# Neighbour-stranger song discrimination in territorial ortolan bunting *Emberiza hortulana* males

## Michał Skierczyński, Kamila M. Czarnecka and Tomasz S. Osiejuk

*M. Skierczyński, Kamila M. Czarnecka and T. S. Osiejuk (correspondence), Dept. of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland. E-mail: t.s.osiejuk@life.pl*

Neighbour-stranger discrimination has been demonstrated in many species, but the mechanisms employed in discrimination vary. We tested whether an oscine bird with small repertoire size, the ortolan bunting *Emberiza hortulana*, discriminated between songs of neighbours and strangers. We performed playback experiments to measure response of males to a repeated single example of a single song type derived from a repertoire of a neighbour or stranger. Thirteen males were tested twice each, and in both cases songs were broadcast from the territory boundary shared by the subject male and the neighbour. Subjects responded more aggressively to songs of strangers than neighbours, i.e. they approached the loudspeaker faster and came closer and did more flights during the playback of stranger song. We found no significant differences in vocal response between treatments. We conclude that ortolan bunting can discriminate between songs of neighbours and strangers. This study provides experimental evidence for ortolan buntings in neighbour-stranger discrimination. It also demonstrates that a single example of song is enough to discriminate between neighbours and strangers. We discuss which song characteristics are the possible acoustic basis for discrimination in the studied species.

Bird song plays a crucial function in defending a territory and usually acts as a first line of defence (Catchpole and Slater 1995). Territorial males of many bird species form communication networks in which song may be uttered in a very sophisticated manner. For example, birds may direct signals toward specific individuals (Beecher et al. 2000) and adjust their response to other signallers with respect to their own status, aggressive motivation or needs and use it to evaluate (e.g. by eavesdropping) the status of signallers (Peake et al. 2002). One of the necessary prerequisites for such refined vocal interactions is the ability to discriminate between individuals based on their vocalization. In over one hundred territorial bird species, "neighbour-stranger" (N-S) discrimination was shown to be crucial for shaping the strength of response of the territory owner during simulated territorial intrusions of strangers in contrast to intrusions of neighbours (Lambrechts and Dhondt 1995, Stoddard 1996). N-S discrimination seems to be a group of processes ranging from simple habituation to sophisticated learning rather than a single method that is widespread among different

species (Wiley and Wiley 1977, Richards 1979, Godard 1991). Most of the former studies stressed that the difficulty of correctly assigning signals to neighbours and strangers should increase with the repertoire size and the number of neighbours within hearing range (e.g. Beecher 1989). N-S discrimination is most often explained in evolutionary terms by the "dear-enemy" effect, where neighbours may reduce the scale of conflicts within a group of familiar males in comparison to interactions with floaters. Such an explanation assumes some kind of 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).

The ortolan bunting *Emberiza hortulana* is a songbird with a relatively small repertoire of 2–3 (up to 5) song types per male according to Cramp and Perrins (1994). Songs of the ortolan bunting have a similar general structure in all studied populations and consists of initial and final phrases, which differ in overall frequency and bandwidth (Fig. 1). Ortolan buntings form apparent dialects in Central and southern Europe.
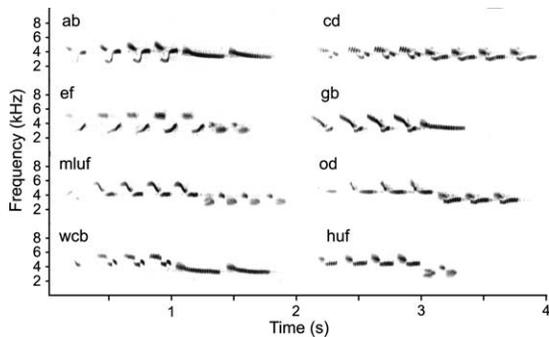
Fig. 1. Sonograms of typical songs of ortolan bunting *Emberiza hortulana* from the studied population in Norway. Each letter denotes single syllable type and sequence of letters is a song type of particular song.

Males within a dialect usually share a single type of final song phrase and have a relatively small repertoire of initial song phrases. A single dialect usually covers an area of several hundreds of square kilometres or more, and dialects seem to be stable over many years (Cramp and Perrins 1994).

In this paper we present a study on an isolated and patchy Norwegian ortolan bunting population, which is characterized by higher song variation (Osiejuk et al. 2003, 2005a, in press). The average repertoire size in this population was close to 5 song types per male (range 1–24), there was no single final phrase of song shared by the majority of males, and particular males often had song types in their repertoires with different final phrases as well as the repertoire of initial phrases was also high.

