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Frequency shift in homologue syllables of the Ortolan Bunting *Emberiza hortulana*

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Abstract

Results of this study indicate that in the Ortolan Bunting *Emberiza hortulana*, syllables of the same shape on sonograms (i.e. homologue syllables) often significantly differ between males in frequency parameters. Typically, homologue syllables of different males in the studied population had a similar bandwidth but shifted minimal and maximal frequencies. We found no strong evidence supporting that the frequency of homologue syllables is affected by the body size variation of males. Besides, frequency parameters of different song types within a male's repertoire did not correlate with each other. Moreover, we found that some males within the population sing two versions of apparently 'the same' song type, which differ in frequency parameters of syllables. Such different frequency versions were sung with eventual variety, which suggests that they are treated as different song types by birds. All these results support the idea that the fine acoustic structure of syllables (and song) is under a strong influence of the acoustic template (i.e. depend mainly on from whom the song was copied). We also found that the frequency of initial syllables within the song strophe is much more variable between males than in case of final syllables. Regardless of the great between-individual variation in initial syllable frequency, the syllables forming the final part of the song are kept within a very restricted bandwidth. These results support our earlier finding that strict syntactic rules of song formation exist in this species. These rules condition the acoustic variation of the initial and final part of the song. At least potentially, such a system enables species recognition and individual variation irrespective of repertoire level. Results of this study indicate that more attention should be paid to the problem of minimal units of song repertoire and to identity of such units within the bird population.
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1. Introduction

Bird song is highly variable both between and within species, and is a sexually selected trait (Catchpole and Slater, 1995). Variation analysed at the species level

is usually related to male quality (Searcy et al., 1985; Horn et al., 1993; Hasselquist et al., 1996; Nowicki et al., 2000) or different song units are presented in ways that allow the males to maintain their territories or other supplies (Weary et al., 1987; Henry et al., 1994; Beecher et al., 1996). One of the crucial problems in linking song functions with song variation is the recognition of real minimal units of song production and perception. Their proper recognition makes it possible to measure the repertoire at a level that is relevant to the function fulfilled by the song, and to analyse interactions between different levels of song complexity (Nowicki and Podos, 1993). In discontinuous singers, each male usually has a repertoire of a limited number of song types, which are presented in time in a specific manner. Each strophe sung could be easily assigned to a particular type and males are known to recognise different types (Catchpole and Slater, 1995). This is typical for many bunting species (Byers et al., 1995), where song types are often considered as basic units of song production (Searcy et al., 1999). Nevertheless, there is also some variation at the song type level (Podos et al., 1992; Nowicki et al., 1994, 1999; Osiejuk et al., 2003a). It is usually connected with relatively small differences in syllable composition within the song type (e.g. Osiejuk et al., 2003a). However, this kind of song variation can also sometimes be distinguished by a signal receiver (Searcy et al., 1995), and presentation of different song variants (i.e. versions within a song type) may suggest that in some situations they could play different functions (Nowicki et al., 1994; Osiejuk, unpublished material).

Most studies analysing song type variation are implicitly based on the assumption that units used for describing song types (typically syllables or their groups) are invariant between different individuals within a studied population. However, it seems reasonable to ask the question if the syllables having the same shape on sonograms (called further homologue syllables) are truly equal in the sense of acoustic structure and function within a population of songbird species. A few studies strongly support this idea. Some songbird species are able to transpose songs or song elements up and down a species-specific frequency range. This shifting is used to match the frequency of rival songs in the Kentucky Warbler *Oporornis formosus* (Morton and Young, 1986), Harris' Sparrow *Zonotrichia querula* (Shackelton et al., 1991), Black-

capped Chickadee *Parus atricapillus* (Shackelton and Ratcliffe, 1994) and Nightingale *Luscinia megarhynchos* (Naguib et al., 2002). In the Black-capped Chickadee, a species with a single-type song, pitch shifts and song structure were also found to indicate male quality (Christie et al., 2004). The problem of syllable identity was also addressed in studies on species recognition, as syllable morphology is often a strong cue involved in discriminative processes (e.g. Weary et al., 1986; Okanoya and Dooling, 1990). The process of categorisation of syllables into discrete classes is still an important topic of bioacoustics research (Shy et al., 1986; Falls et al., 1988; Nelson and Marler, 1989; Kreutzer, 1991). Recently it has been shown that even in suboscine passerines, where song development is apparently genetically programmed (Kroodsma, 1984), species with relatively simple single-type songs may be characterised by a significant and functionally important between-individual song variation (Lovell and Lein, 2004a, 2004b).

Results of our research on the Ortolan Bunting *Emberiza hortulana* (Osiejuk, 2000; Osiejuk et al., 2003a, 2003b, 2004) and yellowhammer *Emberiza citrinella* (Rutkowska-Guz and Osiejuk, 2004) convinced us that this homologue syllable equality assumption is incorrect. When analysing recordings of the Ortolan Bunting, we found that although homologue syllables can be classified as the same syllable type, they may differ in acoustic parameters (Osiejuk et al., 2003a). Such a variation may reflect differences in quality of recordings or influence of the environment due to excessive attenuation, cutting inequitably some frequencies (Bradbury and Vehrencamp, 1998). A preliminary analysis revealed that the syllables, although looking 'the same' in shape on sonograms, significantly differ between individuals with respect to minimal and maximal frequencies, while still maintaining a similar bandwidth. This variation may be functionally significant, so its examination should help us determine what the minimal unit of song production and perception really is, what in song is learned, and what is under a more direct genetic control (Baptista, 1996).

In this paper, we demonstrate that males truly differ in acoustic properties of homologue syllables. Then, we test a few hypotheses that may explain this variation. These hypotheses are derivatives of a simple question: what in song is learned and what results from intrinsic properties of a male?

