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How to identify dear enemies: the group signature in the complex song of the skylark *Alauda arvensis*

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SUMMARY

Song geographic variation and Neighbour–Stranger (N–S) discrimination have been intensively but separately studied in bird species, especially in those with small- to medium-sized repertoires. Here, we establish a link between the two phenomena by showing that dialect features are used for N–S recognition in a territorial species with a large repertoire, the skylark *Alauda arvensis*. In this species, during the breeding season, many pairs settle in stable and adjoining territories gathered in locations spaced by a few kilometres. In a first step, songs produced by males established in different locations were recorded, analyzed and compared to identify possible microgeographic variation at the syntax level. Particular common sequences of syllables (phrases) were found in the songs of all males established in the same location (neighbours), whereas males of different locations (strangers) shared only few syllables and no sequences. In a second step, playback experiments were conducted and provided evidence for N–S discrimination consistent with the dear-enemy effect, i.e. reduced aggression from territorial birds towards neighbours than towards strangers. In addition, a similar response was observed when a ‘chimeric’ signal (shared phrases of the location artificially inserted in the song of a stranger) and a neighbour song were broadcast, indicating that shared sequences were recognized and identified as markers of the group identity. We thus show experimentally that the shared phrases found in the songs of neighbouring birds constitute a group signature used by birds for N–S discrimination, and serve as a basis for the dear-enemy effect.

Key words: microdialects, dear-enemy effect, playback experiment, oscine, *Alauda arvensis*.

INTRODUCTION

The ‘dear-enemy effect’ is defined as a reduced aggression from territorial animals towards familiar individuals, generally neighbours, with whom relationships have already been established (Fisher, 1954). This phenomenon 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 and Slater, 1995; Stoddard, 1996). The ability to discriminate between neighbouring and non-neighbouring cues is a prerequisite for such a phenomenon to occur. Such an ability has been demonstrated using playbacks of tape-recorded vocalizations in animals species like amphibians (e.g. Bee and Gerhardt, 2001), mammals (e.g. Mitani et al., 1996; Frommolt et al., 2003) and birds (e.g. Falls and McNicholl, 1979; Brindley, 1991; Lambrechts and Dhondt, 1995; Stoddard, 1996; Molles and Vehrencamp, 2001; Hardouin et al., 2006), using live introductions of neighbours or strangers on a territory in fishes (e.g. Leiser, 2003) and lizards (e.g. Husak and Fox, 2003), and using olfactory stimuli in mammals (e.g. Vaché et al., 2001; Zenuto and Fanjul, 2002).

In oscines, song production serves to defend territory tenure, and vocal Neighbour–Stranger (N–S) discrimination is believed to be hindered by large size of song repertoire (Kroodsma, 1976). The

‘repertoire constraint’ hypothesis was proposed as a theoretical basis to explain the apparent negative relationship between N–S discrimination and size of song repertoire (Krebs and Kroodsma, 1980; Falls, 1982). 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 is sung proportionately less, which makes the task of learning the whole repertoire of songs more difficult. Comparative analyses of neighbour recognition *versus* song repertoire size have been carried out for 20 (Weary et al., 1992), 26 (Lambrechts and Dhondt, 1995) and 25 (Stoddard, 1996) bird species. None of these studies found the predicted significant negative relationship, although Stoddard suggested that repertoire constraint may exist in species with extremely large repertoires (>100 song types) (Stoddard, 1996).

Vocal discrimination between neighbour and stranger or between neighbours is not possible unless song characteristics vary consistently among individuals (Falls, 1982). In species with small song repertoires, time–frequency structures of songs might support an individual signature. In species with larger song repertoires, song order could be an additional cue for individual recognition (Stoddard, 1996). Each bird may have a unique composition of song types in its repertoire (phonology), or may have a similar repertoire to that of its neighbours but may produce song types in a unique order (syntax). Regardless of its size of repertoire a singer might also be recognizable by distinctive ‘voice’ characteristics (Lambrechts and Dhont, 1995), as found by an operant conditioning experiment in great tits *Parus major* (Weary and Krebs, 1992).

In order to discriminate the song of a neighbour from that of a stranger, a bird may use acoustic features shared by all its neighbours and that do not exist in stranger songs, i.e. the local dialect. In many territorial songbird species, songs of neighbouring males established within a dialect area are more similar to one another than to those of non-neighbouring males. Whole song types (e.g. Griessmann and Naguib, 2002), individual syllables (e.g. Isaac and Marler, 1963; Kreuzer, 1974) or groups of linked syllables (e.g. Becker, 1974) are shared by individuals from the same population. A dialect shared by a small group of neighbours is an example of microgeographic variation, and one shared by a whole population is an example of macrogeographic variation (Mundinger, 1982). Geographic variation is thought to be a consequence of song learning: it is learned, transmitted and shared between birds of a dialect area (Trainer, 1983; Kroodsma, 1996).

Several hypotheses on the function and the maintenance of dialects have been proposed (Trainer, 1983; Catchpole and Slater, 1995). According to the 'genetic adaptation' hypothesis (Nottebohm, 1969; Nottebohm, 1972), geographic variation might be used by birds to recognize and mate with individuals from the same population, which would favour the maintenance and development of local adaptations. The necessary conditions are that males learn their natal dialect and settle to breed in the same area, and that females prefer to mate with males of their natal dialect. According to another model, the 'social adaptation' hypothesis (Payne, 1981a), geographic variation might help social adaptation of young individuals during their first territory settlement. It benefits the young males to learn the songs of their older established neighbours in order to interact more effectively with them (Payne, 1981b). Some studies indeed show that young males may be more successful in establishing territories when they share songs with their new neighbours and that song sharing is positively correlated with breeding success and territory tenure (Payne, 1982; Espmark et al., 1989; Beecher et al., 2000; Wilson et al., 2000).

