

Sharing songs within a local dialect does not hinder neighbour–stranger discrimination in ortolan bunting (*Emberiza hortulana*) males

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Summary

Neighbour–stranger (hereafter N–S) discrimination in birds is common and has most likely evolved to settle repeated disputes more efficiently and without physical fights. We tested whether an oscine bird, the ortolan bunting (*Emberiza hortulana*), with a small repertoire size from a population with a local dialect and a high level of song sharing is able to discriminate between the songs of neighbours and strangers. We performed playback experiments with eighteen males to measure the response to a repeated single rendition of a single song type derived randomly from a repertoire of a neighbour or stranger. Subjects responded more aggressively to the songs of strangers than neighbours (faster approach, more calls and songs uttered), suggesting that ortolan buntings can discriminate between the songs of neighbours and strangers. Our results also suggest that cues for N–S discrimination may be based on individual within-song type variation regardless of song-type repertoire composition. We contrast our results with an earlier study where ortolan buntings from a non-dialect population were tested. Finally, we predict a positive relationship between the level of song sharing and within-song type variation, which may be maintained by selection for N–S discrimination in songbirds with small and moderate repertoire sizes.

Keywords: neighbour–stranger discrimination, song sharing, repertoire size, dialect, within-song type variation.

Introduction

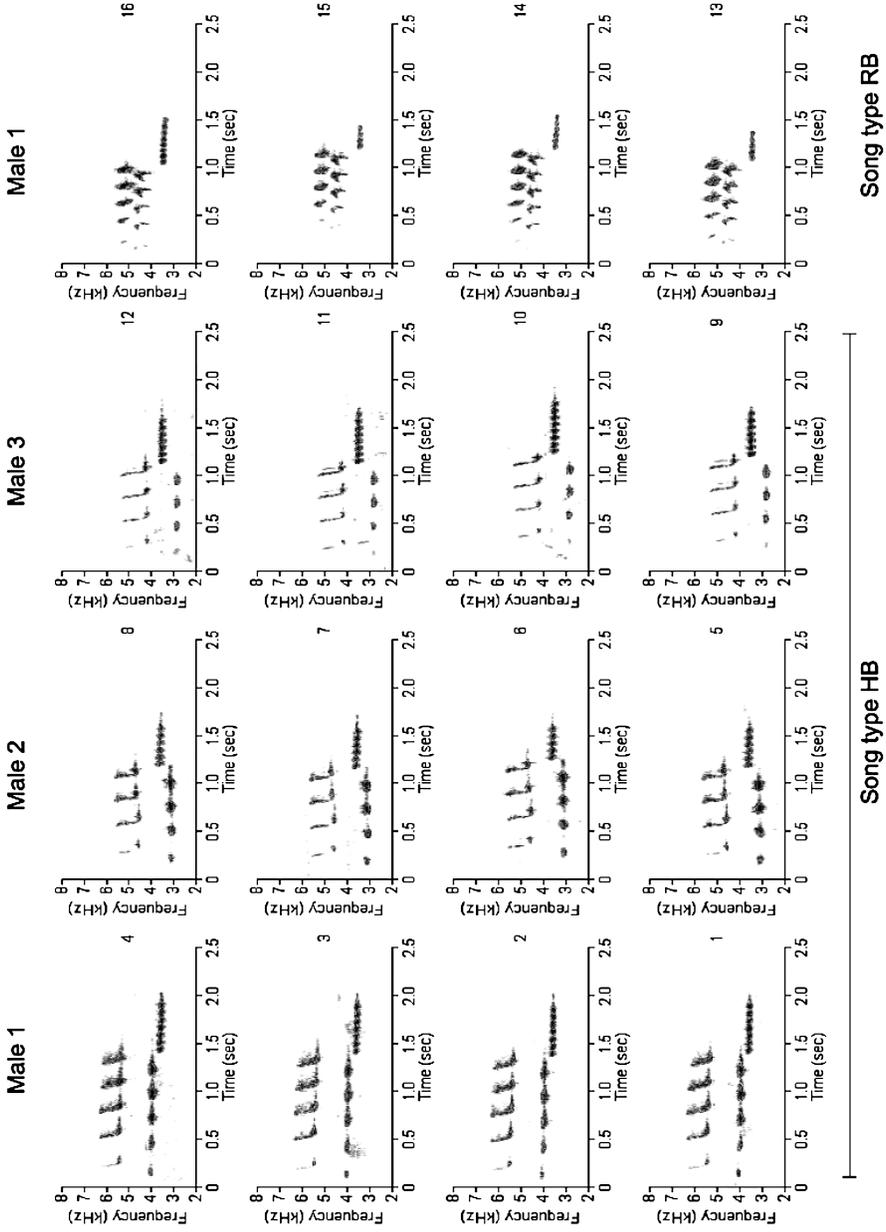
Vocal signalling is usually the primary form of communication in songbirds that enables rival deterrence and mate attraction (Catchpole & Slater, 2008).