1.1. Body size hypothesis

Vocal frequency was found to be inversely proportional to body weight in Northern Bobwhites *Colinus virginianus* (Goldstein, 1978), domestic pigeons (Goodwin, 1965 cited in Baptista, 1996) and tyranid species (Lanyon, 1960, 1978). However, there is no vocal learning in these species (Kroodsma, 1982; Kroodsma and Baylis, 1982). On the other hand, similar relationships were found also in some oscine birds, which acquire their repertoires through learning processes (Schubert, 1976; Bowman, 1979; Wallschläger, 1980; Ryan and Brenowitz, 1985). The body size hypothesis predicts that although song in the Ortolan Bunting is learned from conspecifics (Conrads and Conrads, 1971; Conrads, 1976), its final acoustic properties may depend on the body size of a particular male. We should expect that larger males are able to produce syllables of a lower frequency than smaller ones. As the structural body size is generally stable after the bird becomes adult, we should expect also the acoustic parameters of syllables to be invariable during adulthood. In case of body size influence on the structure of learned songs, we may expect that all song types within a male's repertoire are similarly affected, i.e. are raised or lowered in frequency, depending on the body size of the tutor and learner. Consequently, we should expect that frequency parameters of syllables from different song types from a male's repertoire should correlate positively.

1.2. Acoustic template hypothesis

In general, the acoustic template hypothesis contradicts the body size hypothesis. In this hypothesis, we assume that the learning process incorporates exact copying of a song, including frequency parameters of syllables. In such a case, we should not expect any direct relationships between acoustic parameters of syllables and body size. It is hard to test this hypothesis directly as it is virtually impossible to track in the field from whom exactly the young males learn (or may learn). However, we may expect that if this hypothesis is true, males may have in their repertoires simultaneously song types consisting of syllables that could be characterised as low and high in frequency for a studied population. Therefore, we do not expect any positive correlation between frequency parameters

of different song types from a male's repertoire. Moreover, we may expect that some males, which learned songs from more than one tutor, may sing the same homologue syllables in more than one frequency version.

1.3. Syntax hypothesis

In our earlier study, we found that the main syntax rule for the Ortolan Bunting songs is that the frequency and bandwidth of subsequent syllable series (phrases) decrease within a strophe. We also found some preferences for different syllables to appear in a particular order within the strophe. We found syllables that occurred only at a final or only at an initial position within a strophe, and some universal syllables, which may occur at all possible positions (Osiejuk et al., 2003a). Thus, we may expect that syllable frequency may depend not only on the template acquired or male size, but also on how syllables are positioned within song strophes. If the syntax hypothesis is true, we should expect that frequency parameters of homologue syllables are modified by their position within song strophes. For example, when syllable *x* occurs at an initial position, it should have a higher overall frequency, while when it occurs at a final position, it should have a lower overall frequency. However, we found that it is hard to test this most apparent prediction. In the studied population, a small number of syntactically typical song types predominated and we could not find enough examples to make a rational comparison, however it should be possible to do this in the future (Osiejuk et al., 2003a). For instance, we observed many males with song types *ab* and *cd* but none with *ba* or *dc*. On the other hand, there is no doubt that syntax rules are of key importance in this species (Osiejuk et al., 2003a, 2003b, 2004) and we may expect some differentiation of how initial and final syllables within a song strophe are modified when their frequency is shifted. Regardless of the mechanism of frequency shift, we may expect that it enable keeping the song strophe as a whole within species-specific syntax.

2. Methods

2.1. Study area and population

The study was done in May 2001 and 2002 in Hedmark County, 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 (in 2001) and 16 (in 2002) of those sites, which encompassed all habitats used by the species in Norway (peat 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 (2001: $r_s = 0.95$, $n = 11$, $P < 0.001$; 2002: $r_s = 0.97$, $n = 16$, $P < 0.001$). The total number of males in the population was about 150 (in both years), of which ca. 115 were colour-ringed. We recorded 59 males in 2001 (39% of the population) and 86 males (57%) in 2002. For a more detailed description of the study area and population, see Dale (2000, 2001), and for a detailed description of song repertoire variation, see Osiejuk et al. (2003a, 2003b, 2004). Adult males were captured in mist nets with the aid of song playback, and were given a combination of one metal ring and three colour-rings to permit individual identification. Biometric measurements (body weight, lengths of tarsus and wing) were taken.

2.2. Recording

Birds were recorded between 04:00 and 11:00 h, 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. In 2001, we recorded birds between 9th and 15th May, and in 2002 between 17th and 23rd May. In the studied population, males start singing just after arrival in early- and mid-May. Usually older males appear earlier than younger ones, and the birds sing most intensively until pairing. However, there is a significant insufficiency of females in this population, so many males remain unpaired and sing for longer periods (Dale, 2001).

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 one to three 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 during the previous 1–2 days by other team members and was 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 a unique number and the following notes: time, behaviour of the subject (song, calls, etc.), context status (countersinging or 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 song posts within the territory, and—if necessary—also repertoire analysis.