Although numerous studies have examined geographic variation (e.g. Adret-Hausberger, 1988; Naguib et al., 2001) or N-S discrimination (e.g. Falls and McNicholl, 1979; Brindley, 1991), very few studies have linked both phenomena by testing which dialect features were used for N-S recognition (e.g. Brooks and Falls, 1975; Nelson, 1989). Moreover, with the exception of the European robin [repertoire size between 100 and 200 different phrase types (Brindley, 1991)], the existence of conspecific N-S recognition has never been explored in species with a repertoire of more than 100 different phrase types per individual. Our aim was thus to investigate the relationship between dialects and N-S recognition 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. Thus, both male and female have a strong tendency to return to the same breeding location from year to year (Jenny, 1990), and 1-year-old males show regional philopatry (Delius, 1965). Males display strong territorial behaviour, and intense fights are elicited by newcomers that seem to be harassed, not only by nearby territory owners but

also by skylarks from further afield (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 and Brémond, 1983). Unlike the songs of most songbirds, which are relatively short and discontinuous and 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 repertoire of up to 700 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; Aubin, 1982).

In this study, we first analyzed the syntax of skylark song to understand how such a long and complex song is organized. We then looked for possible microgeographic variation at the syntax level by comparing songs produced by individuals established in different locations. After that, we carried out playback experiments in the field to test their ability to discriminate a neighbour song from a stranger song. Using artificially modified songs, we also tested the hypothesis that microgeographic variations identified during our song analysis are used by birds for N-S recognition.

GENERAL MATERIALS AND METHODS

Study area, subjects and song recordings

Our study was conducted on skylarks *Alauda arvensis* L. during the two successive breeding seasons of 2005 and 2006 (from March to May) in the fields surrounding the University of Paris 11, France. The song analysis was carried out on 9 males established in three different locations (3 males per location), recorded in 2005. The playback experiment was made on 7 males from the same three locations as for the song analysis in 2005, and 8 males from two additional locations in 2006. Within a location, males were established in adjoining and stable territories of circa 1 ha, measured using GPS coordinates (Garmin GPSMAP 76S). Such males will be referred to as 'neighbours'. The mean number of neighbours (group size) within each of the five locations of our study was 8 ± 0.84 ($N=5$ locations; min=6 neighbours; max=10 neighbours). Skylarks remain within their territory boundaries to breed and have never been observed foraging further than 380 m from their nest (Donald, 2004). The different locations considered in this study, i.e. groups of neighbours, were separated by unsuitable breeding habitat (e.g. woods, villages, roads). Thus 'strangers' were defined as males from two different locations situated at least 2 km apart. During the breeding season, site fidelity is very strong (Jenny, 1990; Delius, 1963). Once territories are well established, as boundaries between adjoining territories are stable and males are strongly confined inside (Aubin, 1981), subjects are easily identifiable by observing their position and movements, especially when they perform flight songs. Consequently, 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 day. To help locate and monitor these territories from day to day, GPS coordinates were recorded at the centre of each territory. Recordings of several songs per individual were made between 09:00 h and 12:00 h using a numeric recorder (Marantz PMD 690, Mahwah, NJ, USA; sampling rate: 48 000 Hz) connected to an omni-directional microphone (Sennheiser ME 64 K6, Wennebostel, Germany; frequency response: 30 Hz to 20 kHz \pm 1 dB) mounted on a Telinga Universal parabola (Tobo, Sweden; 50 cm diameter). Songs files were then transferred to a computer and high-pass filtered (cut-off frequency: 1600 Hz) to remove the background noise. The Avisoft

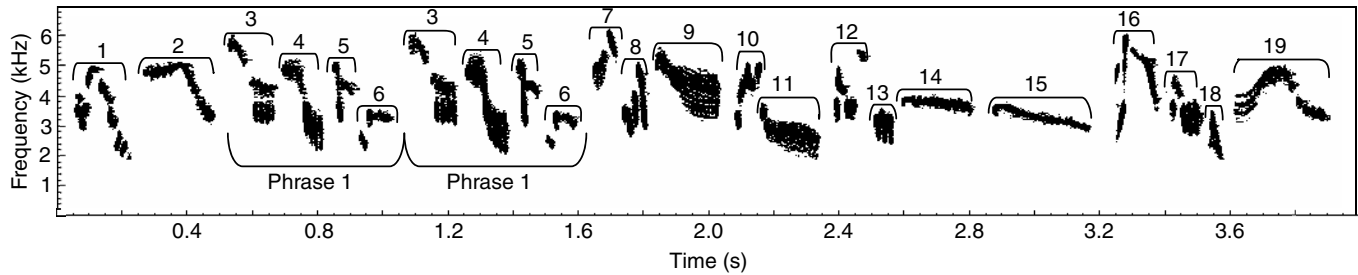


Fig. 1. Sound spectrogram of a part of a flight song of a male skylark. Each syllable is labelled with a number (same syllables have the same number). A phrase corresponds to a succession of at least three different syllables repeated by the same individual or shared by different individuals. Here, the phrase 1 is composed of syllables 3, 4, 5 and 6, and is repeated twice, consecutively.

SASLab pro 4.31 software (Specht, 2004) was used for subsequent analysis and the preparation of songs played back.

(1) SONG ANALYSIS

MATERIALS AND METHODS

Songs were visualized on a sound spectrogram (FFT-length, 1024; frame, 100%; bandwidth, 61 Hz; resolution, 46 Hz, Hamming window). 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 (Fig. 1). A phrase was defined as a sequence of different syllables repeated by the same individual or shared by different individuals.

According to their overall frequency modulation shapes, syllables were labelled on the sound spectrogram with a number. The same syllable found at several places in one song or in different songs of the same individual or of different individuals was labelled with the same number (Fig. 2). In this way, we established a catalogue of the different syllables produced by each individual.

Since skylark song is continuous (i.e. not divided in discrete categories of song types), repertoire size was measured as the total number of different syllables produced. For each individual, the syllable repertoire size was estimated by plotting the number of new syllables produced against their time of occurrence in the songs and calculating the value corresponding to the asymptote (Leitner et al., 2001).

