



## What makes a 'local song' in a population of ortolan buntings without a common dialect?

TOMASZ S. OSIEJUK\*, KATARZYNA RATYŃSKA\* & SVEIN DALE†

\*Department of Behavioural Ecology, Adam Mickiewicz University

†Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences

(Received 1 February 2006; initial acceptance 10 March 2006;  
final acceptance 5 August 2006; published online 7 June 2007; MS. number: 8828R)

Ortolan buntings, *Emberiza hortulana*, have local dialects in central and southern Europe. Neighbouring males typically share the same final phrase of a song, which seems to be important for dialect recognition. We studied ortolan buntings in Norway, where a small and isolated population occurs with no local dialect in the above-mentioned sense. Norwegian males often have song types with different final phrases in their repertoire, and have larger repertoires and less song type sharing than other populations. We experimentally tested (1) whether male ortolan buntings from Norway discriminate between local and foreign or hybrid songs, and (2) what part of the song is used to discriminate between local and foreign songs. We studied the response to typical local songs (L), conspecific foreign songs from a remote population (F), and computer-created hybrid songs with a local final phrase and foreign initial phrase (F–L) and vice versa (L–F). Only local songs evoked a strong response, measured as latency to flight and approach, number of flights and closest distance from the loudspeaker. For F, F–L and L–F song playbacks, the majority of males did not respond at all, or responded significantly less than to L songs. Our results suggest that at least in this population, the final phrase of the song is not a sufficient cue for local song dialect recognition. We discuss the adaptive value of discriminating between own and foreign songs based on specific cues versus full songs in relation to dispersal and song-learning pattern in the ortolan bunting.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** dialect; *Emberiza hortulana*; ortolan bunting; song learning; song perception; song repertoire

In many songbird species, song structure varies on a micro- or macrogeographical scale (Mundinger 1982). Microgeographical variation is related to neighbouring groups of males which, at least potentially, may interact with each other. In several species, one can easily distinguish dialect areas where song structure clearly differs. Areas with a common dialect may be of different sizes, and dialects are common in species with small and large repertoires. However, the song structures that are shared may be very different. In some species males share full songs

from a small repertoire (e.g. white-crowned sparrow, *Zonotrichia leucophrys*: Nelson & Soha 2004a; corn bunting, *Emberiza calandra*: McGregor 1980). In others, only some specific song units such as single syllables or longer motifs are shared (e.g. yellowhammer, *Emberiza citrinella*: Rutkowska-Guz & Osiejuk 2004; redwing, *Turdus iliacus*: Espmark et al. 1989).

In most species, microgeographical variation of song is relatively easy to describe by visual inspection of sonagrams or statistical analysis of quantitative acoustic measurements (e.g. Warren 2002; Leader et al. 2005). However, it is difficult to unravel relations between the geographical pattern of song distribution and its biological significance. This is mostly because researchers usually know only the outcome of the dialect formation process, that is, the distribution of songs in space, while they may only speculate about what kind of factors affected

*Correspondence:* T. S. Osiejuk, Department of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland (email: [osiejuk@amu.edu.pl](mailto:osiejuk@amu.edu.pl)). S. Dale is at the Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway.

this process in the past (Baker & Thompson 1985). There is no doubt, however, that in songbirds dialect formation depends on at least three crucial factors: song learning, dispersal pattern and female choice (see Catchpole & Slater 1995 for a review of hypotheses). Many studies have shown that both male and female birds are able to distinguish between geographically close and distant songs and in most cases respond more strongly to local songs (e.g. Baker et al. 2001; MacDougall-Shackleton et al. 2001; Wright & Dorin 2001; Nelson & Soha 2004b). In contrast, our knowledge of the acoustic cues used for recognition of songs from local populations is still incomplete, which impedes our full understanding of dialect function (Nelson & Soha 2004a).

We tested experimentally how male ortolan buntings, *Emberiza hortulana*, perceive 'locality' of songs. The ortolan bunting is a songbird with a relatively small repertoire, usually two to three, rarely up to five song types per male (Cramp & Perrins 1994). The songs have a similar general structure in all populations studied and consist of two easily recognized parts: (1) an initial phrase of higher overall frequency and wider frequency range, and (2) a final phrase of lower overall frequency and relatively narrow bandwidth. Both the initial and final phrases may be complex, that is, consisting of more than one type of syllable, but in most cases both parts are phrases of a repeated, single-syllable type (Cramp & Perrins 1994; Osiejuk et al. 2003a). Ortolan buntings form apparent dialects in central and southern Europe. 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 (Conrads & Conrads 1971; Conrads 1976, 1994; Helb 1997). Extensive recordings usually show that mixed-dialect singers or foreign-dialect singers are relatively rare in such populations (Conrads & Kupp 1980; Conrads 1997; T. S. Osiejuk, unpublished data). These descriptive studies suggest that the most likely dialect cue in this species is a locally shared final song phrase (the dialect cue hypothesis).

However, this picture of dialect distribution in the ortolan bunting may have to be revised if we compare it with data from Scandinavia. A comparison of song repertoires across Sweden showed that ortolan buntings in this country did not have strict dialect patterns like those in central Europe (Åstrom & Stolt 1993). An isolated population inhabiting Hedmark County in Norway also had no central European-style dialect (Osiejuk et al. 2003a, 2005a; T. S. Osiejuk, unpublished data). In particular, there was no single final phrase of song shared by all or the majority of males. In addition, particular males often had song types in their repertoires with different final phrases, which means that they should be called mixed-dialect singers as defined by Conrads (1994). Comparatively large numbers of different initial phrases were also found at the population level. These results suggest that microgeographical song variation in this species is diverse and may be related to ecological factors such as dispersal pattern, isolation and patchiness of the population (Osiejuk et al. 2005a). The greater song variation in Scandinavia

may also be an effect of shorter breeding seasons than in central Europe. In northern populations males are likely to experience less exposure to their species-specific songs (Nelson et al. 1995, 1996).

