

2011

Microdialect and Group Signature in the Song of the Skylark *Alauda arvensis*

Elodie Briefer

Queen Mary University of London, elodie.briefer@usys.ethz.ch

Fanny Rybak

University of Paris-Sud

Thierry Aubin

University of Paris-Sud

Follow this and additional works at: http://animalstudiesrepository.org/acwp_asie



Part of the [Animal Studies Commons](#), [Comparative Psychology Commons](#), and the [Other Animal Sciences Commons](#)

Recommended Citation

Briefer, E., Rybak, F., & Aubin, T. (2011). Microdialect and group signature in the song of the skylark *Alauda arvensis*. *Bioacoustics*, 20(3), 219-233.

This Article is brought to you for free and open access by the Humane Society Institute for Science and Policy. It has been accepted for inclusion by an authorized administrator of the Animal Studies Repository. For more information, please contact eyahner@humanesociety.org.

Microdialect and Group Signature in the Song of the Skylark *Alauda arvensis*

Elodie Briefer¹, Fanny Rybak^{2,3}, and Thierry Aubin^{2,3}

¹ Queen Mary University of London

² University of Paris-Sud

³ French National Center for Scientific Research

ABSTRACT

*The Skylark *Alauda arvensis* is a territorial species of open landscape in which pairs settle in stable and adjacent territories during the breeding season. Due to the heterogeneity of the habitat, territories are gathered in patches spaced by a few kilometres, in which each male produces very long and complex flight songs as a part of the territorial behaviour. We showed that, in a given patch, all the males (neighbours) share some particular sequences of syllables in their songs, whereas males settled in different patches (strangers) have almost no sequences in common. Such a phenomenon is known as microdialect. To test the hypothesis that these shared sequences support a group signature, we made playback experiments with “chimeric” signals: songs of strangers where the sequences shared by neighbours were artificially inserted. Behavioural responses to playbacks indicated a neighbour-stranger discrimination consistent with the dear enemy phenomenon, i.e. a reduced aggression toward neighbours compared to strangers. Furthermore, the same level of responses, observed when a “chimeric” song and a neighbour song were broadcast, indicated that shared sequences are recognized and identified as markers of the neighbourhood identity.*

INTRODUCTION

In many territorial bird species, vocalisations of neighbouring males established within a given area are more similar to one another than to those of non-neighbouring males. This song geographic variation is thought to be a consequence of learning, as it is transmitted and shared between birds of a given area (Trainer 1983; Kroodsma 1996). Such a phenomenon is called dialect. It has been principally observed in numerous songbirds (e.g. Adret-Hausberger 1988; Naguib *et al.* 2001; Laiolo & Tella 2005), which, within certain genetic limitations or song learning “predispositions”, learn their songs through imitation, improvisation or invention (Beecher & Brenowitz 2005). Whole song types (e.g. Griessmann & Naguib 2002), individual syllables (e.g. Isaac & Marler 1963; Kreutzer 1974) or group of linked syllables (e.g. Becker 1974) are shared between individuals from the same population. Variations occurring between close groups of birds are called microgeographic variations and are often expressed in the syntactic organization of the songs (Mundinger 1982).

Geographic variations might help social adaptation of young individuals during their first territory settlement (Payne 1981), and song sharing has been shown to be positively correlated with breeding

success and territory tenure (Payne 1982; Espmark *et al.* 1989; Beecher *et al.* 2000; Wilson *et al.* 2000). They might also be used by birds in order to discriminate the song of a neighbour from that of a stranger individual established in another dialect area. In birds, such Neighbour-Stranger (N-S) discrimination has been shown in numerous species (Falls & McNicholl 1979; Molles & Vehrencamp 2001; Lovell & Lein 2004; Skierczynski *et al.* 2007) and is often expressed by a reduced aggression toward familiar individuals, generally neighbours, with whom relationships have already been established, compared to strangers or floaters. Such phenomenon, termed the “dear enemy effect” (Fisher 1954), is thought to arise because territory owners avoid wasting time and energy by investing in aggression only against individuals that constitute a serious threat (Temeles 1994). Once boundaries between territories have been set, neighbours may not necessarily be threatening to adjacent territory owners, while strangers may pose more threat, as potential usurpers of territories. The dear enemy effect results in a mutual benefit for neighbours by reducing the cost of the territorial defence of the shared boundary (Ydenberg *et al.* 1988; Catchpole & Slater 1995; Stoddard 1996).

In oscines, N-S discrimination is believed to be hindered by large song repertoire sizes (Kroodsma 1976). The “repertoire constraint” hypothesis was proposed as a theoretical basis by Krebs & Kroodsma (1980) and Falls (1982) to explain the apparent negative relationship between N-S discrimination and song repertoire size. It suggests that more song types should make N-S recognition harder. As repertoire size increases, listeners are indeed exposed to more song types. Moreover, song types become more similar to each other and each of them is sung proportionately less, which makes the task of learning the whole song repertoire more difficult. However, with the exception of the European Robin *Erithacus rubecula* (repertoire size between 100 and 200 different phrase types, Brindley 1991), the existence of conspecific N-S discrimination has never been explored in species with a repertoire of more than 100 different phrase types per individual.