We compared the syllable composition of neighbour and stranger repertoires by calculating a coefficient of repertoire similarity (RS) in which the number of shared syllables was related to the number of unshared syllables using the following equation: $RS = Z / [(X + Y) - Z]$, with X and Y being the total number of syllables produced by males x and y, and Z being the number of syllables shared by males x and y (Hultsch and Todt, 1989).

The sequential organization of syllables was examined using a custom Matlab program. For each song, the numbers corresponding to the syllable labelling were inputted into the Matlab program in the order of production of the corresponding syllables. By classifying sequences of numbers according to their length and the number of times they were repeated, the program allowed us to 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 using the RS coefficient applied to the number of shared and individual phrases.

The following temporal parameters were measured on sound spectrograms: duration of syllables, duration of silences between two successive syllables and duration of sequences. For each

sequence, these parameters were used to calculate the rhythm (sound per silence ratio), the tempo (number of syllables per time unit) and the syllable repetition rating (number of syllables that appear two or more times in a given sequence divided by the total number of syllables in this sequence).

As the data were not normally distributed, we used non-parametric statistics. Two-tailed Wilcoxon matched pair tests were used to compare acoustic parameters of phrases that were shared by neighbours and acoustic parameters of non-shared sequences of syllables. A Friedman test was used to compare the number of phrases shared by individuals between three song parts: beginning, middle and end. All statistical analyses were carried out using Statistica v6 (StatSoft, 2001). Two-tailed permutation tests were used to compare coefficients of similarity between repertoire composition of neighbours and strangers, as 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 neighbour and six times as a stranger) (Sokal and Rohlf, 1995; Mundry, 1999). All results are given as means \pm s.e.m.

RESULTS

Overall characteristics of the flight song

A total of 23 songs produced by the nine studied individuals were analyzed, corresponding to a mean duration of song analysis per individual of 370.7 ± 42.4 s. The mean song duration was of 145.1 ± 15.6 s. Songs comprised a succession of 710.0 ± 61.3 syllables, including 206.9 ± 9.9 different syllables.

Repertoire analysis at the syllable level

For each individual, the number of new syllables produced against their time of occurrence in the songs reached an asymptote, the value of which corresponded to the repertoire size. The studied birds ($N=9$) produced a total of 341 ± 21 different syllables. Neighbours had significantly more syllables in common in their repertoires ($RS=0.4930 \pm 0.0254$, $N=9$) than strangers ($RS=0.1919 \pm 0.0093$, $N=27$) (Permutation test: $N=36$; $P<0.001$). When RS values for all pairs of individuals are placed in a two-dimensional matrix, the dendrogram of Euclidean distances (i.e. the geometric distances) between the RS values illustrates the grouping of neighbours (Fig. 3).

Repertoire analysis at the phrase level

A detailed analysis of the syllable syntax revealed that most of them were arranged in a definite order repeated in the same song or in different songs of each male (phrases). Phrases were made up of an average of 7.2 ± 0.2 syllables ($N=23$ songs) and their duration was $77.2 \pm 1.6\%$ of the total song duration ($N=23$ songs).

In a location, comparisons of phrase repertoire between individuals revealed that pairs of neighbours shared 59.2 ± 6.4 different phrases (two-by-two comparisons, $N=9$), and all individuals within a location shared 30 ± 2 different phrases ($N=3$ locations). An example of such a shared phrase is given in Fig. 4. On the other hand, pairs of strangers had only 0.5 ± 0.1 different phrases in common (two-by-two comparisons, $N=27$). Furthermore, phrases shared by at least two neighbours of a given location were never found in repertoires of individuals established in other locations. Thus, the coefficients of similarity between neighbours' phrase repertoires ($RS=0.2949 \pm 0.0257$, $N=9$) were significantly higher than the coefficients of similarity between strangers' phrase repertoires ($RS=0.0018 \pm 0.0003$, $N=27$) (Permutation test: $N=36$; $P<0.01$).

On average, the duration of the phrases shared by neighbours represented $43.5 \pm 2.6\%$ ($N=23$ songs; min=22.7%; max=79.2%) of the total song duration. If we divided the songs into three parts (beginning, middle and end), these phrases were equally distributed (Friedman test: $F=1.49$; $N=23$ songs; $P<0.48$).

We found that phrases shared by neighbours differed from non-shared sequences of syllables by having a higher rhythm (Wilcoxon matched pairs test: $Z=3.92$; $N=23$ songs; $P<0.0001$), a higher tempo ($Z=2.13$; $N=23$ songs; $P<0.05$), a shorter duration of silences between two successive syllables ($Z=3.95$; $N=23$ songs; $P<0.0001$) and fewer repeated syllables ($Z=3.83$; $N=23$ songs; $P<0.001$). Syllable duration did not differ significantly between shared phrase and non-shared sequences of syllables ($Z=0.67$; $N=23$ songs; $P=0.50$).