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Song is typically species-specific and its multiple roles are facilitated by individual variation which encompasses several dimensions such as song rate, amplitude, repertoire size, temporal organisation, specific syllable structure, etc. (Gil & Gahr, 2002). In birds it is also typical for vocal signalling to take place in a communication network where many individuals may simultaneously at a time may send and receive signals. It is known that songbirds interacting within a social communication network differentiate their response toward specific individuals in a variety of ways, including such sophisticated phenomena as song and repertoire matching. Eavesdropping on interacting rivals and the ability to discriminate between (at least) familiar and unfamiliar individuals based on their vocalisations seem to be necessary prerequisites for such refined interactions (Naguib et al., 1998; Otter et al., 1999; Peake et al., 2001, 2002, 2005; McGregor, 2005; Beecher et al., 2007). In aggressive interactions during territory establishment and maintenance, neighbour–stranger (N–S) discrimination ability is crucial and often results in the dear enemy phenomenon (Temeles, 1994). It can be explained by cooperation between unrelated neighbours who use strategies like ‘tit-for-tat’ and benefit from saving time and energy on boundary disputes (Trivers, 1971; Godard, 1993). However, N–S discrimination may also allow an increase of aggression towards neighbours in social species with intense competition between neighbours (e.g., Müller & Manser, 2007).

To examine the relationships between the capacity for N–S discrimination and song variation, which is likely affected by differences in population ecology (density, sex ratio, pattern of dispersion, etc.), we focused on the ortolan bunting, *Emberiza hortulana*. The ortolan bunting is a Palaearctic songbird with a relatively small repertoire of 2–3 discrete song types per male in the majority of studied populations (Cramp & Perrins, 1994). Ortolan bunting songs have a similar general structure across its geographical range and consist of easy to distinguish (both by ear and visually on sonograms) initial and final phrases. The minimal units of song production in the ortolan bunting are syllables, which are defined as notes with characteristic shapes on sonograms, and different types are denoted in analysis by different letters *A*, *B*, *C*, etc. (Osiejuk et al., 2003). Syllables belonging to one type may differ slightly in duration and could be shifted in frequency among different males (so-called homologous syllables, Osiejuk et al., 2005b) but still have the same shape on a sonogram and sound similar. Songs of the same type consist of exactly the same types of syllables arranged in the same