Although numerous studies have examined geographic variations (e.g. Adret-Hausberger 1988; Naguib *et al.* 2001) or N-S discrimination (e.g. Falls & McNicholl 1979; Brindley 1991), very few studies have linked both phenomena and have attempted to highlight if certain dialect features allow such discrimination (e.g. Brooks & Falls 1975; Nelson 1989). Our aim was thus to investigate the relationship between dialects and N-S discrimination in a species with a very large repertoire. The Skylark *Alauda arvensis* was chosen as an ideal model satisfying all the criteria for displaying song geographic variation and N-S discrimination: large geographical range, strong site fidelity and production of a highly complex song (Donald 2004). The Skylark is a common oscine found in many different open country biotopes in Europe (del Hoyo *et al.* 2004). During the breeding season, several pairs settle in stable and adjoining territories gathered in locations spaced by a few kilometres because of the heterogeneity of the habitat. Skylarks display strong site fidelity within and between breeding seasons. During the whole breeding season, males are fiercely territorial (Delius 1965). As part of this territorial behaviour, males produce a flight song to deter intruders (Delius 1963; Hedenström 1995), in which species identity is encoded by temporal parameters (Aubin & Brémond 1983). Unlike the songs of most song birds which are relatively short and discontinuous and which can be categorized in discrete song types, the Skylark flight song is very long and continuous. It consists of series of song units, named syllables, produced between 2 and 6 kHz. With an estimated syllable repertoire of up to 300 different syllables per individual, this song is one of the most complex among oscines, giving rise to a huge potential for variation at the syntactic level (Aubin 1981, 1982).

In this study, we first analyzed and compared songs produced by individuals established in different locations to find potential microgeographic variations at the syntax level. Then, we carried out playback experiments in the field to test the ability of males to discriminate a neighbour song from a stranger song.

Using artificially modified songs, we also tested the hypothesis that microdialects, identified during our song analysis, support a group signature used by birds for neighbour-stranger discrimination.

METHODS

Study area, subjects and song recordings

The study was conducted during the 2 successive breeding seasons of 2005 and 2006 – from March to May – in the fields surrounding the University of Paris 11, France. The acoustic analysis was carried out on the songs of 9 males established in 3 different locations (3 males per location) recorded in 2005. Playback experiments were made in 2005 on 7 males from the same 3 locations as for the song analysis, and in 2006 on 8 males from 2 additional locations. Within a location, males are established in adjoining and stable territories. They will be referred to as “neighbours” in the following. The mean number of neighbours (group size) within each of the 5 studied locations was 8 ± 0.84 ($N = 5$ locations; Min = 6 neighbours; Max = 10 neighbours). Males from two different locations situated at least two kilometres apart will be referred to as “strangers” (Briefer *et al.* 2008). The boundaries of the studied territories were estimated by the experimenters after numerous and careful visual observations of the birds’ movements at different times of the day. GPS coordinates (Garmin GPSMAP 76S) were recorded at the centre of each territory. Recordings of several songs per individual were made between 9 and 12 a.m. using a Marantz PMD 690 digital recorder (sampling rate: 48000 Hz) connected to a Sennheiser ME 64 K6 omni-directional microphone (frequency response: 30 Hz to 20 kHz \pm 1dB) mounted on a Telinga Universal parabola (diameter: 50 cm). Songs files were then transferred to a computer and high-pass filtered (cut-off frequency: 1600Hz) to remove the background noise. The Avisoft SASLab pro 4.31 (Specht 2004) and Seewave (Sueur *et al.* 2007) softwares were used for subsequent analysis and the preparation of songs played back.

Song analysis – Search of microdialects

A total of 23 songs produced by the 9 studied individuals were analysed, corresponding to a mean number of syllables analysed per individual of 1903.3 ± 248.27 syllables and a mean duration of song analysis per individual of 370.7 ± 42.4 s. As described elsewhere (Briefer *et al.* 2008), a syllable was defined as a continuous trace on the sound spectrogram or a group of continuous traces spaced out by less than 25 ms. Syllables were labelled on a sound spectrogram (FFT-Length: 1024; Frame: 100%; Bandwidth: 61 Hz; Resolution: 46 Hz, Hamming window) with a number according to their overall frequency modulation shapes. Then, their sequential organization was examined using a custom Matlab program, which classified sequences of numbers according to their length and the number of times they were repeated. We could thus detect all sequences that were repeated by the same individual or shared by different individuals. Such sequences are referred to as phrases. We then made further comparisons between the phrase composition of neighbour and stranger repertoires by calculating a coefficient of repertoire similarity (RS) in which the number of shared phrases was related to the number of unshared phrases using the following equation: $RS = Z / ((X + Y) - Z)$, with X and Y being the total number of phrases produced by males x and y, and Z being the number of phrases shared by males x and y (Hultsch & Todt 1989).