For other species such as the blue tit, *Cyanistes caeruleus*, chiffchaff, *Phylloscopus collybita* or goldcrest, *Regulus regulus*, there is evidence that the releasing mechanisms for responding to species-specific song might be broader in peripheral than in central populations. This difference has been interpreted as an increase in song variation in isolated, small populations, which is the consequence of being exposed to a greater variety of sounds than in the centre of a species' range (reviewed in Becker 1982). We should therefore expect a similar situation for ortolan buntings in Norway. Despite having no common dialect (at least in the strict sense of sharing a single final song phrase), more complex songs, larger repertoires and less song type sharing, males in this population recognize songs of conspecifics and interact with them in a normal way (Skierczyński et al. 2007).

Thus, the question arises whether there is a single mechanism of perception of song locality in ortolan buntings and how this 'locality' is perceived in a non-dialect population. Do males from an isolated and patchily distributed population use the final phrase of a song as a dialect indicator even though there is a larger repertoire of these final phrases, or do they use different mechanisms to recognize local and foreign conspecifics? We tested whether male ortolan buntings from Norway discriminate between local, foreign and mixed songs. Then, we tested what part of the song is used to discriminate between local and foreign songs. These tests were based on evaluating the response of males to playback of (1) conspecific foreign dialect songs and (2) two types of artificially mixed songs consisting of (2a) a local initial phrase and a foreign final phrase, and (2b) a foreign initial phrase and a local final phrase of song, in comparison to response to typical local songs. According to the dialect cue hypothesis we predicted that subjects would respond more strongly to local songs and to hybrid songs with the local final phrase than to foreign songs and to hybrid songs with the local initial phrase. If the dialect cue hypothesis is incorrect, it is reasonable to assume that only playback of local songs would evoke a strong response by males (the full song hypothesis).

## METHODS

### Study Area and Subjects

We carried out the study in Hedmark County, south-eastern Norway. The study area covered the main part of the ortolan bunting's distribution range in Norway. The studied population consisted of ca. 150 males inhabiting about 30 well-defined habitat patches with 1–20 or more singing males. The population is heavily fragmented and all sites are distributed over an area of 500 km<sup>2</sup>. The other minor relict population (fewer than 10 males) occurred 50–80 km to the south and southwest in Akershus County but it probably became extinct in 2005 (Dale

et al. 2006). The other closest neighbouring population is in Sweden, about 250 km away. We tested males in all the typical habitats used by this species in Norway, that is, raised peat bogs, forest clear-cuts on poor sandy soils, land being cleared for cultivation and burnt forest (for more details see Dale & Hagen 1997; Dale 2000; Dale & Olsen 2002; Steifetten & Dale 2006). Most males were colour-ringed from a long-term research project started 10 years ago.

### Playback Equipment and Song Stimuli

For the playback experiments we used a Philips Magnavox ESP25 (Koninklijke Philips N.V., Philips, Suzhou, China) compact disc player with a wireless Hama SP433 (Hama GmbH & Co. KG, Monheim, Germany) loudspeaker (frequency range 20–20 000 Hz and linear frequency response within the species-specific frequency range, i.e. 1.8–6.6 kHz). Each experiment used different songs (altogether 78 song samples) belonging to one of three kinds of stimuli: (1) songs from randomly chosen non-neighbours of the subject males; (2) songs from randomly chosen males from a foreign population; (3) computer hybrid songs which consisted of local and foreign phrases (see treatment description for more details). Foreign songs or their parts originated from a Polish population inhabiting the vicinity of Poznań (52° 17'N, 15° 56'E).

All the songs or their parts used as stimuli were common in either Norway or Poland, that is, were shared by at least 10% of males within a given population. We decided to use this threshold because song type diversity in the ortolan bunting is much higher in Norway than in Poland (70 versus 14 different song types per 100 males, respectively; Osiejuk et al. 2005a). Based on this threshold, for the preparation of stimuli we used 78 different songs or phrases belonging to the most typical 18 Norwegian and 14 Polish song types. Each full song or song phrase was derived from the repertoire of a different male. We have studied song of the species in Poland since 1998 and in Norway since 2001, and we have a database of over 40 000 digitized songs from more than 500 males, so the only additional criterion of choice was recording quality. More detailed information about the different song type usage is given in the section [Experiments and Treatments](#).

All the songs used were of good quality and were digitally prepared (2 kHz high-pass filter, amplified or attenuated) to match 86 dB sound pressure level (SPL) at 1 m from the loudspeaker, measured with a CHY 650 (CHY Firemate Co., Ningbo, China) sound level meter. The SPL value was set on the basis of the normal amplitude level of ortolan bunting song, which had been measured in the field previously. In all cases, the amplitude manipulation did not exceed  $\pm 5$  dB and did not affect song structure. All recordings in our database were originally recorded at 48 kHz/16 bit. To prepare an audio CD for playback, we converted to 44.1 kHz/16 bit sampling rate with accuracy 512 and antialiasing filtering 'on'. We used Avisoft SASLab 4.34 software (Specht 2002) to prepare playback cuts.

### Playback Protocol

We carried out the experiments between 7 and 24 May 2005 (between 0400 and 1000 hours local time). On the basis of behavioural observations the experimental period was chosen as the time when males defended territories intensively. We recorded all subject males before the experiments and mapped their territories at least 1 day before the experimental period. All subject males were unpaired and defended territories for at least 1 day before the experiments were conducted. Before each treatment the loudspeaker was placed in a tree about 1.5–2 m above the ground, within the subject male's territory and 30–50 m from his songpost observed during equipment set-up. The loudspeaker was placed in a way that allowed the focal male to move towards the loudspeaker and to land on a tree, bush, rock or elevated ground 5 m or less from it, but that avoided the bird did moving 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 1-min playback followed by 1 min of observation of the behaviour of the focal male. We determined the timing of both stages on the basis of earlier experiments with the species. The playback time was short as we wanted to avoid interacting with males for a long period and we wanted to evoke a simple and clear response to stimuli, where treatment differed only in a single dimension (structure of song). The same songs were played back six times in 1 min, which is a typical song rate and type of song delivery for the species (Osiejuk et al. 2003a) and the playback was started ca. 2 s after the last song of the focal male. The 2-s delay minimized overlapping of the playback songs by the experimental males; the males thus interacted with the playback like they do in typical alternating countersinging (Skierczyński et al. 2007). The postplayback stage was only 1 min long to avoid including in the analysis any behaviour caused by nonplayback factors that might occur after we stopped the playback. Observations of the behaviour of the males were dictated on to a microcassette recorder and notes were transcribed later the same day. The accuracy of extracting variables from a tape was 1 s. We recorded 10 measures of response to playback (Table 1).