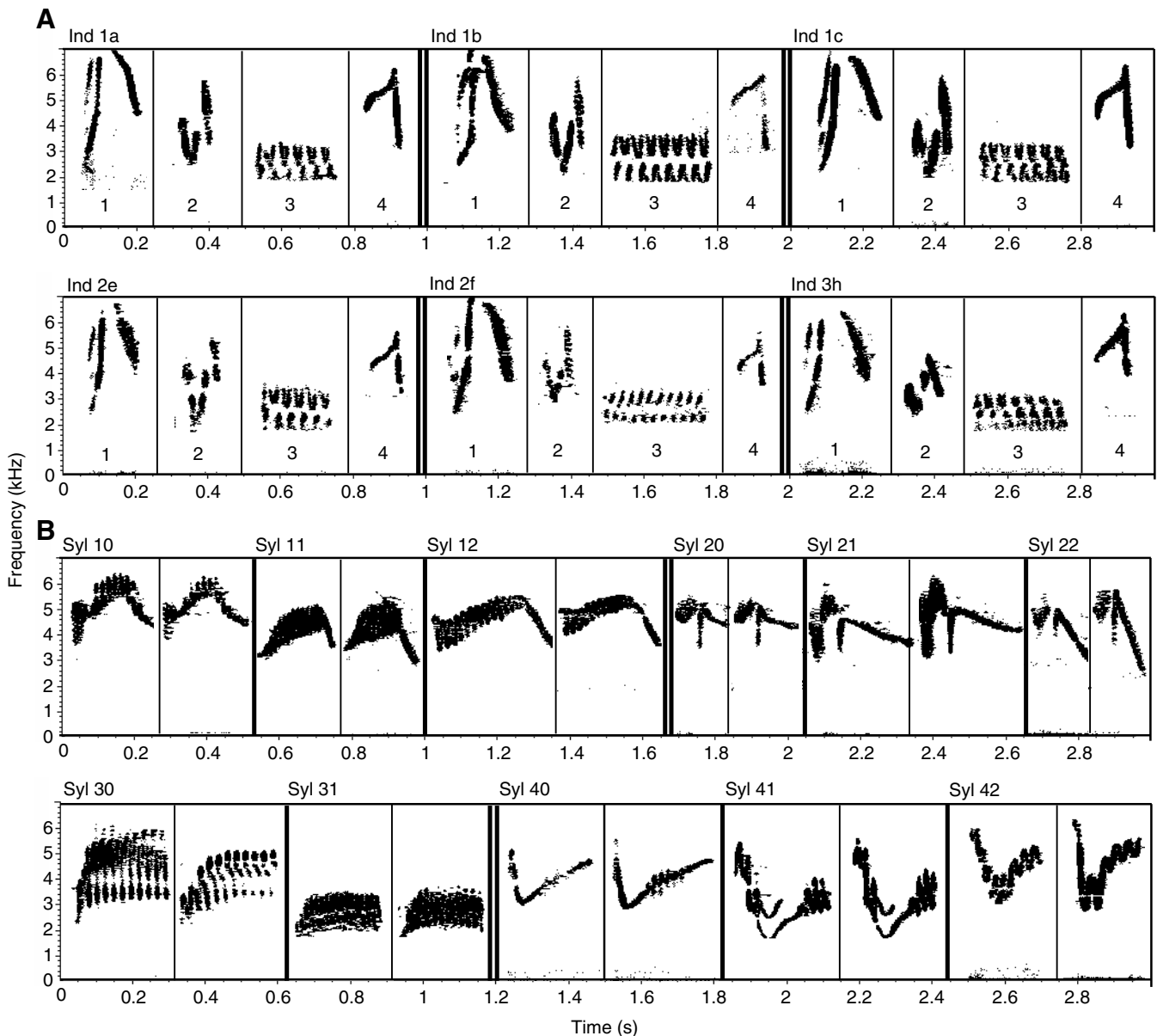


Fig. 2. Syllable classification. (A) Sound spectrogram of four syllables produced by six different individuals (Ind; individuals are identified by a number corresponding to the location and a letter that differentiates them from their neighbours inside the location). (B) Examples of syllables (Syl) classified as 'identical' or 'different'. Sound spectrograms of 11 pairs of 'identical' syllables produced by two different individuals. Double lines separate groups of syllables that have a similar shape but that were classified as 'different'.

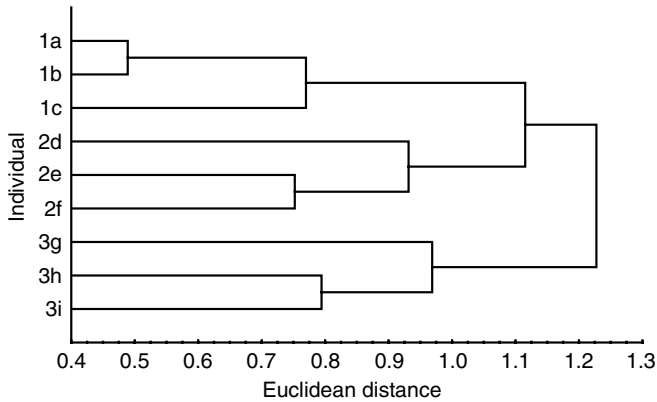


Fig. 3. Dendrogram of Euclidean distances between the repertoire similarity (RS) values calculated for skylark males holding territories in same or different locations (here three locations spaced out by at least 2 km). Subjects are identified by a number corresponding to their location and a letter that differentiates them from their neighbours inside the location.

(2) PLAYBACK EXPERIMENTS

MATERIALS AND METHODS

Principle

To investigate the neighbour–stranger vocal discrimination process, we conducted playback experiments. We tested the hypotheses that males discriminate neighbours from strangers by their songs and that shared phrases found in the songs of neighbouring birds (i.e. group signatures) were used for this discrimination. Playbacks were conducted in May 2005 and 2006, when territories were well established (Delius, 1963; Donald, 2004).

Signals tested

We broadcast three categories of songs to each of the 15 subjects tested: a Neighbour song (N), a Stranger song (S) and a Chimeric song (C), i.e. a stranger song where the shared phrases of the group had been artificially inserted. 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), we rescaled each recorded song to match the root mean square (RMS) amplitude of the different songs at the same output level. For each of the five locations, the N song broadcast to each subject was a song produced by one of its adjacent neighbours and always included phrases shared by the group. One S song was selected among the songs recorded in the most distant location from the one tested (four different S songs were broadcast for the experiment). Each S song was used to prepare the corresponding C song of the given location in the following way: 20–30% of the total duration of the S song was replaced by an equivalent duration of phrases shared by all the birds of the given location. These shared phrases had been previously identified by analyzing and comparing songs produced by at least three birds of each locality using the same protocol as above [(1) Song analysis], i.e. syllable labelling, sequence research using the custom Matlab program, and phrase repertoire comparisons. We inserted these phrases at random temporal positions within the S songs. Then, on the basis of our prior song analysis, we checked the spacing of shared phrases inserted to make sure it was within the natural range. Fewer shared phrases than the amount found in natural songs ($43.5 \pm 2.6\%$ of the total song duration) were inserted, to conserve as much as possible the ‘strangeness’ of the S song. The shared phrases of a given group had the same acoustic characteristics even if they had been produced by different birds. Thus, as the purpose of the experiment was to reveal the group signature, the shared phrases were extracted from songs of at least two different birds of the given location, from