Playback experiments

Playback experiments were carried out to test the hypotheses that males discriminate neighbours from strangers by their songs and that shared phrases found in the songs of all neighbouring birds were used for this discrimination. Playbacks were conducted in May 2005 and 2006, when territories were well established (Delius 1963; Donald 2004).

Signals tested

3 categories of songs were broadcast to each of the 15 subjects tested: a Neighbour song (N), a Stranger song (S) and a Chimeric song (C). We selected songs from our recordings, and all the selected songs were adjusted to the same duration by taking the first 90 s. Using Goldwave V. 5.11 (Craig 2000) software, we rescaled each recorded song to match the root mean square (RMS) amplitude of the different songs at the same output level. For each subject, the N song was a song produced by one of its adjacent neighbours. For each of the 5 locations, one S song was selected among the songs recorded in the most distant location from the one tested. C songs consisted in stranger songs where the shared phrases of the group tested were artificially inserted. C songs were prepared in the following way: each S song selected for a given location was used to prepare the corresponding C song by replacing between 20 and 30% of its total duration by an equivalent duration of phrases shared by all the birds of the location. These shared phrases had been previously identified by analyzing and comparing songs produced by at least 3 birds of each location. The shared phrases were extracted from songs of at least 2 different birds of the given location, from the beginning of the first syllable to the end of the last silence for each phrase. They were then inserted at random temporal positions in the S song replacing original sequences of same duration. In this way, we maintained the average sound per silence ratio in the whole song, this being a key parameter of the species-specific coding (Aubin & Brémond 1983). The spacing of shared phrases inserted was then checked on the basis of our prior song analysis to make sure it was within the natural range. Last, we looked at their overall amplitude level on the oscillogram and eventually adjusted this level to make sure that it was the same as the rest of the resulting C song.

Playback procedure

Songs were broadcast using a Marantz PMD 690 digital recorder connected via a 20 m cable to a 10-W Megavox Pro mega-6000 loudspeaker (frequency response: 400 Hz – 10 kHz, ± 3 dB), at the intensity estimated to be normal for the birds (mean \pm SE: 90.8 ± 0.8 dB SPL measured at 1m from the loudspeaker with a Brüel & Kjaer 2235, linear setting). Trials were conducted between 9 and 12 a.m. The loudspeaker was positioned at about 5 m inside the territory of the tested bird, on the side of the boundary shared with the neighbor whose song was used to prepare the N song. The experimenter stood 20 m away from the loudspeaker. The 3 categories of songs (N, C and S) were played once to each subject, during the same day, in a random order of presentation spaced by at least a 5 min delay to avoid a confounding effect of habituation. The playback was initiated when the subject was standing on the ground inside its territory at more than 10 m from the loudspeaker and when adjacent neighbours were quiet.

Measures of response

For each trial, the response of the bird was scored during 180 s, corresponding to the broadcast of 90 s of continuous song followed by 90 s of post-playback observation. To assess the effects of the different categories of songs played back, the 11 measures of response listed in Table 1 were recorded.

Statistical analyses

Two-tailed permutation tests were used to compare coefficients of similarity between repertoire composition of neighbours and strangers, because conventional parametric and non-parametric tests are not suitable for analyses in which each individual is included several times in the different pair-wise comparisons (twice as a neighbor and six times as a stranger) (Sokal & Rohlf 1995; Mundry 1999).

The measures of response scored during playback experiments, which are likely to be correlated, were plotted in a principal component analysis (PCA) based on the correlation matrix to create a composite

score. As the data were not normally distributed, we used nonparametric statistics. The scores of the first principal component were compared using a Friedman's test and two-tailed Wilcoxon matched pair tests for two-by-two further comparisons. A sequential Bonferroni adjustment was used for post-hoc analyses and all results retained significance when $P < 0.016$ (i.e. $0.05/3$).

All analyses were conducted using Statistica v6 (StatSoft, Inc., 2001), and results are stated as mean \pm SE.

TABLE 1. Measures of response to playback.

| Response category | Measured variable |
|-------------------|--|
| Movements(s) | total duration duration between 10 and 5 m from the loudspeaker duration between 5 and 0 m from the loudspeaker |
| Latency(s) | before the first movement to approach at less than 10 m from the loudspeaker to approach at less than 5 m from the loudspeaker |
| Time spent(s) | between 10 and 5 m from the loudspeaker between 5 and 0 m from the loudspeaker |
| Vocalisations | latency before the first song (s) duration of songs (s) total number of calls |

Figure 1. Spectrograms of song parts produced by three individuals established in the same location (a, b, c). The phrase (*) is shared by all individuals and the phrase () is shared by Ind a and Ind b. (FFT length, 512; frame, 100%; Hanning window).**