We conducted two treatments in random order for each subject. Both treatments for a particular male were done within 3 h (1 h on average) on the same day. The location of the loudspeaker was changed between each treatment, and each time we waited until the male changed his songpost and started singing at a typical rate before restarting the experiment. When several males occurred at a particular site, we usually tested all of them with the first kind of stimulus and then went back to the first male and started the second treatment. This design allowed us to avoid testing the same male in different contexts because the territorial and mating status of a male may change rapidly (personal observation). We also knew from preliminary playback experiments that ortolan bunting males respond in the same way to playbacks within a short period of time if the following stimuli consist of different song types, which was the case in this study.

**Table 1.** Measures of male ortolan bunting responses to playback

Variable	Description
Flight latency	Time between onset of playback and the first flight of the focal male towards the loudspeaker (s)
Approach latency	Time between onset of playback and the appearance of the focal male at 5 m or closer to the loudspeaker (s)
Closest distance	The closest distance between the focal male and the loudspeaker during the whole trial (m)
Flights during playback	No. of flights over 1 m during 1 min of playback
Flights after playback	No. of flights over 1 m during 1 min after playback
Song latency	Time between onset of playback and the first song given by the focal male (s)
Songs during playback	No. of songs given during 1 min of playback
Songs after playback	No. of songs given during 1 min after playback
Calls during playback	No. of calls given during 1 min of playback
Calls after playback	No. of calls given during 1 min after playback

## Experiments and Treatments

Altogether we conducted three series of experiments with the same design and partly different treatments. Each pair of trials for all three series of experiments was done on different males. We tested 13, 14 and 12 males, respectively, in the following experiments.

### *Experiment 1: local versus foreign song*

We tested males with randomly chosen non-neighbour local song (treatment L) and randomly chosen foreign song from a male from a Polish population (treatment F).

### *Experiment 2: local versus mixed song*

We tested males with randomly chosen non-neighbour local song (treatment L) and randomly chosen mixed song consisting of a Polish initial phrase (F) and a Norwegian final phrase (L) (treatment F–L).

### *Experiment 3: local versus mixed song*

We tested males with randomly chosen non-neighbour local song (treatment L) and randomly chosen mixed song consisting of a Norwegian initial phrase and a Polish final phrase (treatment L–F).

### *Choice of song stimuli*

The choice of song stimuli for particular males and experiments was random with the following exceptions. In L and F treatments we avoided using renditions of the same song type within the same experimental series. In the F–L treatment, we used 14 different initial song phrases from Poland and 14 different final song phrases from Norway, but only initial phrases belonged to

different types (i.e. were composed of different syllable types). Final song phrases are less variable among individuals than initial phrases (Osiejuk et al. 2003a, 2005a) and among commonly shared final phrases in Norway we found only seven types that we could use to create hybrid songs. Consequently, in the F–L treatment we used two different examples of each of these seven types of final phrases. Similarly, in the L–F treatment we used 12 different examples of initial song phrases from Norway and 12 different examples of final phrases. Each initial phrase ( $N = 12$ ) belonged to a different type, while all final phrase renditions belonged to the same type, which is characteristic of the Polish population from the Poznań region and seems to be a dialect cue (Fig. 1).

The consequence of using common song types as stimuli was that most tested males or their neighbours shared at least some phrases with the playback stimuli used in all experiments with the L, L–F and F–L treatments. Therefore it is very unlikely that experimental males were unfamiliar with the local song types (or their parts) used in experiments.

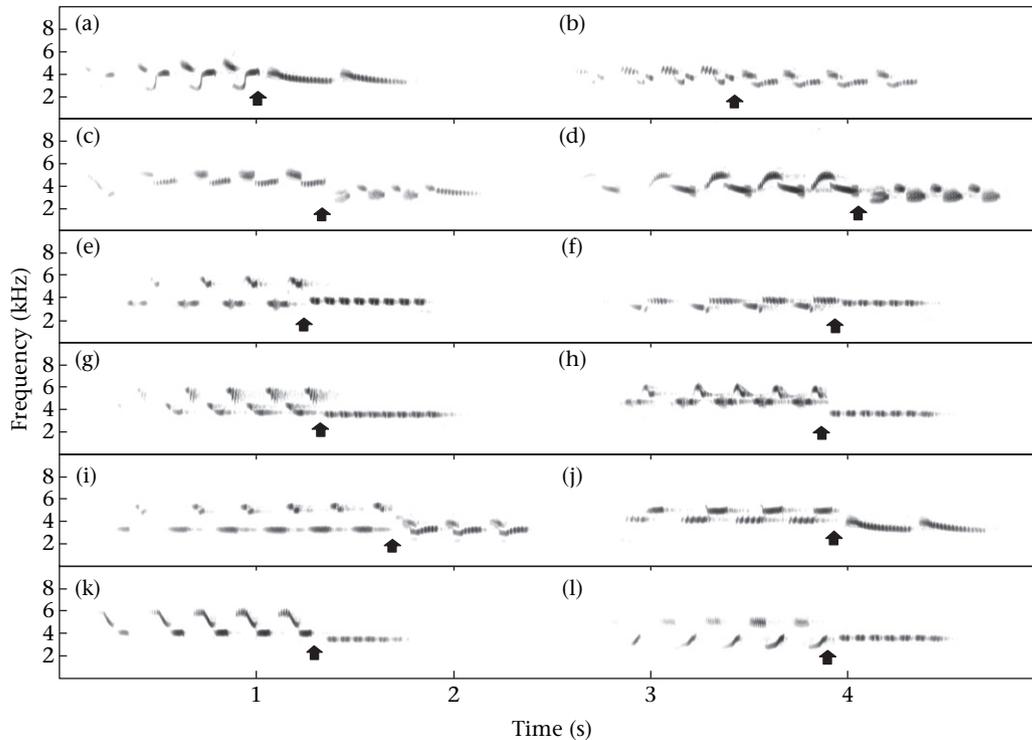
## Analysis

Altogether, we measured 10 response variables that describe the responses of the males to playback, which in about 75% 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 (Rice 1989; McGregor 1992) we combined all log-transformed original variables into three orthogonal principal components (PC1–PC3). The data set appeared to be suited for such an analysis (Kaiser–Meyer–Olkin measure of sampling adequacy = 0.707, Bartlett test of sphericity = 598.57,  $P < 0.001$ ).