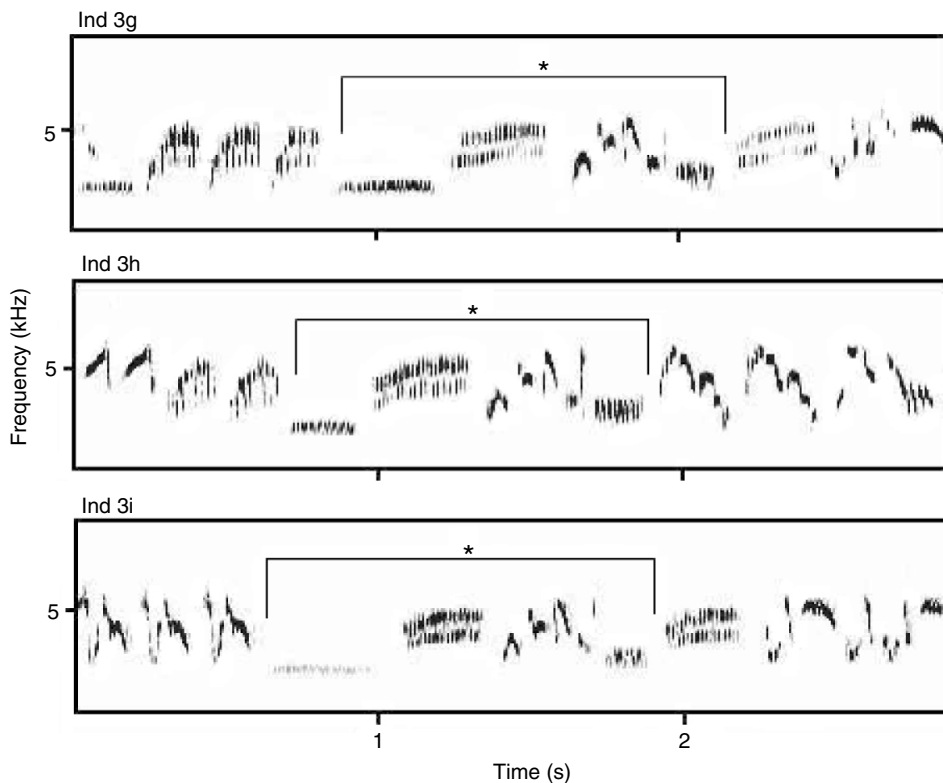


Fig. 4. Spectrograms of song parts produced by three individuals from the same location (3g, 3h and 3i), all including the same phrase (asterisk). (FFT length, 512; frame, 100%; bandwidth, 122 Hz; resolution, 93 Hz, Hamming window.)

the beginning of the first syllable to the end of the last silence for each phrase. They were then inserted 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 and Brémond, 1983). The overall amplitude level of inserted phrases was checked on the oscillogram and eventually adjusted to be sure that it was the same as the rest of the resulting C song.

Playback procedure

Experimental songs were played back with a numeric recorder (Marantz PMD 690) connected *via* a 20 m cable to a 10-W loudspeaker (Megavox Pro mega-6000, Ossining, NY, USA; frequency response, 400 Hz–10 kHz, ± 3 dB), at the intensity estimated to be normal for the birds (mean \pm s.e.m., 90.8 ± 0.8 dB measured at 1 m from the loudspeaker). Trials were conducted between 09:00 h and 12:00 h. The loudspeaker was positioned at about 5 m inside the territory of the tested bird, on the side of the boundary shared with the neighbour whose song was used to prepare the N song. The experimenter stood 20 m away from the loudspeaker. The three categories of tested songs (N, C and S) were broadcast the same day to each subject ($N=15$) 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. The song played back never elicited any song production by the neighbours of the subject tested. Thus the responses observed and scored could not be attributed to an external stimulus. To avoid habituation (Aubin, 1982), each subject was tested only once with the three categories of tested songs. Experiments were not conducted during rainy or windy weather.

Response measured and statistical analysis

For each trial, the response of the bird was scored during 180 s, corresponding to the broadcast of 90 s of song and the 90 s period of silence immediately following. The skylark male displays a very strong territorial behaviour with stereotyped patterns, which are easy to observe (Delius, 1963). It reacts vigorously against territorial intrusion by flying towards the intruder and by landing in its vicinity or flying low over it. It then takes up a fight posture, head and crest up, and emits threat calls. Thus, we chose to score the following qualitative and quantitative responses to assess the effects of the different categories of songs played back.

Qualitative responses

In a first step, we scored qualitative responses with 0 or 1 values: occurrence or not of chases by the subject against other males present in the vicinity, and presence or absence of subjects for any length of time at different regions around the loudspeaker during the playback. These regions were d_2 , d_1 and d_0 , with $10 \text{ m} > d_2 \geq 5 \text{ m}$, $5 \text{ m} > d_1 > 0 \text{ m}$, and d_0 was flying over the loudspeaker.

Quantitative responses

In a second step, we used principal component analysis (PCA) to create a composite score with the following quantitative responses, which are likely to be correlated. The PCA included latency before the first movement, latency to approach at less than 10 m and at less than 5 m from the loudspeaker, and latency before the first song emission. When the subject was present inside the territory during the whole trial without performing this behaviour, a latency of 180 s (corresponding to the total trial duration) was attributed for the

playback. The PCA also included durations of movements (flying or walking on the ground) and of songs: total duration of movements, duration of movements between 10 and 5 m and between 5 and 0 m from the loudspeaker, and duration of songs produced in response. Lastly, the PCA included the time spent 10–5 m and 5–0 m from the loudspeaker, and the total number of calls produced in response.

As the data were not normally distributed, we used non-parametric statistics. Qualitative responses were compared using Q Cochran tests. 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, 2001).