order, e.g., an *AB*-type consists of *A* syllables at the beginning and *B* syllables at the end, and such a song type is treated in analysis as different from a *BA*-type where the same syllable types are arranged in the opposite order (Osiejuk et al., 2003). The songs are short, with typical durations of one to two seconds and are built up from one to five different types of syllables. In most cases, the initial phrases consist of single syllable type repeated as a trill and characterised by a wide frequency bandwidth. Final phrases are built up from syllables, which have lower overall frequencies and narrower bandwidths than in initial phrases. In most cases, the final phrase is also a trill consisting of a repeated single syllable type, however in some populations (like in Norway) a few syllable types may form final phrases and not all of them are repeated (Osiejuk et al., 2003; Łosak, 2007). Males within a local dialect usually share a single type of final song phrase and have a relatively small number of different syllable types, which form initial song phrases (Figure 1). A single dialect usually covers an area of several hundred square kilometres or more, and dialects seem to be stable over many years (Conrads & Conrads, 1971; Conrads, 1976, 1994; Helb, 1997). Recent research in Norway revealed that in the fragmented and isolated population at the northern range limit of the species, males did not exhibit any dialect pattern and song variation was higher, i.e., males had larger song type repertoires (average around 4–5 types and maximally up to 24) and there was no single final phrase indicating any local dialect (Osiejuk et al., 2003, 2005a, 2007a; Łosak, 2007). However, even in this population males shared some song types (or part of songs) and the level of sharing is an important predictor of mating success (Skierczyński, 2009). Males in this population responded strongly to typical Norwegian song types but were nonresponsive to foreign (Polish) songs and hybrid songs, where Norwegian initial or final phrases were replaced with foreign ones (Osiejuk et al., 2007a). Recently, it was experimentally revealed that ortolan bunting males in this population are able to discriminate between neighbours and strangers. During the simulated territorial intrusions, a single song type derived randomly from a respective neighbour or stranger was played back in paired trials and males responded more aggressively to stranger songs (Skierczyński et al., 2007). Consequently, ortolan bunting males in Norway were found to discriminate between neighbour and stranger without having to listen to their whole repertoires and, thus, are likely to base their discrimination on non-repertoire cues.



In this study, we present the results of a playback experiment conducted in Poland where the ortolan bunting population is three times larger in magnitude than in Norway. Experiments were done in Wielkopolska (Western Poland), where the population of the species is relatively continuous and exhibits a typical degree of local dialect song variation. The average male repertoire size in this population was close to three song types per male and the majority of males shared the single final song phrase (see Figure 1, Łosak, 2007). The goal of the present study is to determine whether ortolan bunting males in a population with a local dialect are able to discriminate between neighbours and strangers when repeatedly presented with a single rendition of only one song type from their repertoires. We assume that if discrimination occurs it should be based on individual distinct cues within a song rather than on repertoire composition, similar to what was found in Norway (Skierczyński et al., 2007). On the other hand, due to higher levels of song type sharing among males in Poland compared to Norway, the possible N–S discrimination in this population may be more difficult to perceive. The lower levels of song type sharing and larger male repertoires of ortolan buntings from Norway simply increase the chance that neighbours and/or strangers would sing some distinct song types and, therefore, would be easy to recognise. In the Polish population of this species, frequently shared song types may be non-informative in this respect as many rivals use them. Such an assumption is consistent with findings from an earlier study on the great tit (*Parus major*; McGregor & Avery, 1986) and the banded wren (*Thryothorus pleurostictus*; Molles & Vehrencamp, 2001). We also discuss relationships between song variation, song sharing and discrimination abilities among territorial males and formulate predictions about expected patterns of geographical variation in these traits.

Figure 1. Sonograms of songs of the ortolan bunting from the study area in W Poland. Each song presented belongs to the same local dialect, i.e., shares the common final narrowband phrase. The figure illustrates both between- and within-song type variation. Songs presented in sonograms 1 to 12 belong to the same type (*HB*), where the letters *H* and *B* denote different syllable types and the order of appearance within a song. Presented songs were derived from repertoires of three different males and presented in separate columns (i.e., 1–4 is the first, 5–8 is the second and 9–12 is the third male). Syllables building *HB* songs have similar shapes, but songs of different males may differ in syllable numbers and frequency. Here, a phrase built of *B* syllables is roughly at the same frequency level, while a phrase built of *H* syllables is clearly shifted among males. Songs presented in sonograms 13–16 belong to a different type (*RB*) and were performed by the first male.

Materials and methods

Study area and subjects

The study was carried out in open habitats located south of the city of Poznań in Wielkopolska National Park and its vicinity (W Poland; coordinates of the centre of the study area: 52°17'N 16°56'E). The study area is typical for this region of Poland and is dominated by farmland with a mosaic of fields, meadows, wastelands and forest patches. Ortolan buntings are common there, preferentially breeding along forest edges, in tree lines surrounded by cultivated fields, and in open habitats with scattered trees. The population of ortolan buntings in Poland exceeds several thousand breeding pairs and in the case of the Wielkopolska region it is more or less continuous within farmland landscape (Kuźniak et al., 1997; Kuźniak & Dombrowski, 2007). In the study area, singing males were counted and intensively recorded since 1998. The number of territorial males usually exceeded 50 per year, and they were evenly distributed among six well-defined farmland habitat patches separated by forest (Łosak, 2007; own unpubl. data). Altogether, we conducted N–S discrimination experiments with 18 ortolan bunting males.