We used general linear models (GLM) to test for differences in response to local songs between the three experimental groups and to test for differences in response between local songs and at least partially foreign songs (pooled data from all three experiments). Then we proceeded with the pairwise  $t$  test comparisons of PC1–PC3 compound response measures to evaluate differences in the males' response between treatments within each of the three experiments. When multiple tests were used to compare data relating to a particular hypothesis, we used a Bonferroni adjustment of the alpha value. We used original response variables to present results graphically. In all experiments  $N$  equals the number of subjects and different stimuli. Statistical tests were two tailed.

## RESULTS

Most of the approach-related response measures were strongly correlated with PC1 and lower values of PC1 corresponded to a stronger response, that is, faster approach to a closer distance and more flights during playback (Table 2). PC2 was negatively correlated with the number of songs given after playback, and positively related to the number of calls given (Table 2). This



**Figure 1.** Examples of songs used for the playback experiments. (a–d) Typical songs of Norwegian ortolan buntings. (e–h) Typical songs of Polish ortolan buntings. (i–l) Mixed songs with initial and final parts originating from different populations. Arrows separate initial and final phrases of songs.

compound variable reflects the diversity of the vocal response to stimuli (i.e. call- or song-biased response), but also shows the unchanged vocal behaviour of males that did not react to the playback (i.e. did not stop singing at a typical rate during and after playback, made no flights and did not approach the loudspeaker). PC3 was correlated positively with song latency and negatively with the number of songs given during playback. Therefore, PC3 is an indicator of when the playback caused focal males to cease singing (Table 2).

**Table 2.** Eigenvalues, variance explained and weightings of the original variables in the first three principal components extracted from the 10 original variables of the response to the playback

Statistics and original response variable	Component		
	PC1	PC2	PC3
Eigenvalue	4.45	2.12	1.14
% Variance	32.0	24.2	20.9
Cumulative %	32.0	56.2	77.1
Flight latency	<b>0.81</b>	−0.02	−0.44
Approach latency	<b>0.79</b>	−0.05	0.04
Closest distance	<b>0.89</b>	−0.13	0.11
Flights during playback	− <b>0.87</b>	0.05	0.36
Flights after playback	−0.39	0.23	0.05
Song latency	−0.09	0.14	<b>0.93</b>
Songs during playback	0.07	−0.44	− <b>0.82</b>
Songs after playback	−0.06	− <b>0.90</b>	−0.18
Calls during playback	−0.40	<b>0.71</b>	0.42
Calls after playback	−0.22	<b>0.91</b>	0.13

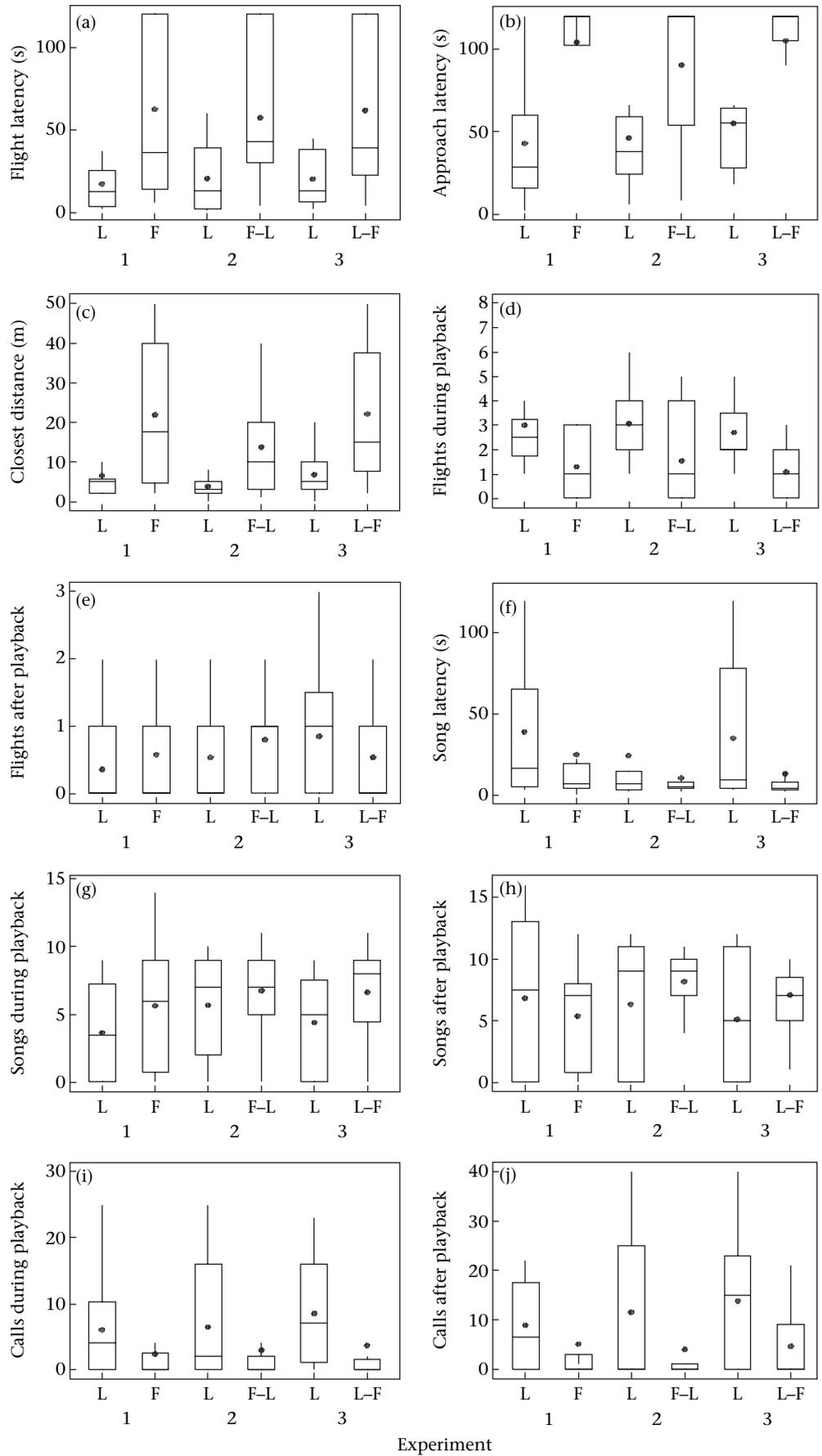
Measures that contributed most to the particular compound variable are in bold.