RESULTS

Although the three categories of songs (N, C and S) were randomly broadcast to a given subject, we tested the possibility of a confounding effect of habituation or increasing aggression due to an order effect. A Friedman's test with the order of presentation of the playback treatments as repeated measures and the responses of subjects as the dependant variables revealed no order effect ($F=4.13$, $N=15$, $P=0.13$).

Qualitative responses

The presence of subjects elicited by the broadcast of the three categories of songs was significantly different at d_2 (Cochran Q test: $Q=16.91$, $N=15$, $P < 0.001$), at d_1 ($Q=11.14$, $N=15$, $P < 0.01$) and at d_0 ($Q=8$, $N=15$, $P < 0.05$). Further comparisons using Cochran Q tests showed that significantly more subjects were present at d_2 in response to S song than to N and C songs (Fig. 5). The presence of subjects at d_1 was also significantly greater in response to S song than to N song, and tended to be greater when elicited by S song than to C song. At d_0 , the presence of subjects tended to be greater in response to S song than to N and C songs. At d_2 , the response to C songs tended to be greater than the response to N songs. Responses to N and C songs were not significantly different at d_1 and d_0 .

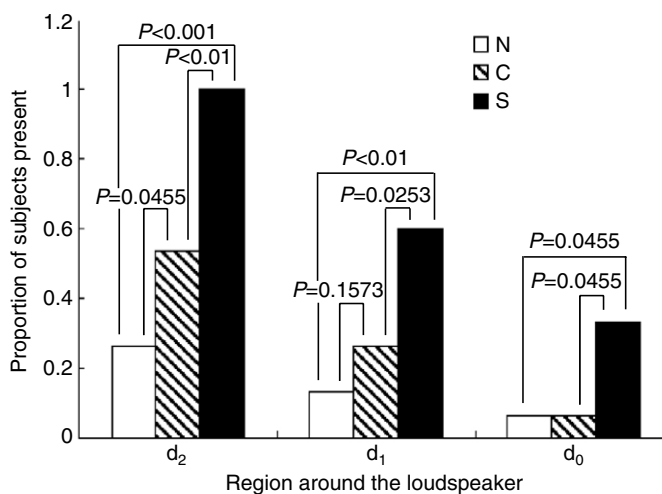


Fig. 5. Proportion of subjects ($N=15$) present 10–5 m from the loudspeaker (d_2), at less than 5 m from the loudspeaker (d_1) and over the loudspeaker (d_0) during playbacks of N, C and S songs (P values refer to *post-hoc* Cochran Q test).

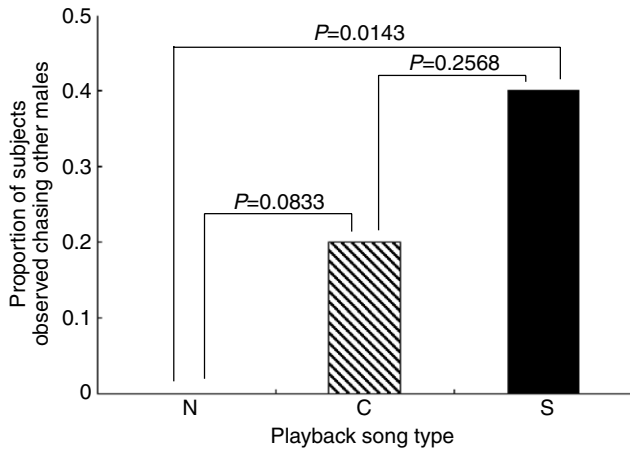


Fig. 6. Proportion of subjects ($N=15$) observed chasing other males present in the vicinity during playbacks of N, C and S songs (P values refer to *post-hoc* Cochran Q test).

The occurrence of chases by the subjects directed against other males present in the vicinity during the playback of the three categories of songs was significantly different (Cochran Q test: $Q=6.75$, $N=15$, $P<0.05$). Comparisons using Cochran Q tests showed that the occurrence of chases by the subjects was significantly greater in response to S song than to N (Fig. 6). Differences between responses to S and C songs and between C and N songs were not significant.

Quantitative responses

The first principal component (PC1) explained 36.1% of the variance in the response measured. Examination of the component loadings, showed in Table 1, reveals 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. Higher negative values of PC1 corresponded to a stronger response, i.e. spending more time moving, approaching closer to the loudspeaker

Table 1. Eigenvalue, variance explained, and loadings of the response measures on the first (PC1) and second (PC2) principal component for playbacks of N, C and S songs

Statistics and response measures	PC1	PC2
Eigenvalue	3.975	1.905
Percent of variance	36.143	17.315
Duration of movements between 5 and 0 m	-0.836	-0.034
Latency to approach at less than 5 m	0.777	0.095
Latency to approach at less than 10 m	0.704	0.084
Total duration of movements	-0.697	-0.269
Duration of movements between 10 and 5 m	-0.686	-0.096
Total number of calls	-0.661	-0.087
Time spent between 5 and 0 m	-0.626	-0.200
Time spent between 10 and 5 m	-0.483	0.153
Duration of songs	0.302	-0.877
Latency before the first song	-0.220	0.843
Latency before the first movement	0.144	-0.505

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

N, neighbour; C, chimeric; S, stranger.

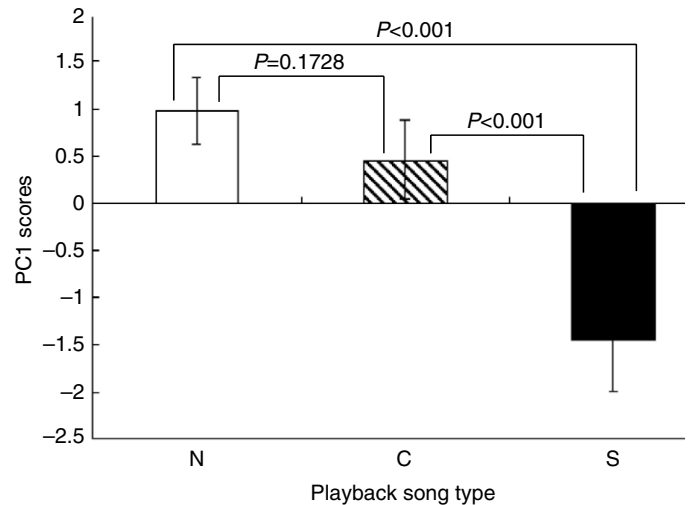


Fig. 7. First principal component scores (means \pm s.e.m., $N=15$) for playbacks of N, C and S songs.