We report here an experiment that aims to find out whether males of ortolan bunting are able to discriminate between neighbours and strangers when presented with a repeated several times single example of a single song type from their repertoires. We assume that if the discrimination occurs it should be based on individual specificity of song rather than on repertoire composition. This is, to our knowledge, the first N-S recognition study on the species.

## Materials and methods

### Study area and subjects

Our study was carried out in Hedmark County, Norway, which includes most of the ortolan bunting range in Norway. The studied population consisted of ca. 100 males inhabiting about 30 well-defined habitat patches with a range of 1 to >20 singing males. The population is heavily fragmented and all sites are distributed over an area of 500 km². The closest neighbouring population is located in Sweden, a

distance of about 250 km. Birds were tested in all typical habitats used by this species in Norway, i.e. raised peat bogs, forest clear-cuts on poor sandy soils, land being cleared for cultivation and burnt forest (more details in Dale and Hagen 1997, Dale 2000). Most males in this population were colour-ringed due to a long-term research project that was started over 10 years ago.

### Playback equipment and preparation of song stimuli

For the playback experiments we used a Marantz PMD670 solid state recorder with a Creative Travel Sound neodymium loudspeaker (linear response within species-specific frequency range, i.e. 1.8–6.6 kHz). Each experiment used different songs (26 song samples altogether) belonging to one of two kinds of stimuli: (1) songs from randomly chosen strangers to the subject males (S-treatment), and (2) songs from a neighbour of the focal males (N-treatment).

Strangers were males that had territories outside the particular patch where the focal male was tested. Ortolan bunting males in Norway may change singing territories during the breeding season if they fail to attract a female at the first site reached after spring migration (Dale et al. 2005, 2006). We were, therefore, very selective in choosing strangers' song for playback experiments, insisting that each stranger was separated from a respective focal male territory by at least 10 km (i.e. much more than hearing range, which probably never exceeds 0.5–1 km). Additionally, in each case we knew that the stranger male did not change his place of singing during the season before the time the experiment with the song derived from his repertoire was conducted. We knew from an earlier study, that strangers from a distance of ≥10 km were not treated as a foreign males in playback experiments (Osiejuk et al. in press).

All the songs used were of good quality and were digitally prepared (2 kHz high-pass filter, amplified or attenuated) to match 86 dB signal pressure level (SPL) at 1 m from the loudspeaker. The SPL value was set on the basis of normal ortolan bunting song amplitude level, which had been measured in the field previously. We used Avisoft SASLab 4.39 software to prepare playback cuts (Specht 2002).

### Procedure for playbacks

We carried out the experiments between 13 and 26 May 2006, (between 05:00 and 09:30 h local time). On the basis of behavioural observations the experimental period was chosen as the time when males defended territories intensively and territorial borders were well

established for at least a few days. In spring 2006, the first males were observed on 3 May. All subject males and their neighbours were recorded and their territories mapped prior to experiments. We conducted experiments only in such places where the arrangement of territories of subject males and neighbours remained unchanged between initial control and following experiments (2−4 d later). Such a procedure ensured that songs used in N-treatments are derived from a repertoire of a well-known neighbour, as territorial males are known to sing up to 370 songs per h during morning hours (Osiejuk et al. unpubl. data from microphone array study).

Before each treatment the loudspeaker was placed in a tree about 1.5−2 m above the ground. The place was always within the subject male's territory and at a distance of 20−40 m to his song post observed during equipment set-up. Two treatments (N and S) were conducted in random order for each subject, and both treatments for a particular male were done on different days separated by a 1−2 d period. Both treatments were only conducted if the subject male was regularly singing and his neighbour was silent and not present at typical song posts. We typically waited for a moment when the neighbour spontaneously stopped singing and started foraging. The location of the loudspeaker was changed slightly (5−10 m) between subsequent treatments to avoid habituation, but in both treatments we played back songs within the focal male territory from a place close to the border with the neighbour male whose song was used in N-treatment. The loudspeaker was placed in a way which allowed the focal male to move towards the loudspeaker and to land on a tree, bush, rock or elevated ground at distances less than or equal to 10 m and 1 m from it. Therefore, each subject had the opportunity (at least potentially) to approach the loudspeaker substantially (10 m), or even very close (1 m), in comparison to its initial position. The loudspeaker was always placed in such a position that the bird did not move towards the observer, who was located approximately 20−30 m perpendicular to the straight line between the loudspeaker and the focal male at the beginning of the trial.