2.3. Sonogram analysis and data selection for testing of hypotheses

We describe songs by using single syllables as minimal units of song production described in detail elsewhere (Osiejuk et al., 2003a). An exemplary song strophe with syllables and phrases indicated is given in Fig. 1. All recordings were transferred from the tape recorder to a PC workstation with SoundBlaster Live! 5.1 (full version) using 48 kHz/16 bit sampling. Recordings were analysed by Avisoft SASLab Pro 4.23b 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 46 Hz frequency and 2.67 ms time resolution (Specht, 2002). We used one-dimensional function called amplitude spectrum (linear) with Hamming evaluation window and typical resolution below 3 Hz. Using this function, we measured in the power spectrum window the following spectral characteristics: FMA: frequency of maximal amplitude [Hz]; MINFREQ: minimal frequency [Hz] and MAXFREQ: maximal frequency [Hz], where the relative to maximal amplitude falls below −20 dB threshold; and BAND: bandwidth [kHz], which is equal to MAXFREQ − MINFREQ.
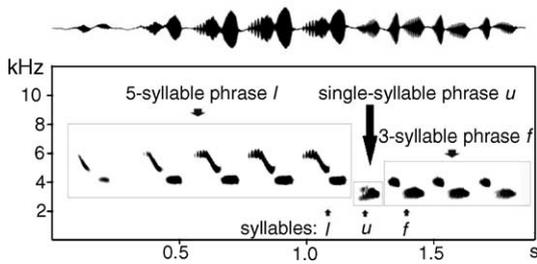
Fig. 1. An exemplary song strophe belonging to song type *luf*. The strophe consists of three different syllable types (*l*, *u* and *f*) presented in exactly such a sequence. The same syllable sequence within a strophe is called phrase. In this particular strophe, we had three different sequences consisting of five, one and three syllables. Notice that the number of syllables within a song type may differ both between individuals and between different performances of a male. The envelope curve is also presented to illustrate that initial and final syllables may have lower amplitudes than other syllables within a strophe.

For bandwidth-related measurements the Spectral Characteristics option 'total' was on. For more details on measurement characteristics, see Specht (2002).

Syllables within a song are characterised by some variation, which depends on position within a song. If a sequence of syllables (usually called a phrase) occurs in a song, the initial syllable has a lower amplitude and frequency range in comparison to others within the series (Åstrom and Stolt, 1993; Osiejuk et al., 2003a). This kind of variation is common to all males and is probably connected with the mechanism of sound production. In this study, we wanted to measure variation, which is connected with an individual specificity, not with acoustics-mechanics. Likewise, if we compare the amplitude of the last syllable in a song strophe, it is often slightly softer, especially if the final phrase consists of more than one syllable (see Fig. 2 and more examples in Osiejuk et al., 2003a). Therefore, we decided to take measurements from carefully selected syllables within a phrase. For the initial phrase, we always measured parameters of the last syllable within the phrase. For the middle and final phrases, we measured the first syllable within the phrase. These rules ensure that measurements were taken from syllables of comparable within-strophe amplitude and are shown in Fig. 2 (compare also Fig. 1 to trace the typical within-strophe amplitude changes on the envelope curve). We measured 10–30 homologue syllables per recording per male (depending on availability) and used average values in the further analysis.
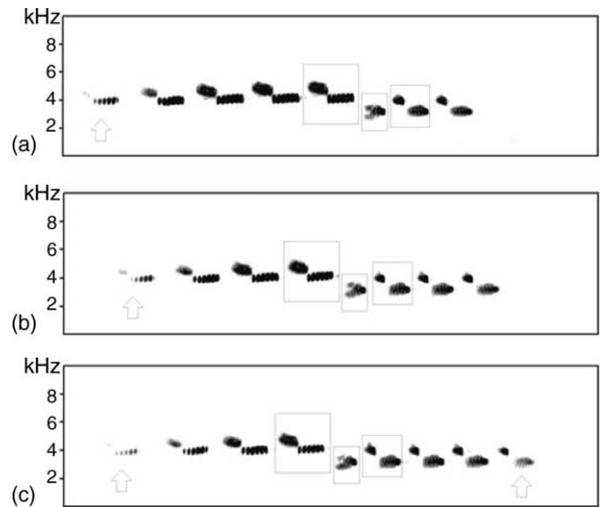

Fig. 2. Exemplary song strophes (type *huf*) of Ortolan Buntings. Syllables for which measurements were taken are indicated by rectangles. Arrows show initial and final syllables that have a lower amplitude, most probably because of the sound production mechanism.

2.4. Statistical analysis

Statistics were calculated by SPSS 10 software (Norusis, 1993). To keep the type I error constant ($\alpha = 0.05$), we used the Bonferroni correction if a multiple test of similar null hypotheses was carried out. *P* values are two-tailed, unless stated otherwise. Acoustic parameters of homologue syllables were usually strongly correlated, therefore in some analyses we reduced their number by using principal components analysis (PCA) based on all four initial variables.

3. Results

3.1. Between-individual variation of homologue syllables

At the first stage, we demonstrated in detail that homologue syllables of different males, although seemingly the same, significantly differ in acoustic parameters. We chose four syllables (*a*, *b*, *c* and *d*), which were sung by many males within the studied population (Osiejuk et al., 2003a). These four syllables were sung

Table 1
Results of four multiway ANOVA models with acoustic parameters of four syllables (*a*, *b*, *c* and *d*) as response variables and males as an independent variable

Variable	Syllable *a* (d.f. = 9, 186)		Syllable *b* (d.f. = 9, 186)		Syllable *c* (d.f. = 8, 245)		Syllable *d* (d.f. = 8, 245)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
FMA	10.10	<0.001	39.88	<0.001	20.32	<0.001	9.23	<0.001
MINFREQ	956.90	<0.001	110.34	<0.001	1364.93	<0.001	69.17	<0.001
MAXFREQ	321.94	<0.001	10.31	<0.001	731.68	<0.001	42.27	<0.001
BAND	117.64	<0.001	7.40	<0.001	98.18	<0.001	45.96	<0.001

The set consists of measurements taken for 10 males in case of syllables *a* and *b*, and for nine males in case of syllables *c* and *d*.

in many of altogether 109 song types recorded in 2001 and 2002 in the studied population. To avoid the potential effect of song type on syllable parameters, we chose only two song types (*ab* and *cd*) to demonstrate the acoustic variation of syllable parameters. These song types were chosen because they were very common in the studied population (36.8% of all 11,656 songs recorded in 2001–2002), and we had enough good-quality recordings for several males to demonstrate this variation.