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: $F=20.80$, $N=15$, $P<0.0001$). As shown in Fig. 7, subjects responded significantly more strongly to S song than to N and C songs. Responses to N and C songs did not differ significantly (Wilcoxon matched pairs test: $Z=1.36$, $N=15$, $P=0.17$).

The second principal component (PC2) explained 17.3% of the variance in the response measured. As shown in Table 1, the duration of songs, latency before first song and the latency before the first movement loaded highly on PC2. No significant effect of the broadcast of the three categories of songs on PC2 scores was found ($F=3.33$, $N=15$, $P=0.18$).

DISCUSSION

Our analysis of the song of the skylark revealed that a majority of syllables were structured syntactically in phrases that recurred several times in a song or in different songs produced by the same individual. These phrases represented more than 75% of the total duration of a song. By comparing the repertoire composition of birds established in the same location ('neighbours') and birds established in different locations spaced by few kilometres ('strangers'), we showed that variation exists in the song of the skylark, at the syllable and at the phrase levels. Neighbours, indeed, shared many more syllables and phrases than did non-neighbouring males, and phrases shared by neighbours of a given location were never produced by individuals from other locations studied. Thus, within each location, the songs of resident males consisted on average of 1/4 individual non-repeated sequences, 1/4 individual phrases and 1/2 shared phrases. Most of the species exhibiting syllable sharing also exhibit song dialects (Mundinger, 1982; Thomson, 1970; DeWolfe et al., 1974; Austen and Handford, 1991). The existence of dialects implies dissimilarities among birds of different localities (Thielcke, 1969; Lemon, 1975; Mulligan, 1975). Variation occurring between close groups of birds is called microgeographic variation and is often expressed in the syntactic organization of the songs. Such microgeographic variation has been identified in many non-oscines, sub-oscines and oscines bird species (Mundinger, 1982), including two species of Alaudidae, namely the flappet lark *Mirafra rufocinnamomea* (Payne, 1973)

and crested lark *Galerida cristata* (Tretzel, 1965), and species with complex songs like the thrush nightingale *Luscinia luscinia* (Griessmann and Naguib, 2002) and the wedge-tailed sabrewing *Campylopterus curvipennis* (Gonzalez and Ornelas, 2005). Skylark songs exhibit microgeographic variation based on both significant differences in the syllable repertoire composition and in the phrase repertoire composition between individuals established in different locations. In that respect, the skylark differs from other species, in which microdialects are based on the sequences of song components but not the basic song components themselves, e.g. the thrush nightingale (Griessmann and Naguib, 2002) and the grey-cheeked fulvetta *Alcippe morrisonia* (Shieh, 2004). The values of coefficient of similarity between the repertoires of strangers in our study ($RS=0.19\pm 0.01$) are comparable with those obtained in similar distance range in other passerine species, such as the thrush nightingale [$RS=0.27\pm 0.01$ (Griessmann and Naguib, 2002)] or the chaffinch [*Fringilla coelebs*; $RS=0.3$ on average at 2 km (Lachlan and Slater, 2003)].

We carried out a playback experiment to test the hypothesis that the phrases shared by all individuals from a given location supported a group signature. When a territorial intrusion was simulated by the broadcast of a stranger's song, subject males spent more time moving, approached closer to the loudspeaker and, after a shorter latency, engaged in more pursuits of other birds, and produced more calls compared to the playback of a neighbour's song. Thus, skylark males discriminated neighbours' from strangers' songs and displayed a stronger territorial behaviour towards the latter, as has been observed in numerous bird species, such as the European robin *Erithacus rubecula* (Brindley, 1991), banded wren *Thryothorus pleurostictus* (Molles and Vehrencamp, 2001), blue grouse *Dendragapus obscurus* (Falls and McNicholl, 1979) and alder flycatcher *Empidonax alnorum* (Lovell and Lein, 2004). 90 s of song (the duration of the songs played back) were sufficient for the birds to differentiate the two categories of songs. This reduced territorial response to intrusion by 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). Thus, neighbour-stranger discrimination results in a mutual benefit for neighbours by avoiding time and energy consuming contests to defend the shared boundary. The fact that neighbours distinguish between familiar and unfamiliar conspecifics does not mean that they necessarily recognize each other individually. The potentiality for individual information to be coded in the song of the skylark exists in the individual syllables and phrases identified by our analysis. To investigate whether individual recognition occurs, further playback experiments are thus required in which, for example, responses of subjects to the broadcast of their neighbours' songs on correct and wrong territory locations are compared.

While numerous studies in songbirds have revealed that N-S recognition based on vocal interactions is a rather common feature, very few have attempted to highlight the vocal parameters coding the information allowing such discrimination. To test the hypothesis that the phrases shared by all individuals from a given location act as a pass signalling the emitter as a member of the group, we carried out playback experiments with 'chimeric' signals: songs of strangers including the 'group signature'. A similar level of responses was observed when a chimeric song and a neighbour 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 markers of the group identity. Microdialects therefore constitute a basis for the dear-enemy phenomenon in the skylark. Despite the fact that 70–80% of the chimeric song broadcast was unknown for each bird tested, 20–30% of inserted shared phrases were sufficient to allow group recognition. Such a proportion of shared phrases was less than the average found in natural songs and thus may indicate that the information carried by the shared phrases is redundant. Nevertheless, the presence of subjects at d_2 (10–5 m from the loudspeaker) tended to be greater in response to the chimeric song than to the neighbour song. This could indicate that the proportion of shared phrases inserted was not entirely sufficient to give exactly the same value to the chimeric song as a neighbour song. It may also be that an adjacent neighbour song would elicit a less intense response than any song of other birds of the group, as a consequence of prior habituation and/or individual recognition. Additionally, we cannot exclude the fact that the recognition process is not based upon the sequential organization of the shared phrases, but more on fine acoustic details of the syllable structure peculiar to neighbours of the group. Thus, the birds could be confused by hearing different 'voices' in the same song, as each chimeric song contained at least 70% of stranger syllables and as shared phrases were extracted from songs of at least two different birds. In the same way, the birds could also be confused by hearing a neighbour 'voice' from a non-expected territory side.