Each treatment consisted of two stages: a three-minute playback (PLAY) followed by three minutes of after playback (POST) observation of the behaviour of the focal male. The timing of the PLAY and POST stages, in respect to adequately measuring the strength and promptness of focal male response to playback, were determined during earlier experiments with the species. The same songs were played back during the PLAY stage with a typical for the species rate of six songs per minute (Osiejuk et al. 2003) and the playback was started ca 2 seconds after the last 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. in press). Observations of the behaviour (flights and distance to the loudspeaker) of the males were dictated to a digital voice recorder and notes were transcribed later the same day using dedicated software, which enables 1 s accuracy of extracting variables. During experiments, all of the focal males were recorded by the second observer using a second Marantz PMD670 recorder coupled with a Telinga V Pro Science microphone. These recordings were used to extract timings of all songs and calls uttered by experimental birds. As preliminary analyses showed no significant differences between treatments according to how frequently different call types were uttered, we only used a simple measure of calling activity in further analysis, i.e. the total number of calls uttered during and after playback. The following ten measures of focal males response were noted: flight latency towards loudspeaker (s), 10 m loudspeaker approach latency (s), 1 m loudspeaker approach latency (s), closest distance to the loudspeaker (m), number of flights over 1 m during and after playback, and number o songs and calls given during the playback and after playback stages.

## Statistical analysis

Altogether, we measured 10 response variables that describe the responses of the males to playback, which in 40% of cases correlated significantly with each other. As separate tests on original variables would not be statistically independent and would not reveal the multivariate character of the response (McGregor 1992) we combined all original variables (Table 1) into two orthogonal principal components (PC1 and PC2, Table 2). The data set appeared to be suited for such an analysis (Kaiser-Meyer-Olkin measure of sampling adequacy = 0.673, Bartlett test of sphericity = 132.78, $P < 0.001$). We used general linear model (GLM) to test for differences in response measure (PC1 and PC2) between treatments (neighbour vs stranger) with the playback order (neighbour first vs stranger first) and interaction between treatment and order included in the model. Statistical tests were two-tailed and calculated by SPSS 12 PL software.

## Results

We conducted experiments with 13 males. The original measures of males' response to playback are presented in Table 1. All the approach-related response measures were strongly correlated with PC1 and lower values of PC1 corresponded to a stronger response, i.e. faster approach to a closer distance and more flights during playback (Table 2). PC2 was positively correlated with

Table 1. Means ($\pm$SE) of the original variables of the response to the playback calculated separately for treatments where neighbour and stranger songs were presented. P-values of paired t-test for original response measures are given.

| Statistics and original response variable | Mean $\pm$ SE | | Paired tests P-value |
| --- | --- | --- | --- |
| | N-treatment | S-treatment | |
| Flight latency (s) | $93 \pm 25.4$ | $57 \pm 12.0$ | 0.219 |
| Approach 10 m latency (s) | $149 \pm 35.0$ | $99 \pm 15.3$ | 0.252 |
| Approach 1 m latency (s) | $327 \pm 23.0$ | $200 \pm 38.4$ | 0.038 |
| Closest distance (m) | $11.2 \pm 3.7$ | $1.6 \pm 0.4$ | 0.003* |
| Flights during playback | $2.3 \pm 0.52$ | $4.6 \pm 0.93$ | 0.034 |
| Flights after playback | $1.0 \pm 0.36$ | $1.3 \pm 0.43$ | 0.810 |
| Songs during playback | $6.6 \pm 1.78$ | $6.6 \pm 2.36$ | 1.0 |
| Songs after playback | $6.2 \pm 1.94$ | $14.3 \pm 3.53$ | 0.044 |
| Calls during playback | $44.7 \pm 12.49$ | $61.3 \pm 17.00$ | 0.355 |
| Calls after playback | $45.8 \pm 13.63$ | $44.8 \pm 16.42$ | 0.964 |

*Test significant after Bonferroni's adjustment.

the number of songs given during and after playback and negatively with the number of calls uttered during both experimental stages. PC2 was also positively related to the number of flights given after playback (Table 2). PC2 reflects the typical bimodality of vocal response for the studied species, where males usually vary constantly between mostly singing and calling (e.g. Osiejuk et al. in press).

A subject usually responded to playbacks by moving toward the loudspeaker, singing and calling. We found substantial differences between response to neighbour and stranger songs. When tested with stranger songs, males approached the loudspeaker faster, came closer and did more flights during the playback (Table 1). GLM analysis revealed that treatment was the only important factor affecting response of ortolan bunting males to playback. There was a significant effect of treatment on PC1 measure, which was reflected by the smaller scores gained during S-treatment ($F_{1,12} = 4.54$, $P = 0.044$). At the same time, we found no significant effect of treatment on PC2 measure ($F_{1,12} = 0.01$, $P = 0.893$), and there was no significant effect of both order (PC1: $F_{1,12} = 0.79$, $P = 0.384$; PC2: $F_{1,12} = 0.32$, $P = 0.576$), and treatment $\times$ order interaction (PC1: $F_{3,12} = 0.10$, $P = 0.759$; PC2: $F_{3,12} = 0.98$, $P = 0.331$). These results suggest that there was no effect of repeated playback and treatment order.