For each syllable, we measured FMA, MINFREQ, MAXFREQ and BAND for at least 10 items (usually 20) from single recordings of males recognised by colour rings. This was a very conservative method, but in this way, we could be sure whose male syllables were measured, and the possible effect of recording quality was minimised. Selected males differed significantly in respect of all syllables and all four measures of acoustic parameters (Tables 1 and 2). The greatest between-individual differences were found in case of MINFREQ, and this concerns all syllables tested. As can be seen in Figs. 3 and 4, in spite of significant between-individual differences, only in case of syllables *a* and *c* some males really diverged in acoustic space. For example, the average MINFREQ for syllable *a* differed between extreme males by 716 Hz, which is easy to perceive even by human ear. Quite variable was FMA of syllables with more than one amplitude peak at quite different frequencies (i.e. syllables *a*, *c* and *d*; presented in this paper and many more within the studied population—compare Osiejuk et al., 2003a). Therefore, as a result of even small differences in energy distribution FMA of homologue syllables within a particular song type may strongly differ even between successive performances of a male. Such differences may be, however, an effect of the acoustic environment and dis-
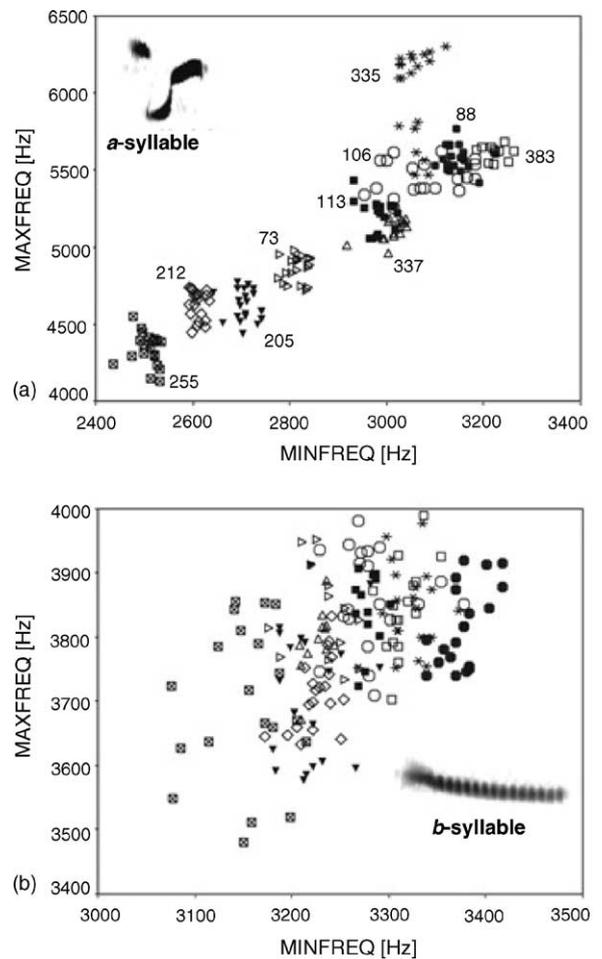

Fig. 3. Minimal and maximal frequencies of homologue syllables *a* and *b* of 10 randomly chosen Ortolan Bunting males from the studied population. In both parts of the figure the same males were presented. Their identity number is given in part (a) of the figure.

Table 2
Basic acoustic parameters of four Ortolan Bunting syllables

Variable	Minimal (kHz)	Maximal (kHz)	Range (max–min) (kHz)	Mean ± S.D. (kHz)	CV (%)
Syllable *a*					
FMA	2.55	5.50	2.95	4.23 ± 0.609	14.4
MINFREQ	2.44	3.26	0.83	2.90 ± 0.229	7.9
MAXFREQ	4.13	6.30	2.18	5.12 ± 0.526	10.3
BAND	1.60	3.20	1.61	2.22 ± 0.343	15.4
Syllable *b*					
FMA	3.18	3.58	0.40	3.40 ± 0.07	2.2
MINFREQ	3.08	3.42	0.34	3.26 ± 0.07	2.1
MAXFREQ	3.48	3.99	0.51	3.79 ± 0.10	2.6
BAND	0.32	0.74	0.42	0.53 ± 0.09	17.1
Syllable *c*					
FMA	3.13	5.20	2.07	3.84 ± 0.49	12.6
MINFREQ	3.02	4.11	1.09	3.43 ± 0.26	7.7
MAXFREQ	4.16	5.42	1.26	4.76 ± 0.31	6.5
BAND	1.06	1.68	0.63	1.33 ± 0.13	9.6
Syllable *d*					
FMA	2.85	3.93	1.08	3.31 ± 0.26	7.8
MINFREQ	2.77	3.06	0.30	2.93 ± 0.06	2.0
MAXFREQ	3.73	5.02	1.30	4.13 ± 0.21	5.0
BAND	0.78	2.14	1.36	1.20 ± 0.22	18.4

(i) Syllable *a* (*n* = 186) and syllable *b* (*n* = 175) were measured for 10 males (*n* = 186); (ii) syllable *c* (*n* = 245) and syllable *d* (*n* = 235) for nine males (*n* = 245). The identity of males is given in Figs. 1a and 2a.

tance between microphone and singer. The larger is the distance and the denser is the environment, the larger is the attenuation of higher frequencies (Bradbury and Vehrencamp, 1998). This was not the case of syllable *b*, which is a whistle with a relatively narrow band. On the other hand, our analysis revealed that the initial syllables (*a* and *c*) are much more variable between individuals than final syllables (*b* and *d*).

3.2. Time stability of homologue syllables

We tested if acoustic parameters of homologue syllables changed between 2001 and 2002 for 10 males, which were recorded in both years of the study and were recognised by colour rings during recording. We analysed differences only for those syllables (altogether 33), for which we had at least 10 good-quality examples per season per male (in most cases we measured 20–30 per male per year). Acoustic parameters of a male's homologue syllables may change between seasons because of (1) differences in recording quality and (2) differences in some male properties related to song production. Only the second case is interesting for us.