## Typical Response to Local Songs

All three experiments showed similar patterns of ortolan bunting response to typical songs from a local population. We found no significant differences in response to local songs between all three groups of males tested (GLM: Wilk's  $\lambda = 0.91$ ,  $P = 0.733$ , all  $P > 0.3$  for variables PC1–PC3). In most cases males commenced their first flight towards the loudspeaker just after the onset of playback and with a few more flights came very close to the loudspeaker. This behaviour was the most obvious response and all the other variables observed showed much higher variation between individuals. After this initial approach males either sang or ceased singing and started calling. Both singing and calling were usually connected with flights, which were usually made during playback of songs and birds usually stopped flying after playback (Fig. 2). The number of songs given during the playback was typically not very high as males usually sang a single song a few seconds after each song played back, or less frequently. If males stopped singing, it was usually connected with giving more calls. Call number was negatively correlated with the number of songs given (Spearman correlation: during playback:  $r_s = -0.71$ ,  $N = 42$ ,  $P < 0.001$ ; after playback:  $r_s = -0.81$ ,  $N = 42$ ,  $P = 0.001$ ; data from all L-treatments were pooled in this analysis).

## Response to Songs with Foreign Phrases

We found substantial differences between responses to local songs and to foreign or partly foreign songs



Experiment

(approaches to the loudspeaker and the number of flights during playback: GLM: Wilk's  $\lambda = 12.40$ ,  $P < 0.001$ ; PC1:  $F_{1,83} = 30.1$ ,  $P < 0.001$ ; PC2:  $F_{1,83} = 1.97$ ,  $P = 0.164$ ; PC3:  $F_{1,83} = 2.04$ ,  $P = 0.157$ ; Fig. 2). In general, this was because most males did not respond to foreign songs and songs with foreign phrases. Comparison of F, F–L and L–F treatments with GLM revealed that there were no significant differences in response to nonlocal songs (Wilk's  $\lambda = 0.895$ ,  $P = 0.65$ , all  $P > 0.4$  for variables PC1–PC3).

Males gave significantly stronger responses to local songs than to songs with foreign phrases, as measured by smaller PC1 scores (Table 3). When tested with foreign-like songs males did not approach the loudspeaker, or approached with a long latency and made fewer flights during playback. We found no significant differences in PC2 and PC3 variables describing the vocal response.

## DISCUSSION

Most of the ortolan bunting males we studied in Norway did not respond to foreign dialect songs or to artificial hybrid dialect songs. We found no significant differences in response to foreign song and artificial hybrid songs. Furthermore, adding a local final phrase of song did not increase response strength in comparison to full foreign song (rejecting the dialect cue hypothesis). Therefore, our results suggest that in ortolan buntings from Norway only the full, local song evoked an immediate and normal response.

In central and southern European populations of ortolan buntings, a single final phrase is typically shared among males within a particular dialect area, while at the same time syllables building initial song phrases seem to be shared over a larger area (Conrads & Conrads 1971; Conrads 1994; Cramp & Perrins 1994). Such a distribution of dialect-specific song cues may lead to an assumption that a hybrid song composed of any species-specific initial phrase and locally specific (dialect) final phrase should evoke a normal response from males inhabiting a dialect area (dialect cue hypothesis). Bird songs often consist of parts that differ in acoustic structure, and these parts may have different functions and/or different receivers. For example, one part may be devoted to individual recognition or dialect recognition, while the other serves as a long-distance 'keep out' signal (e.g. Dabelsteen 1984; Dabelsteen & Pedersen 1988; Lampe 1991). In some Emberizidae species a specific part of the song may be used for dialect discrimination (e.g. yellowhammer: Hansen 1984; white-crowned sparrow: Thompson & Baker 1993). In white-crowned sparrows, different subspecies discriminate between own and foreign dialects based on different parts of the song (Thompson & Baker 1993; Nelson & Soha 2004a).

Ortolan buntings have two-part songs, which have different frequency characteristics (Osiejuk et al. 2003a). Furthermore, the syllables in the final phrase were significantly less variable between males within one population (Osiejuk et al. 2005b), which supports the idea that they may carry more general meaning about the geographical origin of a bird even when there is more than a single version of the final phrase. Nevertheless, we found no experimental support for the dialect cue hypothesis in the Norwegian population of ortolan buntings. Instead, our results suggested that the full song is a basic unit of communication in this population, which enabled discrimination between local and foreign songs (the full song hypothesis). This result is consistent with a study on song sparrows, *Melospiza melodia*, where Searcy et al. (1999) clearly showed that song type is a fundamental unit of song perception in this species, and that songs are categorized at this particular level (however, see also Horning et al. 1993).