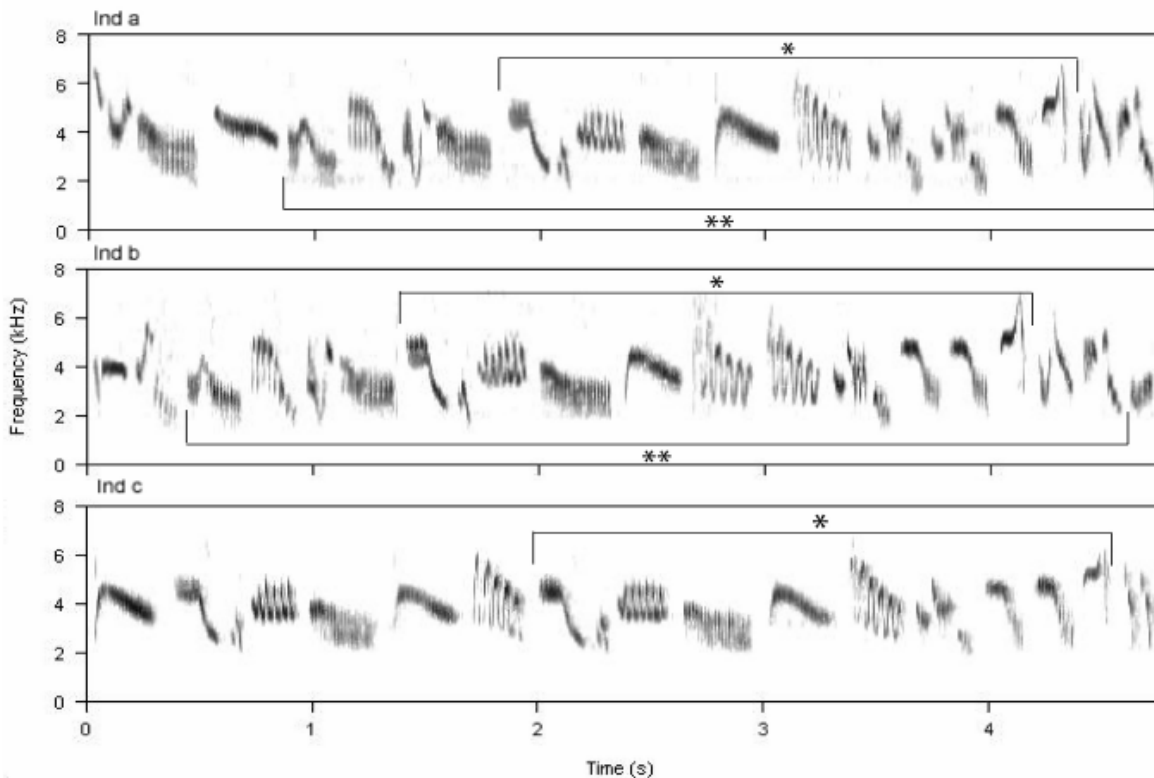


Figure 2. Coefficients of phrase repertoire similarity (RS values, mean \pm s.e.m) between pairs of neighbours (N = 9 pairs) and between pairs of strangers (N = 27 pairs). The asterisks indicate a significant difference (Permutation test, *** < 0.001).

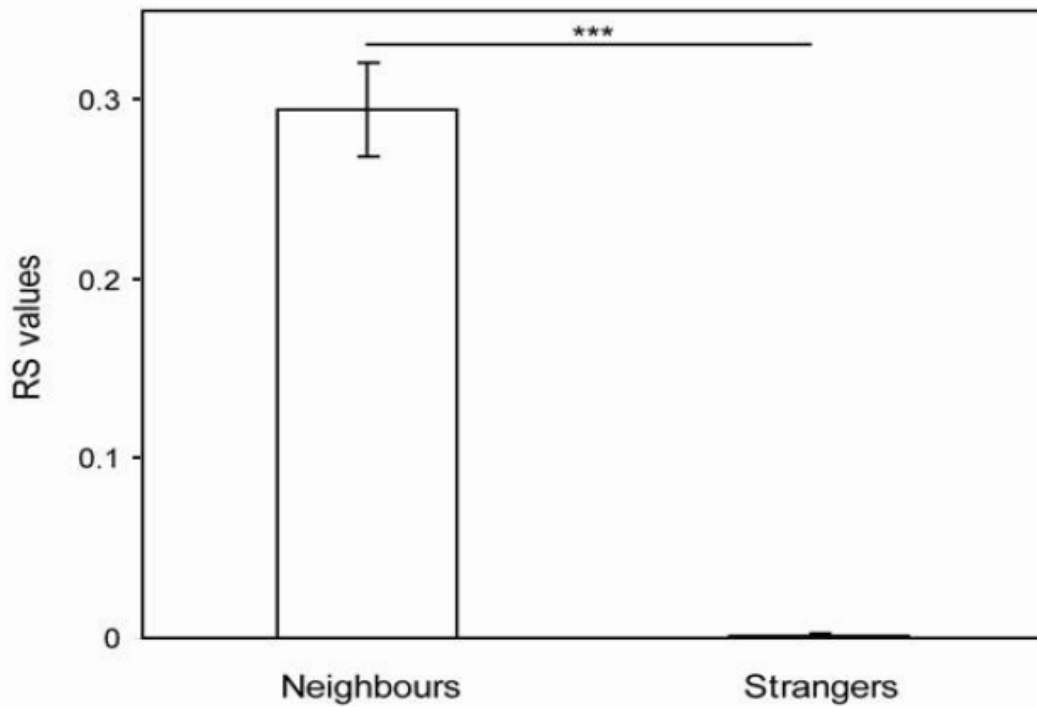


TABLE 2. Eigenvalue, variance explained, and loadings of the response measures on the first (PC1) principal component for playbacks of N, C and S songs. Measures that contributed most to the PC1 are in bold.

