observed in populations with a lower song variation and clear dialect membership (Conrads & Quelle 1986, Bülow 1990).

Levels of song variation — possible function(s)

All three repertoire size indices were significantly correlated. Values of correlation coefficients suggest that although the number of song variants in a male's repertoire depends on the syllable and song type repertoire size, most of its variation (ca. 67%) is related to another factor, namely the number of songs recorded. The correlation between song type and syllable repertoires was strong and significant, in contrast to the insignificant correlations between those indices and number of recorded song phrases. This resulted from the way in which new syllables, song types and song variants are delivered during song performance. Each male seems to have a finite number of syllables and song types in its repertoire and consequently the level of this variation decreases during the song bout. The number of song variants increased linearly with the number of phrases performed. This clearly indicates that there must be a substantial difference between song variability at the variant level vs. syllable and song type levels. The presence of dialect and contextual usage of song types (Osiejuk 2000) suggests that the ultimate functions of syllable/song type variation level are: territory maintenance and, consequently, female attraction (Catchpole & Slater 1995). We cannot go further into the details of mechanisms underlying such processes, but they are certainly connected with song learning processes and social adaptation of males to the local population (Catchpole & Slater 1995).

Distribution of song variants within song bouts suggests that both the source and function of this variation are different. One of the possible explanations is that song variants occur because of production errors caused by some structural or neuro-motoral constraints in song production (Lambrechts & Dhont 1988, Podos 1996, 1997). However, it is still possible that males differ substantially in making mistakes, and that variation of this kind may also carry an important message to the potential receiver.

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