To answer the question whether the pattern of response we found in Norway is typical of this isolated population only or is representative for the species in general, similar experiments in other populations of ortolan buntings need to be conducted. However, some studies (e.g. Thompson & Baker 1993; Nelson & Soha 2004a) suggest that both options are possible. It is worth considering both the dialect cue and full song hypotheses as they may have far-reaching consequences for our understanding of dialect functions and origin.

If we consider a continuous population with a common dialect indicated by the final phrase of the song, the model of acquiring full songs from tutors and being responsive to known full songs should enable interaction between males and maintain the dialect over time, which is known to occur in ortolan buntings (Conrads 1986). If males typically learn only two or three song types from neighbours and then settle close to the place of hatching, that is, within a local dialect, they should always match the repertoires of at least some neighbours. The most important thing in this model is that there is no need to think about any specific 'dialect cue' within a song. Males may just copy full songs and react to known songs, that is, songs similar to their own and probably also to those heard earlier in neighbours' repertoires, but not incorporated into their own repertoires. In this case temporal stability of a dialect and low within-population song variation will be maintained by short natal dispersal (and a lack of, or a short, breeding dispersal), which is in fact observed in such populations (e.g. Conrads 1986).

In the Norwegian population of ortolan buntings males have large repertoires, which is probably a by-product of learning from the large number of tutors. Lemon (1975) and Becker (1982) suggested that in isolated populations variation between songs may increase. The Norwegian

**Figure 2.** Box plots showing response measures to playback of local (L), foreign (F) and artificially mixed songs (F–L and L–F): (a) flight latency, (b) approach latency, (c) closest distance, (d) flights during playback, (e) flights after playback, (f) song latency, (g) songs during playback, (h) songs after playback, (i) calls during playback and (j) calls after playback. The lower and upper edges of the boxes represent the first and third quartiles; the median divides each box. The vertical lines ('whiskers') include the range of values within 1.5 times the interquartile range. Solid circles are means.

**Table 3.** Results of paired *t* tests testing differences in response measured by compound PC1–PC3 variables to local (L), foreign (F) and artificially mixed songs (F–L and L–F)

	PC1			PC2			PC3		
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
Experiment 1 L versus F	–3.27	13	0.006*	0.27	13	0.824	1.34	13	0.203
Experiment 2 L versus F–L	–4.25	14	0.001†	1.016	14	0.327	0.47	14	0.645
Experiment 3 L versus L–F	–4.43	12	0.001†	1.73	12	0.109	1.476	12	0.166

\*Bonferroni-corrected *P* value = 0.018.

†Bonferroni-corrected *P* value = 0.003.

population is isolated and patchy. Males have longer breeding than natal dispersal distances and often actively seek new suitable patches to establish territories if they fail to attract a female at the place initially chosen after wintering (Dale et al. 2005; Osiejuk et al. 2005a; Steiffen & Dale 2006). Such behaviour is also promoted by the male-biased sex ratio in this population (Dale 2001a, b). The result of such a change in ecology and dispersal may be an enlarged repertoire if males have the capability to memorize and sing more song types. In fact, we found that some males from Norway had extremely large repertoires (between 10 and 24 song types); furthermore, such large repertoires were found only in young males in the second calendar year of life. Recordings of the same individuals in the following seasons revealed that they drop many song types and later in their life typically used, on average, only five song types, which is still twice as many as in central Europe (Osiejuk et al. 2005a; T.S. Osiejuk, K. Ratyńska & S. Dale, unpublished data). Similar overproduction of song types and later attrition of learned song types was found in the white-crowned sparrow (Nelson 2000).

The more males are spatially separated the greater the chance that cultural drift in song learning may occur. In Norway we observed many unique song types, which clearly appear because of some disturbance to the learning process (Osiejuk et al. 2003a, b, 2004, 2005a). This increase in song variation between males (i.e. lower song sharing) may negatively affect territory maintenance, especially in young males attempting to establish a territory for the first time among older neighbours who know each other and share repertoires (e.g. Beecher et al. 2000). We have examples from the microphone array study in Norway that show that new males appearing within a patch may have problems interacting with older males at the beginning of the season (T.S. Osiejuk, K. Ratyńska, M. Skierczyński & S. Dale, unpublished data). Our current experiments support this observation because even when typical local songs were played back we found some males reacting very weakly or not reacting at all. This might mean that they were unfamiliar with these particular song types taken from the local population. All these observations suggest that the recognition of local songs based on any specific dialect cue, for example the common final phrase, should be an advantage in our study population. Instead, male ortolan buntings in Norway learn a larger number of song types, probably over a longer time and from a larger number of tutors than in continuous populations. Later in

life they selectively drop some song types that are unnecessary for interactions with neighbours (e.g. song types not shared with neighbours). Hence, such a change in the song-learning programme (more tutors, selective attrition) seems to be a rather maladaptive outcome of changes in the ecology of this isolated and patchy population.

In conclusion, our results suggest that, at least at the moment, there is no reason to label the final song phrase of ortolan buntings a 'dialect cue'. The observed pattern of local dialects in relatively dense and continuous populations and the lack of such local dialects in patchy, isolated populations may result from the same general mechanism based on reacting to familiar songs. Familiarity in this case may mean both songs that are used actively by a male and songs that were memorized during a lifetime. There is, however, an urgent need to repeat these experiments in a continuous population of ortolan buntings with a single form of the final song phrase.

The support for the full song hypothesis comes from studies on some North American sparrows. Searcy et al. (2003), studying foreign/local song discrimination in song sparrows, found that geographical discrimination is not accomplished simply by recognition of a small number of phonological markers for example, typical notes shared by most local males. Stoddard et al. (1992) showed that song sparrow males are capable of memorizing the full song repertoire of their neighbours and that evolution of song type repertoire in this species is not constrained by the individual recognition of neighbours. This result could also be interpreted in a different way, that is, an increase in repertoire size might not constrain the recognition of a local dialect if it is followed by an increase in memorized song types that are not sung but are used as templates for neighbour–stranger recognition. In fact, one of the assumptions of the full song hypothesis is that males are able to memorize large numbers of song types. Studies of white-crowned sparrows also support our results. Indeed, several populations of sedentary or short-distance migratory subspecies show clear dialect variation with distinguishable dialect discrimination cues of different character (reviewed in Chilton et al. 2002). On the other hand, dialects are less prominent or not discernible at the microgeographical scale in the long-distance migratory subspecies *Z. l. gambelli* inhabiting the northern part of the species' range (Nelson 1998; Chilton et al. 2002). The ortolan bunting is migratory within the whole species' range, but the observed differences in song behaviour between the

peripheral Scandinavian populations and those from central Europe seem to result from differences in demography, analogously to the white-crowned sparrow.