## Discussion

We found that the ortolan bunting males we studied in Norway responded noticeably stronger to the playback of strangers' songs in comparison to the song of neighbours. There were significant differences in approach-related measures of response, but not in vocal response. Such results are consistent with our earlier experiments with this species, which also showed that approach-related measures of response usually differ the most between treatments of different threat value (Osiejuk et al. in press).

The results of the present study indicate that ortolan buntings can discriminate between neighbours and strangers. Similar results were found in other members of the Emberizidae family, including species with single song type repertoire (field sparrow *Spizella pusilla*, Goldman 1973), small repertoire size (e.g. yellowhammer *Emberiza citrinella*, Hansen 1984), or moderate repertoire size, song sparrow *Melospiza melodia*, Stoddard et al. 1991a).

Moreover, our study suggests that N-S discrimination in ortolan bunting results from a mechanism, which enables the extraction of information from a single example of a particular song type from a neighbour's repertoire. Differentiating response to a single song type (neighbour vs stranger) presented during playback suggests that the repertoire composition is not important for the recognition process in the ortolan bunting. Stoddard et al. (1991a,b) showed similar results in song

Table 2. Eigenvalues, variance explained and weightings of the original variables in the first two principal components extracted from the ten original variables of the response to the playback. Measures that contributed most to the particular compound variable are in bold.

| Statistics and original response variable | PC1 | PC2 |
| --- | --- | --- |
| Eigenvalue | 3.576 | 3.025 |
| Percent of variance | 35.759 | 30.246 |
| Cumulative percent | 35.759 | 66.005 |
| Flight latency | **0.721** | 0.196 |
| Approach 10 m latency | **0.856** | 0.138 |
| Approach 1 m latency | **0.775** | −0.180 |
| Closest distance | **0.893** | 0.002 |
| Flights during playback | **−0.833** | −0.003 |
| Flights after playback | −0.191 | **0.797** |
| Songs during playback | 0.163 | **0.832** |
| Songs after playback | −0.153 | **0.775** |
| Calls during playback | −0.368 | **−0.676** |
| Calls after playback | −0.100 | **−0.742** |

sparrow, moreover it was also demonstrated that song sparrow males are able to learn all song types of their neighbours in a typical natural situation (Stoddard et al. 1992). However, possible familiarity with large number of song types may be not be sufficient for explaining N-S and N-N discrimination as song types shared among many neighbours may discontinue being informative on signaller identity (Schroeder and Wiley 1983). Therefore, the proper recognition system should involve some extra information apart from the repertoire composition of particular neighbours.

Lambrechts and Dhondt (1995) proposed two other mechanisms underlaying individual recognition: "song rendition" and "individual voices". They reflect observations of many authors that shared song types are in fact not identical and these small differences within shared songs could be potentially a good cue for individual recognition as are characterized by greater between- than within-individual variation of acoustic parameters. Ortolan bunting males usually sing different variants of the same song types, which differ in numbers of particular syllables within song renditions (Osiejuk et al. 2003). This within song-type variation was not thoroughly investigated, but preliminary results suggest that particular males tend to sing more often particular variants (own unpubl. data), and other bunting species are known to perceive such small variation in the structure of songs (Stoddard et al. 1988). In ortolan bunting we also found substantial differences in frequency parameters between syllables derived from same song types among males (Osiejuk et al. 2005b). Some shared syllables and song types were shifted in frequency by up to 1 kHz when several males were compared, and these differences remained individually stable between following years. These results suggest that in ortolan bunting clear between-individual differences may exist regardless of repertoire size and sharing-pattern.

We would like to stress necessity of further studies on N-S and N-N discrimination, which involve manipulation of the song acoustic parameters.

# References

Beecher, M. 1989. Signalling systems for individual recognition: an information theory approach. – Anim. Behav. 38: 248–261.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. and Nordby, J. C. 2000. Song-type matching between neighbouring song sparrows. – Anim. Behav. 59: 21–27.

Catchpole, C. K. and Slater, P. J. B. 1995. Bird song. Biological themes and variations. – Cambridge University press, Cambridge.

Cramp, S. and Perrins, C. M. 1994. Birds of the western Palearctic: handbook of the birds of Europe, the Middle East and North Africa. Vol. 9. – Oxford University Press, Oxford.