Our analysis revealed that the continuous song of the skylark included 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. Shared phrases indeed differed from non-shared ones by a faster rhythm and tempo, due to a shorter duration of silences between successive syllables, and a lower repetition rate of identical syllables. Such a song structure could be compared to that of the canary *Serinus canaria* song, in which some special 'sexy' phrases differ acoustically from other phrases by a larger frequency bandwidth, a faster frequency modulation and a faster frequency of repetition of the syllables. These sexy phrases have a particularly strong potential to sexually stimulate the females (Vallet and Kreutzer, 1995; Vallet et al., 1998).

In some studies of oscines and non-oscines species, a more intense response was elicited by the local dialect than by a dialect from some distance away (for reviews, see Nelson, 1998; Wright and Dorin, 2001), which apparently contrasts with our results. The mechanism of such a response pattern has been hypothesized to be driven by the species song recognition process, in which the songs that elicit the strongest behavioural responses are those that most closely match an individual's internal representation of their species' standard song (Dabelsteen and Pedersen, 1992; Lampe and Baker, 1994; Nelson, 1998). As the individual's internal representation is built by listening to the local dialect, a foreign dialect is 'simply' not recognized as conspecific. The parameters used by the skylarks to identify other individuals as conspecifics have already been identified (Aubin and Brémond, 1983), and all the songs broadcast in our study were carrying them. Furthermore, these other studies aimed to emphasize the function of dialects in the species recognition process. Thus, they chose local songs that were not produced by immediate neighbours and were not likely to be known by the birds subjected to playback. In our case, we broadcast songs of adjacent neighbours known by the subjects and of strangers, established only few kilometres away, not known by the subjects.

Within certain genetic limitations or song learning 'predispositions', most songbirds acquire particular songs through

imitation of models produced by conspecifics, although improvisation or invention may occur. Song sharing is a typical consequence of this imitation strategy (Beecher and 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 and 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. We cannot exclude that neighbours in our study were related and were partial siblings or fathers and sons. Thus, some parts of their song might share genetically determined components. Another possibility is that 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 the redwings *Turdus iliacus* (Espmark et al., 1989), and the white-crowned sparrows, *Zonotrichia leucophrys nuttalli* (Trainer, 1983). The only aspect of song learning in skylarks known to date is that they are able to imitate the song of other bird species (e.g. Peter, 1997). 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 1-year-old skylarks exhibit strong site fidelity, most returning in the year after hatching to within 1 km of their natal nest. Thus the conditions for the maintenance of dialects in this species are fulfilled.

Depending on the hypothesis, song learning leads to birds having a large song repertoire, or producing songs that they share with their neighbours. According to the 'repertoire' hypothesis, large song repertoires are selected by female choice, and according to the 'sharing' hypothesis, small repertoires of shared songs are selected by male-male competition. These two selection trends are at least partially contrary because song-learning strategy cannot optimize both goals (Beecher and Brenowitz, 2005). Indeed, maintaining high stereotypy in learned songs becomes increasingly difficult as song repertoires become larger (Kroodsma, 1974). Nevertheless, it seems that the song-learning strategy of the skylark succeeded in selecting a very large repertoire and also consequent phrase sharing among songs of neighbours. To our knowledge, only one study explored the N-S discrimination in a species with a very large repertoire (Brindley, 1991). We found that skylarks are exceptional among songbirds because they produce continuous songs lasting, on average, 145 s with very long streams of syllables. Because most other songbirds deliver their songs according to a discontinuous pattern, numerous studies have measured song repertoire size as the number of song types sung by males. Thus, comparison of repertoire size, estimated in number of syllables, between the skylark and these other species is difficult. Compared with the few species where the repertoire was estimated in number of different syllables produced, like the meadow pipit *Anthus pratensis* [3-6 syllables (Elfström, 1990)], house finch *Carpodacus mexicanus* [25-40 different syllables (Mundinger, 1982)], thrush nightingales [49 basic song components (Griessmann and Naguib, 2002)], or canary [81 syllables (Leitner et al., 2001)], the skylark produces a highly diversified and complex continuous song, containing more than 200 different syllables per song, with a total repertoire size of more than 300 syllables per individual.

The results of our study do not support the 'repertoire constraint' hypothesis (Krebs and Kroodsma, 1980), which predicts a negative

relationship between N-S discrimination and 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. The 'repertoire constraint' hypothesis supposed that the task of memorizing a repertoire becomes more difficult as the size of the repertoire increases (Kroodsma, 1976). It would be interesting to determine the amount of time necessary for skylarks to be able to perform such discrimination by testing the birds several times from the very beginning of their settlement in stable territories to the end of the breeding season. The onset of recognition may take more time in such species, as hypothesized by Lambrechts and Dhondt (Lambrechts and Dhondt, 1995). Neighbour identification could be coded in only a few features of the repertoire, for example in characteristic sequences of songs (Stoddard, 1996), in one distinct song, or in voice characteristics (Lambrechts and Dhont, 1995), which may be more easily memorized. In these cases, listening to the whole neighbour repertoire is not necessary for recognition. This could be the case for skylarks. Birds, as indicated above, may learn only a part of their neighbours' song, i.e. some of the shared phrases supporting the group signature.

In conclusion, we have shown that skylark dear-enemies sing a common code signing the group and use it so as not to attack each other. We established a clear relationship between microdialects and N-S discrimination in a species with a very large repertoire.

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