We can easily separate between those two effects. If the homologue syllable of a male shifted in frequency between years, then we should observe a simultaneous increase (or decrease) in MINFREQ, MAXFREQ and FMA with a relatively invariant BAND. In fact, any other changes in acoustic properties should be more probably linked with differences in quality of recordings (compare, however, Hoese et al., 2000 for effect of beak movements on song production). We found only one case that fulfils these conditions: syllable *c* from song type *cd* of male 88 (Table 3). In this case, both average MINFREQ and MAXFREQ decreased by ca. 80 Hz. There was no such effect of any three other syllables from song types *ab* and *cd* analysed for this male. In general, we found that the measured acoustic parameters of homologue syllables may change between seasons in both directions, but in most cases mean differences were smaller than frequency resolution of measurements (Table 3), consequently they should be considered as inconclusive. The modulus of mean difference was always below 150 Hz, with MINFREQ being the most invariant feature. Simultaneously, as was stated above, MINFREQ varied the most between
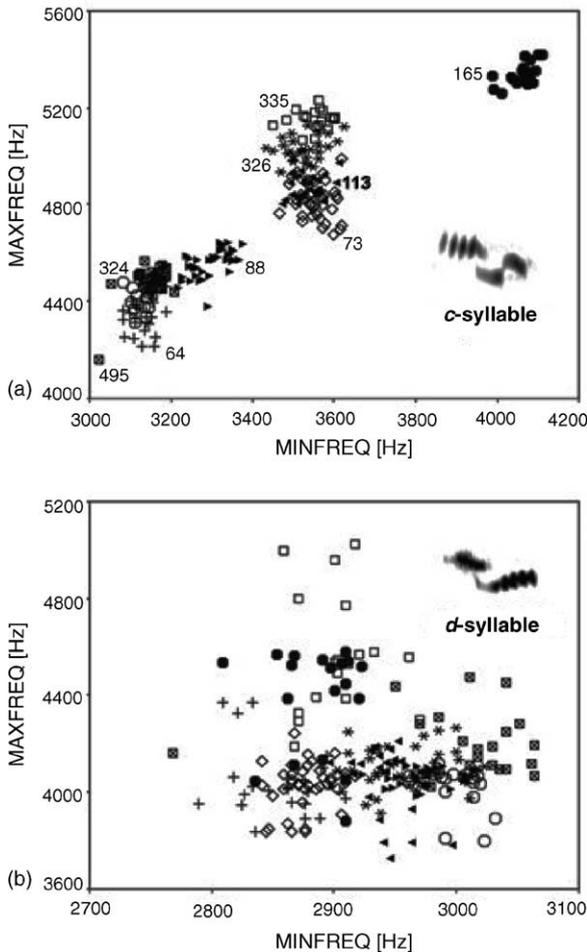
Fig. 4. Minimal and maximal frequencies of homologue syllables *c* and *d* of 10 randomly chosen Ortolan Bunting males from the studied population. In both parts of the figure the same males were presented. Their identity number is given in part (a) of the figure.

ables by using principal components analysis (PCA). In case of syllable *a*, PCA extracted only one component called COMP_A, which was strongly correlated with FMA ($r = 0.82$), MINFREQ ($r = 0.91$), MAXFREQ ($r = 0.98$) and BAND ($r = 0.85$), and explained 79.35% of initial variation. Multiple stepwise regression of COMP_A on all three body size measures revealed that it was significantly affected by wing length (adjusted $R^2 = 0.15$, $t = -2.294$, $P = 0.031$). In case of syllable *b*, PCA extracted two compound variables COMP_B1 (correlated with FMA $r = 0.96$ and MINFREQ $r = 0.97$) and COMP_B2 (correlated with MAXFREQ $r = 0.96$ and BAND $r = 1.00$), which explained 97.8% of initial variation. We found that both variables were not affected significantly by any body size measure. In case of syllable *c*, PCA extracted one compound variable COMP_C (correlated with FMA $r = 0.72$, MINFREQ $r = 0.90$, MAXFREQ $r = 0.97$ and BAND $r = 0.46$), which explained 62.0% of initial variation. It was not affected significantly by any body size measure. In case of syllable *d*, PCA extracted two compound variables COMP_D1 (correlated with FMA $r = 0.81$ and MINFREQ $r = 0.87$) and COMP_D2 (correlated with MAXFREQ $r = 0.97$ and BAND $r = 0.98$), which explained 90.2% of initial variation. Also here in both cases, the two compound variables were not affected significantly by any body size measure.

3.4. Body size versus acoustic template hypothesis

To check the potential effect of body size versus acoustic template, we selected males that had simultaneously in their repertoires both common song types, i.e. *ab* and *cd*. As was suggested in Section 1, if body size matters, we should expect positive correlation between analogous frequency parameters measured for different song types across males sharing repertoires. We correlated frequency parameters of syllables taken from *ab* and *cd* songs of selected males and found no significant correlations. For example, correlation between the most individually invariant feature, i.e. MINFREQ was $r = -0.09$ ($n = 13$, $P = 0.773$).

Our analysis of frequency parameters of homologue syllables revealed that as a rule each male has single frequency versions of each syllable. However, analysis of parameters of song type *ab* from all males recorded in 2001–2002 revealed some strik-

males (Table 3). Note that all $P > 0.05$ in Table 3 after Bonferroni correction.