| Statistics and response measures | PC1 |
|--|---------------|
| Eigenvalue | 3.9758 |
| Percent of variance | 36.143 |
| Duration of movements between 5 and 0 m | -0.836 |
| Latency to approach at less than 5 m | 0.777 |
| Latency to approach at less than 10 m | 0.704 |
| Total duration of movements | -0.697 |
| Duration of movements between 10 and 5 m | -0.686 |
| Total number of calls | -0.661 |
| Time spent between 5 and 0 m | -0.626 |
| Time spent between 10 and 5 m | -0.483 |
| Duration of songs | 0.302 |
| Latency before the first song | -0.220 |
| Latency before the first movement | 0.144 |

RESULTS

Song analysis

Comparisons of phrase repertoires between individuals revealed that $70.7 \pm 2.9\%$ ($N = 9$) on average of the repertoire of each individual was composed of phrases shared by at least one neighbour of its location. An example of such a shared phrase is given in Figure 1.

The duration of shared phrases represented $43.5 \pm 2.6\%$ ($N = 23$ songs) on average of the total song duration. Pairs of neighbours shared 59.2 ± 6.4 different phrases (two-by-two comparisons, $N = 9$), whereas pairs of strangers had only 0.5 ± 0.1 different phrases in common (two-by-two comparisons, $N = 27$). Thus, the coefficients of similarity between neighbours' phrase repertoires were significantly higher than the coefficients of similarity between strangers' phrase repertoires (Figure 2).

Playback experiments

The first principal component (PC1) explained 36.1% of the variance in the response. The examination of the component loadings revealed that the durations of movements at different distances from the loudspeaker, the latencies to approach at less than 10 and 5 m, the number of calls and the times spent at different distances from the loudspeaker loaded highly on PC1 compared to the other responses (Table 2). Higher negative values of PC1 corresponded to a stronger response, *i.e.* spending more time moving, approaching closer to the loudspeaker after a shorter latency and producing more calls. A comparison of PC1 scores showed that subjects' responses were significantly different depending on the category of song played back (Friedman's test: $F = 20.80$, $N = 15$, $P < 0.0001$). Subjects responded significantly more strongly to S songs than to N songs (Wilcoxon matched pairs test: $Z = 3.41$, $N = 15$, $P < 0.001$) and more strongly to S songs than to C songs ($Z = 3.29$, $N = 15$, $P < 0.001$). Responses to N and C songs did not differ significantly ($Z = 1.36$, $N = 15$, $P = 0.17$) (Figure 3).