### Acknowledgments

We thank Øyvind Steiffeten and Anne Karen Darrud for their help with the field work, and Thorsten Balsby and the anonymous referees for their helpful comments on the manuscript. Matt Smith kindly improved our English. The study was supported by the State Committee for Scientific Research (grant no. 3 P04C 083 25 to TSO). T.S.O. was supported by the foreign postdoc fellowship of the Foundation for Polish Science to Cornell University and Université Paris-Sud.

### References

- Åstrom, G. & Stolt, B.-O. 1993. Regional song dialects of the ortolan bunting *Emberiza hortulana* L. in Sweden. *Ornis Svecica*, **3**, 1–10.
- Baker, M. C. & Thompson, D. B. 1985. Song dialects of white-crowned sparrows: historical processes inferred from patterns of geographic variation. *Condor*, **87**, 127–141.
- Baker, M. C., Baker, E. M. & Baker, M. S. A. 2001. Island and island-like effects on vocal repertoire of singing honeyeaters. *Animal Behaviour*, **62**, 767–774.
- Becker, P. H. 1982. The coding of species-specific characteristic in bird sounds. In: *Acoustic Communication in Birds. Vol. 1. Production, Perception, and the Design Features of Sounds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 213–252. New York: Academic Press.
- Beecher, M. D., Cambell, S. E. & Nordby, J. C. 2000. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour*, **59**, 29–37.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song. Biological Themes and Variation*. Cambridge: Cambridge University Press.
- Chilton, G., Wiebe, M. O. & Handford, P. 2002. Large-scale geographic variation in songs of Gambel's white-crowned sparrows. *Condor*, **104**, 378–386.
- Conrads, K. 1976. Studien an Fremddialekt-Sänger und Dialekt-Mischsängern des Ortolans (*Emberiza hortulana*). *Journal für Ornithologie*, **117**, 438–450.
- Conrads, K. 1986. Chronik, insbesondere des Gesangsrepertoires, eines ( $x + 8$ ) jährigen Ortolan (*Emberiza hortulana*) aus der Senne (Ostmüsterland). *Bericht des Naturwissenschaftlichen Vereins fuer Bielefeld und Umgegend E.V.* **28**, 173–189.
- Conrads, K. 1994. Dialektklassen des Ortolans, *Emberiza hortulana*, im mittleren Europa: eine Übersicht. In: *I. Ortolan-Symposium Wien* (Ed. by H. M. Steiner), pp. 5–30. Wien: Institute für Zoologie, Universität für Bodenkultur.
- Conrads, K. 1997. Ein Während des Ortolansymposium 1996 in Westfalen aufgenommenen Dialektmischsänger. In: *II. Ortolan-Symposium Westfalen 1996* (Ed. by B. von Bülow), pp. 13–14. Haltern: Verlag Th. Mann.
- Conrads, K. & Conrads, W. 1971. Regionaldialekte des Ortolans (*Emberiza hortulana*) in Deutschland. *Vogelwelt*, **92**, 81–100.
- Conrads, K. & Kupp, M. 1980. Ökologische und bioakustische Indizien für die Annahme einer Neuansiedlung nordskandinavischer Ortolane (*Emberiza hortulana*) in einem nordwestdeutschen Hochmoor. *Vogelwelt*, **101**, 41–47.
- Cramp, S. & Perrins, C. M. 1994. *Birds of the Western Palearctic: Handbook of the Birds of Europe, the Middle East and North Africa Vol. 9*. Oxford: Oxford University Press.
- Dabelsteen, T. 1984. An analysis of the full song of the blackbird *Turdus merula* with respect to message coding and adaptations for acoustic communication. *Ornis Scandinavica*, **15**, 227–239.
- Dabelsteen, T. & Pedersen, S. B. 1988. Song parts adapted to function both at long and short ranges may communicate information about the species to female blackbirds *Turdus merula*. *Ornis Scandinavica*, **19**, 195–198.
- Dale, S. 2000. The importance of farmland for ortolan buntings nesting on raised peat bogs. *Ornis Fennica*, **77**, 17–25.
- Dale, S. 2001a. Causes of population decline of the ortolan bunting in Norway. In: *Bunting Studies in Europe* (Ed. by P. Tryjanowski, T. S. Osiejuk & M. Kupczyk), pp. 33–41. Poznań: Bogucki Wydawnictwo Naukowe.
- Dale, S. 2001b. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos*, **92**, 344–356.
- Dale, S. & Hagen, Ø. 1997. Population size, distribution and habitat choice of the ortolan bunting *Emberiza hortulana* in Norway. *Fauna Norvegica, Series C, Cinclus*, **20**, 93–103.
- Dale, S. & Olsen, B. F. G. 2002. Use of farmland by ortolan buntings (*Emberiza hortulana*) nesting on a burned forest area. *Journal für Ornithologie*, **143**, 133–144.
- Dale, S., Lunde, A. & Steiffeten, Ø. 2005. Longer breeding dispersal than natal dispersal in the ortolan bunting. *Behavioral Ecology*, **16**, 20–24.
- Dale, S., Steiffeten, Ø., Osiejuk, T. S., Losak, K. & Cygan, J. P. 2006. How do birds search for breeding areas at the landscape level? Interpatch movements of male ortolan buntings. *Ecography*, **29**, 886–898.
- Espmark, Y. O., Lampe, H. M. & Bjerke, T. K. 1989. Song conformity and continuity in song dialects of redwings *Turdus iliacus* and some ecological correlates. *Ornis Scandinavica*, **20**, 1–12.
- 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 Scandinavica*, **15**, 240–247.
- Helb, H.-W. 1997. Gesangsdialekte des Ortolans, *Emberiza hortulana*, in Südeuropa. In: *II. Ortolan-Symposium Westfalen 1996* (Ed. by B. von Bülow), pp. 23–49. Haltern: Verlag Th. Mann.
- Horning, C. L., Beecher, M. D., Stoddard, P. K. & Campbell, S. E. 1993. Song perception in the song sparrow: importance of different parts of the song in song type classification. *Ethology*, **94**, 46–58.
- Lampe, H. M. 1991. The response of male redwings *Turdus iliacus* to playback of conspecific songs with or without the terminating twitter. *Ornis Scandinavica*, **22**, 137–142.
- Leader, N., Wright, J. & Yom-Tov, Y. 2005. Acoustic properties of two urban song dialects in the orange-tufted sunbird (*Nectarinia osea*). *Auk*, **122**, 231–245.
- Lemon, R. E. 1975. How birds develop song dialects. *Condor*, **77**, 325–406.
- MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A. & Hahn, T. P. 2001. Physiological and behavioural responses of female mountain white-crowned sparrows to natal- and foreign-dialect songs. *Canadian Journal of Zoology*, **79**, 325–333.
- McGregor, P. K. 1980. Song dialects in the corn buntings (*Emberiza calandra*). *Zeitschrift für Tierpsychologie*, **54**, 285–297.
- McGregor, P. K. 1992. Quantifying responses to playback: one, many, or composite multivariate measures? In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 79–96. New York: Plenum.
- Mundinger, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalization of birds. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 147–208. New York: Academic Press.