3.3. Body size of males versus acoustic parameters of homologue syllables

We used each male's mean frequency parameters of syllables *a*, *b*, *c* and *d* taken exclusively from song types *ab* and *cd*, respectively. Only for these two song types we had a higher number of males measured. We reduced the number of acoustic vari-

Table 3

Mean between-year differences in acoustic parameters of shape syllables of 10 males recorded in 2001 and 2002 and recognised by colour rings

Male	Song type	Syllable	Mean difference (Hz) and significance of between-year difference			
			FMA	MINFREQ	MAXFREQ	BAND
72	*ab*	*a*	262 ns	−10 ns	−30 ns	−19 ns
72	*ab*	*b*	4 ns	−6 ns	57[*]	64[*]
72	*cd*	*c*	203[*]	−24[*]	69[**]	94[***]
72	*cd*	*d*	44 ns	−9 ns	11 ns	20 ns
88	*ab*	*a*	247 ns	−22 ns	−2 ns	20 ns
88	*ab*	*b*	−15 ns	−60[***]	278[***]	338[***]
88	*cd*	*c*	492[***]	−82[***]	−76[***]	6 ns
88	*cd*	*d*	−7 ns	−27[***]	19 ns	46[***]
165	*eb*	*e*	−49[***]	−106[***]	−19 ns	87[***]
165	*eb*	*b*	32 ns	−42[***]	1 ns	42[**]
171	*guf*	*g*	213 ns	−32[*]	85[***]	117[***]
171	*guf*	*u*	−7 ns	−28 ns	61 ns	90[*]
171	*guf*	*f*	−274[**]	−56[**]	−18 ns	38 ns
205	*pb*	*p*	−8 ns	−24 ns	−62[**]	−38 ns
205	*pb*	*b*	65[**]	18 ns	114 ns	96 ns
322	*cd*	*c*	−38 ns	−5 ns	62[*]	66 ns
326	*ab*	*a*	−619[*]	−18 ns	35 ns	54 ns
326	*ab*	*b*	−13 ns	−75[***]	65 ns	140[*]
326	*cd*	*c*	154[**]	53[***]	−22 ns	−75[***]
326	*cd*	*d*	165[**]	50[***]	46 ns	−4 ns
328	*ab*	*a*	−45 ns	−10 ns	12 ns	22 ns
328	*ab*	*b*	−29 ns	−1 ns	184[*]	186[*]
328	*gb*	*g*	−97 ns	−47[*]	3 ns	51 ns
328	*gb*	*b*	−12 ns	11 ns	11 ns	−1 ns
340	*ab*	*a*	−79 ns	42 ns	120 ns	77 ns
340	*ab*	*b*	73[***]	56[***]	180[***]	125[**]
340	*cb*	*c*	423[***]	153[***]	427[***]	275[**]
340	*cb*	*b*	16 ns	−39 ns	−29 ns	9 ns
385	*e*	*e*	−337 ns	4 ns	9 ns	5 ns
385	*ef*	*e*	−24 ns	−30[*]	−49 ns	−19 ns
385	*ef*	*f*	423 ns	−52 ns	−132 ns	−81 ns
385	*h*	*h*	−30 ns	−48[***]	15 ns	64[*]

The sign '−' indicates that the average variable value in 2002 was lower than in 2001. ns, not significant.

　　[*] $P \leq 0.05$.

　　[**] $P \leq 0.01$.

　　[***] $P \leq 0.001$.

ing exceptions to this rule. Namely, we found males that had in their repertoires song type *ab* represented by two frequency versions. Such versions significantly differed in respect of the parameters of syllable *a*, having syllable *b* at a roughly similar level. A typical example is illustrated in Fig. 5. A male with four song types in their repertoires sang a low-frequency version (LFV) and a high-frequency version (HFV) of song type *ab*. Mean value of MINFREQ (kHz) was 2.29 ± 0.049 for LFV and 2.64 ± 0.036 for HFV, respectively ($t_{87} = -29.68$, $P < 0.001$). Mean

value of MAXFREQ (kHz) was 5.19 ± 0.119 for LFV and 5.70 ± 0.122 for HFV, respectively ($t_{87} = -19.02$, $P < 0.001$). We carefully checked variation of MINFREQ and MAXFREQ across 58 males singing song type *ab*, and found that at least five males (and most probably two more) had two frequency versions of syllable *a*. This gives a rough estimation between 8.6 and 12% of males having two versions of a homologue syllable. If we consider only 31 males for which we had longer recordings (at least 30 strophes), this estimation is even higher, reaching 18–20%. Males with such
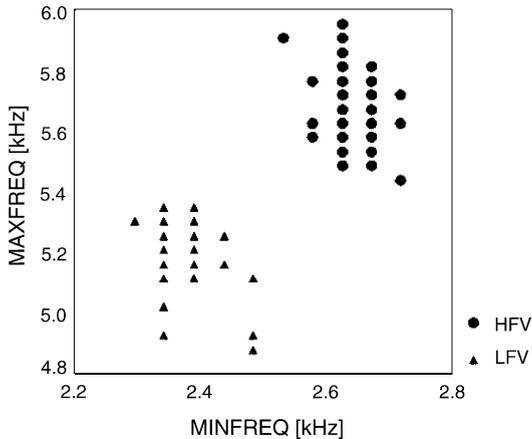
Fig. 5. Scatter plot of minimal and maximal frequencies of syllable *a* of male no. 312. The male was recorded four times and had four song types in his repertoire (*ab*, *huf*, *hufb*, *jufb*). Besides the typical switching between different song types, we found that the male sang sequences of *ab* songs in two distinct versions: with a low and high frequency (LFV and HFV, respectively).

double versions of syllables (and consequently song types) used such versions in the same manner as different song types, i.e. they tended to sing one version in a sequence before switching to a different song type or different song version (i.e. with eventual variety).