Playback equipment and preparation of song stimuli

For the playback experiments we used a Philips Magnavox ESP25 (Suzhou, P.R. China) compact disc player with a wireless Sekaku WA-320 (Taichung, Taiwan) loudspeaker with a 20 W amplifier (frequency range 50–15 000 Hz and linear frequency response within a species-specific frequency range, i.e., 1.8–6.6 kHz). All songs used in the experiments were recorded during field study using a Marantz PMD670 solid state recorder coupled with a Telinga V Pro Science microphone. The songs used for playback were derived from larger set of recordings from the study area. Starting from the end of April 2008 we made an effort to record whole song type repertoires of all territorial males in the study area. All the songs used for playback were of good quality, recorded at short distances during windless mornings and with no other sounds in the background. The songs selected for playback had a minimum frequency of 2.7 kHz or more; therefore, we first applied a 2 kHz high-pass filter (Avisoft SASLab Pro 4.39, R. Specht, Germany) and then amplified or attenuated samples to match 86 dB sound pressure level (SPL, A-weighting) at 1 m from the loudspeaker. The SPL value was set on the basis of typical

ortolan bunting song amplitude level, which had been measured in the field previously with a CHY 650 (Ningbo, P.R. China) sound level meter. In all cases, the amplitude manipulation did not exceed ± 5 dB, and did not affect song structure. All recordings in our database were originally recorded at 48 kHz sampling rate and 16 bit resolution.

Once all songs were signal-processed, we decreased the sampling rate to 44.1 kHz using a sampling frequency conversion function of Avisoft SASLab Pro, and burned standard compact discs used in the field for playback. During the experiment we used different song renditions (36 songs from 36 different males) belonging to one of two kinds of stimuli: (1) songs from randomly chosen strangers to the subject males (S-treatment) and (2) songs from an adjacent neighbour of the focal males (N-treatment). In the majority of cases, the song stimuli used were song types unshared with the birds tested. However, in four cases for N-treatment and two cases for S-treatment, the song stimuli used were shared with tested males. We did not remove these cases from further analysis as we found no significant effect of adding a shared/unshared song variable into GEE analyses (all p between 0.222 and 0.879). Strangers were males that had territories outside the particular patch where the focal male was established. As the patches were isolated by unsuitable habitats (forest) and distances of over 1 km, we were sure that experimental males were not able to hear strangers from their territories. Ortolan buntings are known to sing with an amplitude around 86 dB SPL measured at 1 m from the source, which means that the hearing range of their songs in open habitats never exceeds 0.5–1 km (Skierczyński et al., 2007).

Procedure for playbacks

We carried out the experiments between 5 May and 17 May 2008 (between 05:00 and 10:00 local time). Each male was subjected to two treatments with identical procedures except that different sounds were played back, i.e., songs of a neighbour (N-treatment) or a stranger (S-treatment), respectively. On the basis of behavioural observations, the experimental period for each male was chosen as the time when unpaired males defended territories intensively and territorial borders with neighbours were well established for at least a few days. All subject males and their neighbours were recorded and their territories mapped prior to the experiments. We only conducted experiments in such places where the arrangement of territories of male subjects