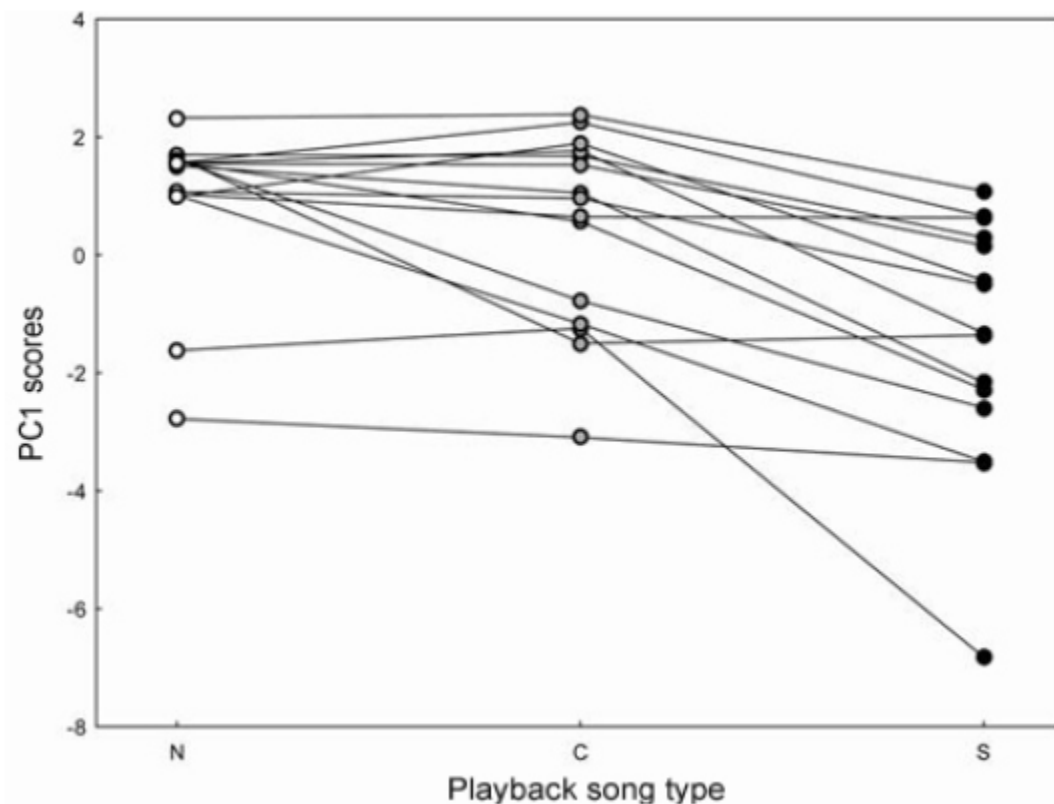
DISCUSSION

Microdialects

We showed recently that microgeographic variations exist in the syllable repertoire composition (Briefer *et al.* 2008). In the present paper, comparisons between the phrase repertoire composition of birds established in the same location ("neighbours") and birds established in different locations spaced by a few kilometres ("strangers") showed the existence of microgeographic variations at the phrase level. Indeed, neighbours shared much more phrases than did non-neighbouring males. Thus, Skylark song displays microdialects based both on basic song components and on the organisation in sequence of these song components, *i.e.* their syntactic order. Microgeographic variations have been identified in many non-oscines, sub-oscines and oscines bird species (Mundinger 1982), including two species of Alaudidae (Crested Lark *Galerida cristata*, Tretzel 1965; Flappet Lark *Mirafra rufocinnamomea*, Payne 1973), and species with complex songs like the Thrush Nightingale *Luscinia luscinia* (Griessmann & Naguib 2002) and the Wedge-Tailed Sabrewing *Campylopterus curvipennis* (Gonzalez & Ornelas 2005). In bird species that learn their songs, the young acquire their songs through imitation of models produced by conspecifics, although improvisation or invention may occur, and song sharing is a typical consequence of this imitation strategy (Beecher & Brenowitz 2005). Dialects are thus vocal traditions passed on to subsequent generations by vocal imitative learning and are therefore the product of cultural evolution (reviewed in Mundinger 1982; Catchpole & Slater 1995; Kroodsma 1996). No study has, to our knowledge, ever been carried out on song learning in Skylarks and the origin of shared phrases is unknown. Apart from some components of their song that could be genetically determined, young birds might learn shared phrases heard in their birthplace before autumn dispersal and return each breeding

period to the same location, like in the Song Sparrow *Melospiza melodia* (Nordby *et al.* 1999). Males might also be able to learn new song features throughout their life and incorporate new shared phrases by imitation of their neighbours each breeding season, like in Redwing *Turdus iliacus* (Espmark *et al.* 1989), and the White-crowned Sparrow *Zonotrichia leucophrys nuttalli* (Trainer 1983). Strong site fidelity from year to year has been recorded in male Skylarks remaining in the same region all year round and also in migratory populations (reviewed in Donald 2004). Furthermore, the post-natal dispersal occurs over short distances and one-year-old Skylarks exhibit strong site fidelity. Thus the conditions for the maintenance of dialects in this species are fulfilled.

Figure 3: Individual first principal component scores (N = 15) for playbacks of neighbour (N), chimeric (C) and stranger (S) songs. There is a significant difference between responses to S and C songs, and between responses to S and N songs (see text).



Neighbour-stranger discrimination and group signature

Our playback experiment showed that, when a territorial intrusion was simulated by the broadcast of a stranger's song, subject males responded with a stronger territorial behaviour, by spending more time moving, approaching closer to the loud-speaker and after a shorter latency and producing more calls, compared to the playback of a neighbour's song. Thus, Skylarks males discriminated neighbours' from strangers' songs as observed in numerous bird species, like the Banded Wren *Thryothorus pleurostictus*, (Molles & Vehrencamp 2001), the Blue Grouse *Dendragapus obscurus*, (Falls & McNicholl 1979) and the Alder Flycatcher *Empidonax alnorum* (Lovell & Lein 2004). This reduced territorial response to intrusion by familiar neighbours could be attributed to the dear enemy effect which leads to a reduced aggression from territory owners towards conspecific neighbours with whom relationships have been already established (Fisher 1954).

While numerous studies in songbirds have revealed that Neighbour-Stranger (N-S) recognition based on vocal interactions is a rather common ability, very few have attempted to find which song features were used by birds for N-S recognition. To test the hypothesis that the microdialect, i.e. the phrases shared by all individuals from a given location, supports a group signature, we carried out playback experiments with “chimeric” signals: songs of strangers including the “group signature”. Despite the fact that 70 to 80% of the chimeric song broadcasted was unknown for each bird tested, a similar level of responses was observed when a chimeric song and a neighbor song were played back. Thus, a stranger song lost its potential for eliciting aggressive behaviour when it included shared phrases of the location, showing that these phrases were recognized and identified as a signature shared by all neighbouring birds of the group. The continuous song of the Skylark seems therefore to include some parts that are potentially distinguishable from the rest of the song and that carry a particular meaning for the birds, e.g. the neighbourhood identity. These markers of the group identity can provide a basis for the dear enemy effect to occur.