3.5. Syntax and frequency of homologue syllables

The Ortolan Bunting song is constructed with simple syntax rules, namely the successive phrases within the song strophe decrease in frequency and bandwidth. It has also been shown that some syllables tend to occur at particular positions within the strophe (Osiejuk et al., 2003a). Consequently, we may expect that acoustic parameters of some syllables building the song may be under a strong influence of their position within the song. In fact, we found that the initial syllables of song types *ab* and *cd*, were much more variable than final syllables of these two song types. We can imagine two possible mechanisms of changing the frequency of homologue syllables (and whole song phrases). First, birds may alter homologue syllables by changing the frequency by a certain number of Hz. For instance, song type *xy* with the following frequency ranges 3.0–6.0 kHz for *x*, and 3.5–4.0 kHz for *y*, should change to 3.5–6.5 kHz and 4.0–4.5 kHz, respectively, after raising the frequency by 500 Hz. Second, males may alter homologue sylla-

bles by transposing them, i.e. by multiplying the frequencies by a certain factor. If we use the same values as above, and take the multiplying factor 1.1(6), we will obtain shifted song characteristics: 3.5–7.0 kHz for *x*, and 4.08–4.67 kHz for *y*. Only in the first case, source and shifted homologue syllables look exactly the same on sonograms, but simultaneously only in the second case the melody line of the song remained unchanged (Hansen, personal communication). It is possible to test the two hypotheses by correlating any measure of overall syllable frequency (e.g. MINFREQ or FMA) with syllable frequency range. If the first hypothesis is true, frequency range should remain unchanged, whatever the overall frequency of the homologue syllable. If the second hypothesis is true, the frequency range should be positively correlated with the overall frequency of the homologue syllable. We found that both MINFREQ and FMA of syllable *a* from song type *ab* correlated significantly with BAND of this syllable ($r = 0.60$, $n = 28$, $P = 0.001$ and $r = 0.50$, $n = 28$, $P = 0.007$, respectively). We did not find any similar correlation for syllable *b* within song type *ab* ($r = 0.18$, $n = 27$, $P = 0.37$ and $r = 0.23$, $n = 27$, $P = 0.244$, respectively). We did not find any significant correlation for a similar comparison in song type *cd*. If we assume that the song is copied from a tutor as a whole, we may expect that changing the frequency or multiplying the frequency should affect the whole strophe, i.e. there should be some fixed relationship between the frequency of initial and final syllables. We found that MINFREQ and FMA of the initial syllable in song type *ab* ($r = 0.32$, $n = 27$, $P = 0.104$ and $r = 0.321$, $n = 27$, $P = 0.103$) and song type *cd* ($r = 0.52$, $n = 12$, $P = 0.085$ and $r = 0.374$, $n = 12$, $P = 0.231$) correlated positively but insignificantly with BAND of the final syllable. On the other hand, we found that within individuals, MINFREQ of syllable *a* was strongly correlated with MINFREQ of the following syllable *b* ($r = 0.71$, $n = 27$, $P < 0.001$). However, the strongest within-strophe relation was between MINFREQ of syllable *a* and the difference between MINFREQ of syllables *a* and *b* ($r = -0.97$, $n = 27$, $P < 0.001$; Fig. 5). A parallel relationship was found for syllables *c* and *d* within *cd* songs ($r = 0.99$, $n = 12$, $P < 0.001$, Fig. 5b), where MINFREQ of syllables *c* and *d* did not correlate significantly ($r = -0.45$, $n = 12$, $P = 0.139$). These results indicate that although the frequency of initial syllables may markedly vary between individuals, the final syllables are preserved at
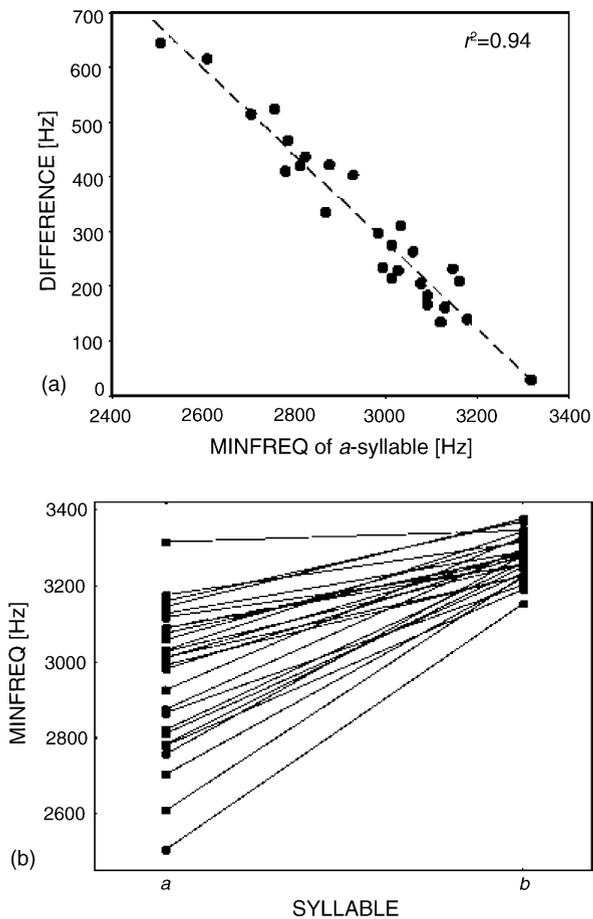
Fig. 6. The ceiling effect on final syllable(s) frequencies, exemplified by the relationships between minimal frequencies (MINFREQ) of initial and final syllables within song type *ab*. (a) The DIFFERENCE variable is the mean, absolute difference between MINFREQ of syllables *a* and *b* of 28 males. Below (b), you can see the same relationships shown in a more illustrative way. Each line links mean male's MINFREQ of syllables *a* and *b* within song type *ab*.

a relatively stable level within the studied population (Fig. 6).

4. Discussion

This study confirms our preliminary observations that in the Ortolan Bunting, syllables of the same shape (i.e. homologue syllables) significantly differ between males in basic acoustic parameters. We found some between-year differences in acoustics of homologue syllables when comparing songs of the same males from two seasons, but these differences were negligible. We found this variation unlikely to be responsible for between-individual variation observed at the population level. It is also possible, in cases where greater between-year differences were found, that in fact we did not observe any change in homologue syllable frequency parameters but just recorded in the second year a different frequency version from the male's repertoire. Conrad's (1986) observations support our findings, as he did not observe any substantial changes in song properties (including frequency) for males recorded even during 7 successive years.