and neighbours remained unchanged between the initial field inspection and the following experiments (2–4 days later). Such a procedure ensured that songs used in N-treatments were derived from a repertoire of a well-known neighbour. The loudspeaker was fixed in a tree about 1.5–2 m above the ground before each treatment and its location was changed slightly (5–10 m) between subsequent treatments with the same male to avoid habituation. Despite some loudspeaker movement, all songs were played back within the focal male territory from a place close to the border of the neighbour male whose song was used in the N-treatment. The loudspeaker was always within the subject male's territory and at a distance of 20–50 m to the song-post used by the male during equipment set-up. We made an effort to place the loudspeaker in a way which allowed the focal bird to take flight towards it and land on a tree or other elevated place at distances lower than 1 m from it. Thus, each male had the potential opportunity to come close to the loudspeaker in comparison to its initial position and without getting closer to the observer, who was located 20–30 m perpendicular to the loudspeaker–focal male line. The N- and S-treatment for each subject were conducted in a random order and were separated by a 1–2-day period. Experiments were only conducted if subject males were regularly singing and their neighbours were silent and not present at typical song posts.

Each treatment consisted of two stages: a three-minute playback (PLAY) followed by three minutes of post-playback silence (POST). During both stages, the behaviour of the focal male was observed. To adequately measure the strength and rapidity of a male's response to playback, the duration of the PLAY and POST stages was determined during earlier experiments with the species. During each treatment, the same song rendition was played back with a species-typical rate of six songs per minute (Osiejuk et al., 2003) and the playback was started ca. 2 s after the song of the focal male. This allowed the focal male to avoid overlapping with the following playback songs, especially because an increase in song rate during a playback phase is not a typical response (Osiejuk et al., 2007b). The POST stage was relatively short to avoid including any behaviour into the analysis caused by non-playback factors, which might occur after we stopped the playback. Observations of the behaviour of the males were recorded on an Olympus VN-240PC Digital Voice Recorder and notes were transcribed later the same day using dedicated software (Olympus Digital Wave Player 2.0.2), which enables 1 s accuracy of extracting variables. Distance measurements were done with a

Bushnell Yardage Pro Sport 450 laser rangefinder (1 m accuracy). The following nine original response measures were recorded: flight latency toward loudspeaker (s), latency to approach at the closest distance(s), closest distance to the loudspeaker (m), and number of flights, songs and calls during and after the playback.

Statistical analysis

The birds' responses to playback usually have multidimensional character and were, thus, measured by a set of response variables. Separate tests on original variables would not be statistically independent and would not reveal the multivariate character of the response (Rice, 1989; McGregor, 1992). Therefore, we initially combined all original variables into orthogonal principal components through a principal components analysis. Results of this analysis were ambiguous as we obtained the relatively large number — in comparison to earlier playback experiments with ortolan bunting — of four principal components with eigenvalues over 1.0 (Osiejuk et al., 2007a,b; Skierczyński et al., 2007). We assessed the factorability of the data and according to the Bartlett test of sphericity (113.41, $p < 0.001$) the data set should be considered appropriate. The Kaiser–Meyer–Olkin measure of sampling adequacy, however, had a value of 0.505, suggesting that the degree of common variance among the nine original variables was inadequate (Pallant, 2001; Tabachnick & Fidell, 2001). Therefore, we tested the effect of treatments on separate variables with the Generalized Estimating Equation (GEE) method. We used GEE with a normal or Poisson probability distribution (depending on which variable was tested), an independent working correlation matrix structure and an identity link function in SPSS 16. GEE is an extension of the quasi-likelihood approach that accounts for the nested structure in an experimental design (two treatments for each male in our case). The advantage of GEE is that it could be applied to data with different distribution patterns (not all of our variables were normally distributed) and enables incorporating additional predictors (treatment order in this study). Values of original variables are presented as 95% confidence interval for GEE or as means \pm SE or medians, depending on the data distribution.

Results

We found significant differences between the response to playback of neighbour and stranger songs. There are two characteristic aspects of response to

Table 1. Estimated 95% Wald confidence intervals of the response to the playback, calculated for N- and S-treatments, where neighbour and stranger songs were presented.