The results of our study do not support the “repertoire constraint” hypothesis (Krebs & Kroodsma 1980), which predicts that N-S discrimination is hindered by large song repertoire size. The male Skylark produces one of the longest and most complex territorial songs among oscines and is yet able to discriminate a neighbour song from a stranger one. To our knowledge, only one study found such NS discrimination in a species with a very large repertoire (European Robin, Brindley 1991). The “repertoire constraint” hypothesis supposed that the task of memorizing a repertoire becomes more difficult as the size of the repertoire increases (Kroodsma 1976). However, neighbor identification could be coded only in a few features of the repertoire which may be more easily memorized, for example in particular sequences of songs (Stoddard 1996) or in voice characteristics (Lambrecht & Dhont 1995). Thus, listening to the whole neighbor repertoire will not be necessary for recognition. This could be the case of Skylarks that may learn only a part of their neighbours’ song, i.e. some of the shared phrases supporting the group signature.

To conclude, we showed that, despite a long song and a very large repertoire, Skylarks have the ability to discriminate between the song of a neighbour and that of a stranger. Such ability is accomplished by the recognition of particular sequences of the song making up the microdialect that act as a pass signalling the emitter as a member of the group.

ACKNOWLEDGMENTS

This study was supported by the CNRS and the University of Paris 11. EB was funded by a grant from the French Minister of Research and Technology during data collection. We are grateful to the anonymous referees for comments and suggestions.

REFERENCES

- Adret-Hausberger, M. (1988). Song differentiation and population structure: the example of the whistled songs in an introduced population of European starlings *Sturnus vulgaris* in Australia. *Ethology*, 79, 104-115.
- Aubin, T. (1981). Etude expérimentale du chant territorial de l'alouette des champs (*Alauda arvensis* L.). Caractéristiques physiques, valeur sémantique et spécificité. Ph.D. thesis, University of Besançon, Nancy 1, Strasbourg.
- Aubin, T. (1982). Habituation au chant territorial chez l'alouette des champs (*Alauda arvensis* L.). *Biol. of Behav.*, 7, 353-362.
- Aubin, T. & Brémond, J.-C. (1983). The process of species-specific song recognition in the skylark *Alauda arvensis*. An experimental study by means of synthesis. *Z. Tierpsychol.*, 61, 141-152.

- Becker, P. H. (1974). Der Gesang von Winter und Sommergoldhähnchen (*Regulus regulus*, *Regulus ignicapillus*) am westlichen Bodensee. *Vogelwarte*, 27, 233-243.
- Beecher, M. D. Campbell, S. E. & Nordby, J. C. (2000). Territory tenure in song sparrows is related to song sharing with neighbors, but not to repertoire size. *Anim. Behav.*, 59, 29-37.
- Beecher, M. D. & Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends Ecol. Evol.*, 20, 143-149.
- Briefer, E., Aubin, T., Lehongre, K. & Rybak, F. (2008). How to identify dear-enemies: the group signature in the complex song of the skylark *Alauda arvensis*. *J. Exp. Biol.*, 211, 317-326.
- Brindley, E. L. 1991 Response of European robins to playback of song: neighbor recognition and overlapping. *Anim. Behav.*, 41, 503-512.
- Brooks, R. J. & Falls, J. B. (1975). Individual recognition by song in white-throated sparrows III: song features used in individual recognition. *Can. J. Zool.*, 53, 1749-1761.
- Catchpole C. K. & Slater, P. J. (Eds.) (1995). *Bird Song: Biological themes and variations*, pp. 45-69; 131-137; 196-218. Cambridge: Cambridge University Press.
- Craig, C. (2000). Goldwave V. 5.11. Goldwave. St John's, Canada.
- del Hoyo, J., Elliott, A. & Christie, D. A. (Eds.) (2004). In *Handbook of the Birds of the World. IX: Cotingas to Pipits and Wagtails*, pp. 598-599. Barcelona: Lynx Edicions.
- Delius, J. D. (1963). Das Verhalten der Feldlerche. *Z. Tierpsychol.*, 20, 297-348. Delius, J. D. (1965). A population study of skylarks *Alauda arvensis*. *Ibis*, 107, 466-492.
- Donald, P. F. (2004). Song and song flight. In *The skylark*, pp. 72-88. London: T and AD Poyser.
- 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. Scand.*, 20, 1-12.
- Falls, J. B. (1982). Individual Recognition by Sound in Birds. In *Acoustic Communication in Birds. II* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237-274. New York: Academic Press.
- Falls, J. B. & McNicholl M. K. (1979). Neighbour-stranger discrimination by song in male blue grouse. *Can. J. Zool.*, 57, 457-462.
- Fisher, J. (1954). Evolution and bird sociality. In *Evolution as a process* (Ed. by J. Huxley, A. C. Hardy, & E. B. Ford), pp. 71-83. London: Allen & Unwin.
- Gonzalez, C. & Ornelas J. F. (2005). Song structure and microgeographic song variation in wedge-tailed sabrewings (*Campylopterus curvipennis*) in Veracruz, Mexico. *Auk*, 122, 593-607.
- Griesmann, B. & Naguib, M. (2002). Song sharing in neighboring and non-neighboring thrush nightingales (*Luscinia luscinia*) and its implications for communication. *Ethology*, 108, 377-387.
- Hedenström, A. (1995). Song flight performance in the skylark *Alauda arvensis*. *J. Avian Biol.*, 26, 337-342.
- Hultsch, H. & Todt, D. (1989). Context memorization in the song-learning of birds. *Naturwissenschaften*, 76, 584-586.
- Isaac, D. & Marler, P. (1963). Ordering of sequences of singing behaviour of mistle thrushes in relationship to timing. *Anim. Behav.*, 11, 179-188.
- Krebs, J. R. & Kroodsma, D. E. (1980). Repertoire and geographical variation in bird song. In *Advances in the study of behaviour II* (Ed. by J. S. Rosenblatt, R. A. Hinde, C. Beer & M. C. Busnel), pp. 134-177. New York: Academic Press.
- Kreutzer, M. (1974). Stéréotypies et variations dans les chants de proclamation territoriale chez le Troglodyte (*Troglodytes troglodytes*). *Rev. Comp. Animal.*, 8, 270-286.
- Kroodsma, D. E. (1996). Ecology of passerines song development. In *Ecology and Evolution of Acoustic Communication in Birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 3-19. Ithaca: Cornell University Press.
- Kroodsma, D. E. (1976). The effect of large song repertoires on neighbor "recognition" in male song sparrows. *Condor*, 78, 97-99.

