

Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark

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Summary

1. Males of many bird species match song with neighbours during territorial interactions. Although bird vocal mimicry has received much attention, the relationships between song variation and ecological factors such as landscape geometry and habitat fragmentation are still poorly known, and most previous research has been limited to one or a few populations of a species. In this study we analysed the spatial patterns and ecological determinants of song matching in Dupont's lark *Chersophilus duponti*, a rare and specialized steppe passerine.

2. By recording bird songs from 21 Spanish and Moroccan localities, we analysed the effect of habitat fragmentation and the availability of suitable steppe habitat on the patterns of song matching in Dupont's lark, controlling for other potential determinants such as period in the breeding season, intensity of competition, geographical location and spatial distribution of individuals.

3. Both song-type sharing (match of song types in the repertoire) and spectrotemporal matching (convergence in the acoustic features of the same song type) were greater between counter-singing neighbours than between non-neighbours, and spatial autocorrelation (similarities between singing individuals) only occurred at short distances. The study localities differed in the amount of overall acoustic matching between individuals, seemingly as a consequence of local differences in the intensity of male competition and in the availability of suitable habitat.

4. The levels of song-type sharing between non-neighbours tended to increase and those among neighbours to decrease with the increase of steppeland availability. Moreover, the existing differences in sharing between neighbours and non-neighbours were significantly affected by the presence of elements of fragmentation in the steppe. In fragmented habitats, song sharing among neighbours was enhanced, possibly because of harsher competition for limited resources; conversely, sharing among non-neighbours dropped, probably because of the lack of interactions among individuals isolated by habitat barriers.

5. Synthesis and applications. Anthropogenic habitat barriers could alter bird perception of the spatial distribution of rivals over distance, leading to a contraction of the spatial range of the individual acoustic niche. We suggest that communication systems of habitat-sensitive species might be used as a behavioural indicator of anthropogenic environmental deterioration. Because of their rapidly evolving cultural nature, bird vocalizations might become an early warning system detecting the effects of fragmentation over relatively short times and before other indicators (such as genetic markers) show any change.

Key-words: *Chersophilus duponti*, cultural evolution, habitat loss, steppe

Introduction

Sharing song types with neighbours is common in birds with a pool of song types that are learned after natal dispersal (Beecher *et al.* 1997; Hill *et al.* 1999). Song-type sharing occurs when a male replies to a rival's song with the same song sequence, with the supposed purpose of signalling an increased likelihood of attack on the singing opponent (Bremond 1968 modified by Krebs, Ashcroft & Van Orsdol 1981; Vehrencamp 2001; Anderson, Searcy & Nowicki 2005). The use of song matching as a threat signal between males has been thought to explain the evolution of complex song repertoires, given that the possession of a large song pool increases the number of rivals that can be matched (Hughes *et al.* 1998). There is both direct and indirect evidence that sharing song types with neighbours may bring fitness advantages, related to territory tenure (in the song sparrow *Melospiza melodia* Wilson; Beecher, Campbell & Nordby 2000), mating success (in the brown-headed cowbird *Molothrus ater* Boddaert; Dufty 1985) and reproductive success (in the great reed warbler *Acrocephalus arundinaceus* L.; Catchpole 1986). In addition, male quality can determine the amount of song-type sharing in a population (in the western meadowlark *Sturnella neglecta* Audubon; Horn, Dickinson & Falls 1993). In simulated territorial games, Lachlan, Janik & Slater (2004) found that vocal matching (conformity) was a more successful strategy (it spread more frequently) than ignoring conformity. Notably, conformism is one of the most important components of human social learning, and genes leading to conformist transmission might have been favoured by natural selection in a wide range of environmental conditions (Boyd & Richerson 1985; Henrich & Boyd 1998).

Levels of song sharing in birds have proven to vary with respect to time in the breeding season, migratory status of the species and geographical location. Song sparrows, for instance, were more likely to song-type match early in the breeding season, when territory boundaries were unstable, than late in the season, when territories were already well established (Beecher *et al.* 2000). Moreover, migratory populations might share less song types than sedentary and stable ones, and differences in the proportions of migratory and resident birds in a population might account for geographical variations in the levels of song sharing (Ewert & Kroodsma 1994).

Although songbird vocal mimicry has been widely studied (for a comprehensive review see Beecher & Brenowitz 2005), to our knowledge no study has focused on variation in song-matching patterns in relation to ecological factors such as landscape geometry and habitat fragmentation driven by human intervention, and most previous research has been limited to one or a few populations. In this study, we analysed the spatial patterns and ecological determinants of song variation in a large number of populations of Dupont's lark *Chersophilus duponti* Vieillot, an ecologically as well as geographically restricted songbird that exclusively inhabits flat steppeland

fragments of Spain and northern Africa (Cramp 1988). Spanish populations of Dupont's lark have dropped to 1300–1900 breeding pairs and are increasingly threatened by anthropogenic habitat loss and fragmentation (Garza, Suárez & Tella 2003; Garza, Traba & Suárez 2003; Tella *et al.* 2005). Less known is the species status in northern Africa, where overgrazing and agricultural development has led to population declines in Tunisia (Isenmann *et al.* 2005) and the population in Morocco has not increased above 2000–3000 breeding pairs (BirdLife International 2005).