Statistics and original response variable	95% Wald confidence interval		Wald χ^2	Treatment effect p -value
	N-treatment	S-treatment		
Flight latency (s)	19.47–81.20	10.01–21.10	8.92	0.003
Approach closest distance latency (s)	86.89–147.45	58.72–111.73	3.99	0.046
Closest distance (m)	2.32–9.57	1.25–4.42	2.80	0.095
Flights during playback	4.74–9.03	7.32–12.68	4.55	0.033
Flights after playback	2.50–4.61	3.12–6.21	1.42	0.233
Songs during playback	10.33–22.45	13.12–25.10	1.22	0.269
Songs after playback	15.0–23.44	21.22–32.89	4.80	0.028
Calls during playback	9.72–42.50	25.23–69.43	5.60	0.018
Calls after playback	4.48–29.08	3.83–18.95	0.44	0.507

Wald χ^2 and p -values concern separate GEE analyses for original response measures.

rival songs in the ortolan bunting, which could be defined as rapidity and the strength of response (Osiejuk et al., 2007b). Rapidity is best reflected by the time in which one may observe changes in focal male behaviour; in our experiments it is related to flight and approach latency. Males responded more promptly to stranger songs (flight latency median = 12.5 s) in comparison to neighbour songs (median = 22.5 s) and these differences were statistically significant (Table 1). The strength of response was well reflected by the number of flights, closest distance and the relation between numbers of songs and calls given. Analyses of original variables obtained in this study indicate that males responded stronger to playback of stranger songs compared to playback of neighbour songs. The median number of calls during playback for S-treatment was 14, while for N-treatment was only 2.5 (see Table 1). The average number of songs given after playback was significantly larger when males responded to stranger songs (27.1 ± 3.06) in comparison to neighbour songs (19.2 ± 2.21). Males tested with stranger songs had significantly more flights towards the loudspeaker (10.0 ± 1.4) than when tested with neighbour songs (6.9 ± 1.13 ; Table 1). Also the closest distance of approaching to the loudspeaker was shorter in case of S-treatment (2.8 ± 0.83 m) than of N-treatment (5.9 ± 1.90 m).

Ortolan bunting males typically sing with a rate of around 6 songs per minute and give no calls when they are not interacting with other individuals.

When males respond to rivals they usually cease singing or substantially decrease their song rate and start calling (Osiejuk et al., 2007a,b). Thus, the number of songs and calls is usually negatively correlated and an increase of song rate, if any, is observed after playback, i.e., when a focal male finished direct interaction with the playback. Thus, if response to S-songs is stronger, we should expect a stronger negative correlation between the number of songs and calls given during the PLAY stage of the experiment for the S-treatment. In fact, when N-songs were played back the correlation between the number of songs and calls uttered during playback was $r_s = -0.57$ ($p = 0.013$), while for S-songs this relation was stronger ($r_s = -0.79$, $p < 0.001$).

We found that the order of the treatments did not significantly affect any of the measured response variables (all $p > 0.21$ in GEE analysis).

Discussion

The results of this study indicate that ortolan bunting males in a population with a local dialect and high levels of song type sharing are able to discriminate between neighbours and strangers based on a single song rendition (played back repeatedly) derived from the respective rivals' repertoire. These results are consistent with an earlier study on this species (Skierczyński et al., 2007) and show that N–S discrimination is a widespread phenomenon, acting somewhat independent of song type diversity and sharing, which may substantially differ between ortolan bunting populations (Osiejuk et al., 2003, 2007a; Łosak, 2007). N–S discrimination behaviour was observed in several other Emberizidae species, regardless of song repertoire size (e.g., Goldman, 1973; Hansen, 1984; Stoddard et al., 1991a). Moreover, there is an increasing amount of data indicating that N–S discrimination occurs in birds regardless of whether they learn their songs or not (Lovell & Lein, 2004, 2005; Mackin, 2005) and even in those species which have extremely large repertoires (Briefer et al., 2008). It seems plausible that species with song repertoire sizes differing in an order of magnitude might use different routes for discriminating between neighbours and strangers. On the other hand, within-species comparisons may help us understand how different ecological factors shape discrimination processes or abilities in a similar way as was revealed for relations between migration and song development (Nelson et al., 1996a;

Nelson, 1999) and memory capacity (Nelson et al., 1996b). This study, together with our earlier experiments (Skierczyński et al., 2007) gives an opportunity for such a comparison.