We demonstrated in this study that homologue syllables of the Ortolan Bunting may significantly differ between individuals. Simultaneously, we found that this variation does not involve all homologue syllables evenly, and probably has a complex origin. We found that syllable *a*, which is common in the studied population, is slightly but significantly affected by the male's wing length. Wing length is often correlated to migration distance but not necessarily to other morphological traits. In the Ortolan Bunting, wing length was shown to correlate significantly but weakly with body weight (Gawroński, 2001). Therefore, we can conclude that our study gave no substantial support for the body size hypothesis. Singing more than one frequency version of syllables (and song types) by some males and the lack of significant correlation between frequencies of different song types of particular males support the acoustic template hypothesis. On the other hand, clear relationships between syllables within song strophes and differentiated variation of initial and final syllables show that syntax rules also affect strongly the final effect, i.e. acoustic details of songs performed by a male. When formulating hypotheses we expected that acoustic parameters of homologue syllables are controlled mainly by a single factor. In practice, we observed a pattern suggesting that the final acoustic structure of song is a common effect of learning processes (syllable parameters) and inheritance (syntax). However, in the last case, an alternative hypothesis might be that syntax rules are extracted by listening to a number of males. Observation of atypical singers revealed that Ortolan Bunting males may sing syntactically normal strophes even when particular syllables are copied from other species or conspecifics singing a foreign dialect (Osiejuk et al., 2003b, 2004). There is no doubt however, that our sug-

gestions about learning and inheritance effects on song structure in Ortolan Bunting should still be regarded as initial hypotheses, which should be experimentally tested (e.g. as in Baptista and Petrinovitch, 1984). So, the "syntax inheritance" should rather be considered as a catchword, and in our opinion most probable is that inherited are some learning mechanisms, which ensure syntax persistence (Baptista, 1996; Janik and Slater, 2000).

Our data suggest that Ortolan Bunting males may learn songs from more than one individual. This is supported by the observation of males singing two frequency versions of homologue syllables of the same song type. Ortolan Buntings in Norway usually have a larger song type repertoire size (on average around four song types per male; Osiejuk et al., 2003a) than in other studied populations of this species (see Cramp and Perrins, 1994 for review). In Norway, we observed males that had up to 11 (Osiejuk et al., 2003a) or even 24 different song types in the repertoire (Osiejuk et al., unpublished data). Song types from so large repertoires consisted mainly of syllables typical for the population (i.e. shared by other males), but it is unlikely that they were copied from a single tutor. Those observations also support the idea that Ortolan Bunting males can copy songs from many males (Osiejuk et al., in preparation). Also other bunting species were found to learn songs from multiply tutors (e.g. Nordby et al., 2000). We also found that males with two frequency versions of a song type used such song types with eventual variety, which means that birds treat such versions as belonging to different song types. Such observations indicate that new syllables within a population may appear not only because of 'a point mutation' of culturally transmitted units but also by gradual changes in frequency of syllables from the existing repertoire.

Relationships between frequencies of initial and final syllables forming a song strophe indicate that irrespective of the details of the mechanism of cultural transmission, the mechanism preserves the stability of song syntax at the species level, despite obvious repertoire differences between populations (e.g. Conrads, 1994; Åstrom and Stolt, 1993; Helb, 1996; Osiejuk et al., 2003a). As was shown in our earlier study, the structure of songs of the Ortolan Bunting are based on the rule that successive phrases within a strophe have decreasing frequencies, and narrowing frequency bandwidths (Osiejuk et al., 2003a). This study indicates that those rules result from different 'behaviour' of initial and final syllables forming phrases within the strophe. Final syllable(s) are very conservative as they maintain relatively invariant frequency parameters, no matter to what extent the initial syllables shift in frequency. Initial syllables are more likely to vary between individuals. To some extent this could be explained by a multiplying frequency mechanism, but results obtained only for a single syllable (i.e. *a*) showed a predicted positive correlation between overall frequency and bandwidth.

Cultural transmission of song in the Ortolan Bunting ensures the stability of some song features, which are probably crucial for species recognition (invariant features hypothesis—Catchpole and Slater, 1995). It is known that Ortolan Bunting males do not react to songs with broken syntax (Osiejuk et al., 2003b, 2004). On the other hand, such a pattern of transmission permits some level of within-population variation in the acoustic character of homologue syllables; besides, males differ in song type repertoire (Osiejuk et al., 2003a). The questions are: (1) is the variety described here adaptive; and (2) what are its possible functions? We are, at this point, unable to give definite answers to these questions. However, in our opinion at least two hypotheses described below should receive research attention in the near future.

Ortolan Buntings breed in Norway in clearly separated groups, which differ in song type repertoire. We found that usually a few song types predominate within the studied subpopulations (Osiejuk et al., in preparation). It is not such a clear microgeographic pattern as the so-called local dialects in the Corn Bunting *Miliaria calandra* (e.g. McGregor, 1980; Latruffe et al., 2000; Osiejuk and Ratyńska, 2003). On the other hand, it is certainly different from the random pattern observed in the yellowhammer *E. citrinella*, where there is no tendency to share repertoires with neighbours (Hansen, 1981; Hiett and Catchpole, 1982; Rutkowska-Guz and Osiejuk, 2004). So, typically signal receivers are able to hear simultaneously homologue syllables of more than one individual. Thus, the first hypothesis is that differences in the acoustic pattern of homologue syllables are helpful in individual recognition, for both males and females. Although the relationship between body size and the initial syllable frequency was not strong, we cannot reject the second hypothesis that it is sufficient to be a cue for females choosing between neighbour-

ing males. Both hypotheses need to be experimentally tested in the future. Finally, we would like to encourage researchers to study topics related to the variation of homologue syllables discussed above. To our knowledge, a similar variation occurs also in other bunting species and may be a quite widespread but overlooked phenomenon among passerines.

Acknowledgements

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