- Laiolo, P. & Tella, J. L. (2005). Habitat fragmentation affects culture transmission : patterns of song matching in Dupont's lark. *J. Appl. Ecol.*, 42, 1183-1193.
- Lambrechts, M. M. & Dhondt, A. A. (1995). Individual voice discrimination in birds. *Curr. Ornithol.*, 12, 115-139.
- Lovell, S. F. & Lein, M. R. (2004). Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behav. Ecol.*, 15, 799-804.
- Molles, L. E. & Vehrencamp, S. L. (2001). Neighbor recognition by resident males in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. *Anim. Behav.*, 61, 119-127.
- Mundinger, P. C. (1982). Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In *Acoustic communication in birds II*. (Ed. By D. E. Kroodsma & E. H. Miller), pp. 147-208. New York: Academic Press.
- Mundry, R. (1999). Testing related samples with missing values: a permutation approach. *Anim. Behav.*, 58, 1143-1153.
- Naguib, M., Hammerschmidt, K. & Wirth, J. (2001). Microgeographic variation, habitat effect and individual signature cues in calls of chiffchaffs *Phylloscopus collybita canarensis*. *Ethology*, 107, 341-355.
- Nelson, D. A. (1989). Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). *J. Comp. Psychol.*, 103, 171-176.
- Nordby, J. C., Campbell, S. E. & Beecher, M. D. (1999). Ecological correlates of song learning in song sparrows. *Behav. Ecol.*, 10, 287-297.
- Payne, R. B. (1973). Wingflap dialects in the flappet lark *Mirafra rufocinnamomea*. *Ibis*, 115, 270-274.
- Payne, R. B. (1981). Population structure and social behaviour: models for testing the ecological significance of song dialects in birds. In *Natural selection and social behaviour: recent research and new theory*. (Ed. by R. D. Alexander & D. W. Tinkle), pp 108-120. New York: Chiron Press.
- Payne, R. B. (1982). Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo bunting. *Ecology*, 63, 401-411.
- Skierczynski M., Czarnecka K. M. & Osiejuk, T. S. (2007). Neighbour-stranger discrimination in territorial ortolan bunting *Emberiza hortulana* males. *J. Avian Biol.*, 38, 415-420.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. 3rd edition (ed. W. H. Freeman), New York.
- Specht, R. (2004). Avisoft-SASLab pro v4.31. Avisoft, Berlin.
- StatSoft, Inc. (2001). Statistica v6.0. for Windows (Computer program manual). StatSoft, Inc., Tulsa: Oklahoma.
- Stoddard, P. K. (1996). Vocal recognition of neighbors by territorial Passerines. In *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356-374. Ithaca, New York: Cornell University Press.
- Sueur, J., Aubin, T. & Simonis, C. (2007). Seewave: Time wave analysis and graphical representation. R package version 1.4.4.
- Temeles, E. J. (1994). The role of neighbours in territorial systems: when are they 'dear enemies'? *Anim. Behav.*, 47, 339-350.
- Trainer, J. M. (1983). Changes in song dialect distributions and microgeographic variation in song of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *Auk*, 100, 568-582.
- Tretzel, A. (1965). Imitation und Variation von Schäferpfeifen durch Haubenlerchen (*Galerida c. cristata* L.). Ein Beispiel für spezielle Spottmotiv-Prädisposition. *Z. Tierpsychol.*, 22, 784-809.
- Ydenberg R. C., Giraldeau L. A. & Falls J. B. (1988). Neighbours, strangers, and the asymmetric war of attrition. *Anim. Behav.*, 36, 343-347.