Population differences in N–S discrimination

Ortolan bunting males from Poland (this study) and Norway (Skierczyński et al., 2007) both responded differently to neighbour and stranger songs, giving a stronger response to the song of an unfamiliar individual. However, male subjects from Poland responded to stranger song playback with shorter flight latency and gave more calls during playback than males from Norway (Skierczyński et al., 2007). These differences in response may reflect variation in male spatial arrangement in both populations. Neighbouring males in Poland had a typical linear distribution as birds settled down along tree alleys or forest–open habitat edges (Goławski & Dombrowski, 2002). Thus, in the study area most males usually had up to two neighbours (unpublished data). In Norway, the arrangement of males was more complicated. The preferred habitats were wider patches, within which territories often occurred in clumps (Dale & Hagen, 1997; Dale et al., 2005, 2006). Moreover, there are observations suggesting that males in the Scandinavian population in general tend to aggregate (Vepsäläinen et al., 2007; Berg, 2008; Skierczyński, 2009). It is also characteristic that, within a typical territory in Norway, a male has very many song posts; in burned forest areas and peat bogs there are hundreds of shrubs or small trees available (Dale & Hagen, 1997; pers. obs.). In the study area in Poland, relatively small numbers of song posts occur within a typical territory and consequently birds are more restricted in their movements. Therefore, it was not surprising that we observed some differences in movement patterns during response to playback between these two populations. We suppose that habitat characteristics facilitate a step-by-step approach toward the loudspeaker in Norway, as birds are not limited by song post availability. In fact, the placement of the loudspeaker in relation to a focal male and his neighbour territory was much more similar between experiments in Norway than in Poland. Secondly, males in Poland with fewer direct neighbours might have a more rapid response to playback because discriminating between two neighbours and a stranger is perceptually an easier task than discriminating between four or five neighbours and a stranger. Such an explanation seems to be reasonable regardless of what kind

of cue is used for N–S discrimination. For the reasons mentioned above, the overall response of ortolan bunting males in Poland was more variable which affected the relationships between original response measures (see Materials and methods).

Repertoires and alternative N–S discrimination cues

In the experiments presented here and those conducted in Norway (Skierczyński et al., 2007), a single song rendition was used for each playback. This suggests that the N–S discrimination in both populations results from the same mechanism, which enables the extraction of information about rival identity from a single example of a particular song type from a neighbour's repertoire. This assumes that the repertoire composition is not crucial for the discrimination process in the ortolan bunting. Similar results were found for the song sparrow, *Melospiza melodia*, a species with a moderate repertoire size, which was shown to discriminate between neighbours and strangers and among different neighbours on the basis of a single song type (Stoddard et al., 1991a,b). These good discrimination skills of male song sparrows were linked with their memory capacity. Stoddard et al. (1992) showed that they can learn up to 64 different song types, which is probably not the limit for their memory capacity. Ortolan bunting are usually regarded as small repertoire singers, as the majority of studied males in the population had only two or three different song types (Cramp & Perrins, 1994). However, recent findings showed that under specific conditions males could learn and use much more song types than was previously believed (up to 24, Osiejuk et al., 2003, 2008; Łosak, 2007). It is not known how many songs ortolan buntings are able to learn or remember, without singing them, although it seems that repertoire size and learning ability are not limiting factors for N–S discrimination (Skierczyński et al., 2007). We expected that birds would categorize songs first to a particular song type (Searcy et al., 1999), but due to song type sharing it is clearly not enough to discriminate between rivals.

Song diversity, measured as the number of different song types found per male, differs substantially between Norwegian and Polish ortolan bunting populations (i.e., 0.7 vs. 0.11 types per male; Osiejuk et al., 2005a), which is also reflected by a much higher level of song sharing among neighbours in Poland. So, even if one may imagine that birds in Norway discriminate between neighbours and strangers because they remember song types of neighbours and because strangers are likely to sing different types than neighbours,