- Nelson, D. A. 1998. Geographic variation in song of Gambel's white-crowned sparrow. *Behaviour*, **135**, 321–342.
- Nelson, D. A. 2000. Song overproduction, selective attrition and song dialects in the white-crowned sparrow. *Animal Behaviour*, **60**, 887–898.
- Nelson, D. A. & Soha, J. A. 2004a. Perception of geographical variation in song by male Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. *Animal Behaviour*, **68**, 395–405.
- Nelson, D. A. & Soha, J. A. 2004b. Male and female white-crowned sparrows respond differently to geographic variation in song. *Behaviour*, **141**, 53–69.
- Nelson, D. A., Marler, P. & Palleroni, A. 1995. A comparative approach to vocal learning: intraspecific variation in the learning process. *Animal Behaviour*, **50**, 83–97.
- Nelson, D. A., Marler, P. & Morton, M. L. 1996. Overproduction in song development: an evolutionary correlate with migration. *Animal Behaviour*, **51**, 1127–1140.
- Osiejuk, T. S., Ratyńska, K., Cygan, J. P. & Dale, S. 2003a. Song structure and repertoire variation in ortolan bunting (*Emberiza hortulana* L.) from isolated Norwegian population. *Annales Zoologici Fennici*, **40**, 3–16.
- Osiejuk, T. S., Ratyńska, K., Cygan, J. P. & Dale, S. 2003b. Ortolan bunting *Emberiza hortulana* singing like yellowhammer *E. citrinella*. *Ornis Fennica*, **80**, 38–42.
- Osiejuk, T. S., Ratyńska, K., Dale, S., Steifetten, Ø. & Cygan, J. P. 2004. Ortolan bunting *Emberiza hortulana* mimicking other species and other dialects of own species. *Ornis Norvegica*, **27**, 73–79.
- Osiejuk, T. S., Ratyńska, K., Dale, S. & Cygan, J. P. 2005a. Isolation, patchiness and dispersal pattern strongly affect singing behaviour in ortolan bunting (*Emberiza hortulana*). In: *XXIX International Ethological Conference Abstracts. Budapest, Hungary. August 20–27, 2005. Page 166*. Budapest: Készült a Codex Print Nyomdában.
- Osiejuk, T. S., Ratyńska, K., Cygan, J. P. & Dale, S. 2005b. Frequency shift in homologue syllables of the ortolan bunting *Emberiza hortulana*. *Behavioural Processes*, **68**, 69–83.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Rutkowska-Guz, J. M. & Osiejuk, T. S. 2004. Song structure and variation in yellowhammers *Emberiza citrinella* from western Poland. *Polish Journal of Ecology*, **52**, 333–345.
- Searcy, W. A., Nowicki, S. & Peters, S. 1999. Song types as fundamental units in vocal repertoires. *Animal Behaviour*, **58**, 37–44.
- Searcy, W. A., Nowicki, S. & Peters, S. 2003. Phonology and geographic song discrimination in song sparrows. *Ethology*, **109**, 23–35.
- Skierczyński, M., Czarnecka, K. M. & Osiejuk, T. S. 2007. Neighbour–stranger song discrimination in territorial ortolan bunting *Emberiza hortulana* males. *Journal of Avian Biology*, **38**, doi:10.1111/j.2006.0908-8857.04123.x.
- Specht, R. 2002. *Avisoft-SASLab Pro Sound Analysis and Synthesis Laboratory. A PC-software for MS-Windows 95/98/ME/NT/2000/XP*. Berlin: Avisoft Bioacoustics, <http://www.avisoft.com>.
- Steifetten, Ø. & Dale, S. 2006. Viability of an endangered population of ortolan buntings: the effect of a skewed operational sex ratio. *Biological Conservation*, **132**, 88–97.
- Stoddard, P. K., Beecher, M. D., Loesche, P. & Campbell, S. E. 1992. Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour*, **122**, 274–287.
- Thompson, A. D. & Baker, M. C. 1993. Song dialect recognition by male white-crowned sparrows: effects of manipulated song components. *Condor*, **95**, 414–421.
- Warren, P. S. 2002. Geographic variation and dialects in songs of the bronzed cowbird (*Molothrus aeneus*). *Auk*, **119**, 349–361.
- Wright, T. F. & Dorin, M. 2001. Pair duets in the yellow-naped amazon (*Psittaciformes: Amazona auropalliata*): responses to playbacks of different dialects. *Ethology*, **107**, 111–124.