Dale, S. 2000. The importance of farmland for ortolan buntings nesting on raised peat bogs. – Ornis Fenn. 77: 17–25.

Dale, S. and Hagen, Ø. 1997. Population size, distribution and habitat choice of the ortolan bunting *Emberiza hortulana* in Norway. – Fauna Norvegica, Ser. C, Cinclus 20: 93–103.

Dale, S., Lunde, A. and Steifetten, Ø. 2005. Longer breeding dispersal than natal dispersal in the ortolan bunting. – Behav. Ecol. 16: 20–24.

Dale, S., Steifetten, Ø., Osiejuk, T. S., Losak, K. and Cygan, J. P. 2006. How do birds search for breeding areas at the landscape level? Interpatch movements of ortolan buntings. – Ecography 29: 886–898.

Godard, R. 1991. Long-term memory of individual neighbours in a territorial songbird. – Nature 350: 228–229.

Godard, R. 1993. Tit for tat among neighboring hooded warblers. – Behav. Ecol. Sociobiol. 33: 45–50.

Goldman, P. 1973. Song recognition by field sparrows. – Auk 90: 106–113.

Hansen, P. 1984. Neighbour-stranger song discrimination in territorial yellowhammer *Emberiza citrinella* males, and a comparison with responses to own and alien song dialects. – Ornis Scand. 15: 240–247.

Lambrechts, M. M. and Dhondt, A. A. 1995. Individual voice discrimination in birds. – Curr. Ornithol. 12: 115–139.

McGregor, P. K. 1992. Quantifying responses to playback: one, many, or composite multivariate measures? – In: McGregor, P. K. (ed.). Playback and studies of animal communication. Plenum Press, New York, pp. 79–96.

Osiejuk, T. S., Ratynska, K., Cygan, J. P. and Dale, S. 2003. Song structure and repertoire variation in ortolan bunting (*Emberiza hortulana* L.) from an isolated Norwegian population. – Ann. Zool. Fenn. 40: 3–16.

Osiejuk, T. S., Ratynska, K., Dale, S. and Cygan, J. P. 2005a. Isolation, patchiness and dispersal pattern strongly affect singing behaviour in ortolan bunting (*Emberiza hortulana*). – XXIX Int. Ethol. Conf. Abs. Budapest, Hungary. August 20–27, 2005, p. 166.

Osiejuk, T. S., Ratynska, K., Cygan, J. P. and Dale, S. 2005b. Frequency shift in homologue syllables of the ortolan bunting *Emberiza hortulana*. – Behav. Proc. 68: 69–83.

Osiejuk, T. S., Ratynska, K. and Dale, S. 2007. What makes a 'local song' in a population of ortolan buntings without a common dialect? – Anim. Behav. in press.

Peake, T. M., Terry, A. M. R., McGregor, P. K. and Dabelsteen, T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? – Proc. R. Soc. B 269: 1925–1929.

Richards, D. 1979. Recognition of neighbors by associative learning in rufous-sided towhees. – Auk 96: 688–693.

Schroeder, D. J. and Wiley, R. H. 1983. Communication with shared song themes in tufted titmice. – Auk 100: 414–424.

Specht, R. 2002. Avisoft-SASLab Pro sound analysis and synthesis laboratory. A PC-software for MS-Windows 95/98/ME/NT/2000/XP. – Avisoft Bioacoustics, Berlin.

Stoddard, P. K. 1996. Vocal recognition of neighbors by territorial passerines. – In: Kroodsma, D. E. and Miller, E. H. (eds). Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca and London, pp. 356–374.

Stoddard, P. K., Beecher, M. D. and Willis, M. S. 1988. Response of territorial male song sparrows to song types and variations. – Behav. Ecol. Sociobiol. 22: 125–130.

Stoddard, P. K., Beecher, M. D., Horning, C. L. and Willis, M. S. 1991a. Strong neighbor-stranger discrimination in song sparrows. – Condor 92: 1051–1056.

Stoddard, P. K., Beecher, M. D., Horning, C. L. and Campbell, S. E. 1991b. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. – Behav. Ecol. Sociobiol. 29: 211–215.

Stoddard, P. K., Beecher, M. D., Loesche, P. and Campbell, S. E. 1992. Memory does not constrain individual recognition in a bird with song repertoires. – Behaviour 122: 274–287.

Trivers, R. L. 1971. The evolution of reciprocal altruism. – Q. Rev. Biol. 46: 35–57.

Wiley, R. H. and Wiley, M. S. 1977. Recognition of neighbours' duets by stripe-backed wrens (Campylorhynchus nuchalis). – Behaviour 62: 10–34.