such a scenario is unlikely for Polish ortolan buntings. In this population, practically all birds sing the same dialect (i.e., have the same final phrase in all songs, see Figure 1) and usually share initial phrases with both neighbours and non-neighbours, as the number of rare song types is low (Łosak, 2007). Small repertoire sizes, low population song type diversity and the high level of song type sharing are typical for the ortolan bunting within a continuous range (Cramp & Perrins, 1994). We suggest that it is unlikely that N–S discrimination in this species relies on repertoire differences between males and that observed sizes and composition of repertoires have evolved under strong selection on individual recognition. The study on Norwegian ortolan buntings supports this idea, too. Despite higher song variation in this population, N–S discrimination experiments were conducted with commonly shared songs only (for details see Skierczyński et al., 2007). We agree with Lambrechts & Dhondt (1995) that individual recognition processes might be accomplished due to song variation at a level different than repertoire variation. These authors have suggested such mechanisms as “song rendition” and “individual voices”, which reflect many observations that even shared songs differ between individuals and such relatively small differences are often individually specific and could potentially be a good cue for discrimination between familiar and unfamiliar males (Stoddard et al., 1988; Osiejuk et al., 2007c).

We have observed such consistent between-male differences in both studied populations of ortolan bunting. First, males singing particular song types often differed in the numbers of particular syllables, while they still produced them in the same order. Analysis of long recordings clearly show that males tended to sing in their own way and that such differences are easy to observe even by a human, e.g., if one male is singing the *AAAABB* version of an *AB*-song type all the time, while the other is singing *AABB* (Osiejuk et al., 2003; Łosak, 2007). Second, shared song types both in Norway and in Poland often differed in frequency parameters and might be shifted between males, even by over 1 kHz, while within-individual variation in frequency remained below 0.1 kHz (see Figure 1) and frequency parameters were stable between seasons (Osiejuk et al., 2005b; Łosak, 2007). Both types of within-song type variation are, thus, good candidates for N–S discrimination cues.

Song sharing and N–S discriminating — expected patterns

Our findings suggest that there could be an interesting link between repertoire variation and cues used for N–S discrimination. We hypothesise that

for species with small and moderate repertoire sizes, the task of N–S discrimination is more difficult when the level of repertoire sharing is high. Consequently, if the within-song type variation is related to discriminative processes, one should expect positive correlations between within-song type variation and song type sharing. As sharing is affected by males' dispersal levels and repertoire size, one may expect that across a species' range there should be visible patterns of within-song variation related to these factors. We predict that if N–S discrimination selection is relatively equivalent in a species (which might not be true for some wintering and migrating populations; Kroodsmas et al., 1999), within-song type variation should increase with an increase of song type sharing.

Recent comparisons of ortolan bunting song structure between Norway and Poland partially supports this hypothesis. Łosak (2007) found significantly higher within-song type variation measured by the number of different variants in Poland while at the same time those males had significantly smaller song type repertoires and higher song type sharing. We suggest that both types of within-song type variation, i.e., variation in syllable numbers and shifted frequencies of songs, could be involved in discrimination processes in the ortolan bunting and, in general, they may explain why song repertoires in other species do not hinder N–S discrimination (Weary et al., 1992). The issue of how repertoire size and N–S discrimination are related is very important. First, repertoire composition could aid N–S discrimination if repertoires of individuals differ enough. However, the larger repertoires are the more discrimination process based on this trait would be affected by memory capacity. Discrimination between rivals with large and partially shared repertoires would demand time and it would be additionally affected by the style of singing. The content of repertoires could be presented in different ways, e.g., immediate variety singing could provide more recognition cues than eventual variety singing (Naguib & Todt, 1998; Molles & Vehrencamp, 1999). Second, there is growing evidence that song repertoires evolved under selection towards being large and function as an honest trait in sexual selection (e.g., great reed warbler *Acrocephalus arundinaceus*; Hasselquist et al., 1996), or towards being shared with neighbours (e.g., song sparrow; Hughes et al., 2007). However, to our knowledge there is a lack of data suggesting that repertoires evolved primarily under selection to serve in N–S discrimination. Here we propose the proximate mechanisms (i.e., within-song type variation) that enabled the release of discrimination tasks

from the repertoire level. We further predict the relationships between variations in discrimination cues among males and the level of song type sharing, which could easily be tested by comparing populations with different levels of song type sharing.

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