We assessed the occurrence of song matching between Dupont's lark males from Spanish and Moroccan populations, and examined a set of ecological and ethological factors, such as the amount of steppe cover, geographical location, period in the breeding season, intensity of male competition and spatial distribution of individuals. In particular, we tested whether local habitat fragmentation could affect the degree of song matching between counter-singing neighbours and non-neighbours. As Dupont's lark is strictly dependent upon steppe habitats to feed, nest and shelter (Garza & Suárez 1990), we expect that the occurrence of habitats other than this in the landscape might alter the perception of the spatial distribution of rivals, affecting the magnitude of cultural transmission of acoustic variants. Holland, McGregor & Rowe (1996) hypothesized that rapid change in land use might have driven microgeographical differentiation in the song of the corn bunting *Miliaria calandria* L., but so far no previous study has analysed the role played by habitat loss and fragmentation on song-matching patterns. Most studies on song matching have been carried out on type or repertoire matching, where one bird's reply is unambiguously similar to the others' song (Burt *et al.* 2002), but there is less evidence on the convergence of acoustic (frequency and temporal) properties within the same song type (Bell, Trail & Baptista 1998). In this study, we analysed vocal mimicry at both qualitative and quantitative scales, by expressing song matching as song-type sharing, counter-singing males that shared song types, and spectrotemporal matching, male songs that converged in their physical properties.

Methods

We recorded Dupont's larks throughout Spain in March–June 2004, and in Morocco at the end of February 2005 during the breeding period. Males were recorded in their territories from 1 to 1.5 h before until 1–2 h after dawn. We used a TC-D8 DAT recorder (Sony Corporation, Tokyo, Japan) and a ME67 microphone (Sennheiser, Berlin, Germany) to record birds, and a GPS eTrex(r) Navigator (Garmin, Olathe, KS, USA) to establish male positions during singing bouts.

We recorded 326 singing males, from which we selected a subsample of localities with at least seven birds and where each individual repeated its complete song at least

three times (to record the complete song repertoire). Hence, sample size was 204 birds from 20 Spanish localities (196 birds, 7–18 individuals per locality) and one Moroccan site (eight birds) (see Appendix S1). In Spain, the species occurs in patches or groups of nearby patches in each locality (frequently hosting < 10 territories), isolated from other localities by a large matrix of unsuitable habitat. In the Moroccan study area, steppeland cover was more continuous, although locally degraded by overgrazing.

During dawn choruses, males from neighbouring territories approached each other to counter-sing along territory boundaries. Interacting neighbours reduced interindividual distances, often showing a clumped distribution. Singing clusters comprised up to seven birds but birds also sang alone. Males from adjacent territories interacting during bouts of counter-singing were considered as members of the same song cluster (neighbours), for which the mean pairwise distance was 201 m ± 28 SE. Conversely, pairs of males from different singing clusters or birds alone were classified as non-neighbours (mean pairwise distance 1914 ± 363 m).

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The Dupont's lark song unit is made up of several discrete sequences (three to 11 per individual); song sequences (types) are made up of one to 13 notes (Fig. 1). The most common sequence of Dupont's lark song is the so-called 'whee-ur-wheeee' (Cramp 1988) (Fig. 2). This sequence is composed of a number of notes that varies among localities (from four to 10) but always ends with a characteristic tonal note of increasing pitch. We focused on this sequence to quantify song spectrotemporal matching. In the time domain, we measured total sequence duration and the duration of each note, whereas in the frequency domain we quantified the maximum frequency of each note and its frequency range. In the final tonal element, we also measured the fundamental frequency. We measured 842 sequences (on average four per bird) but all the analyses were carried out using individual means.

To quantify individual repertoire size, we classified song types by inspecting sonograms by eye. Visual inspection of sonograms was carried out by the same investigator, thus avoiding any interobserver bias. To measure song-type sharing, we compared the bird's song repertoire with that of all the recorded males in the same locality. To be considered as shared songs, two sequences had to match at least 3/4 of their component notes and the matching portions had to be similar in note shape, timing and frequency. Classification was facilitated by restricting interindividual comparisons within localities, where borderline cases were rare. Once song type had been classified, we built a binary matrix of song types, scoring the presence (1) or absence (0) of a song type in the pool of an individual.

Sound analyses were carried out with Avisoft SASLab Pro 3.91 (Specht 2003), performing a Fast Fourier

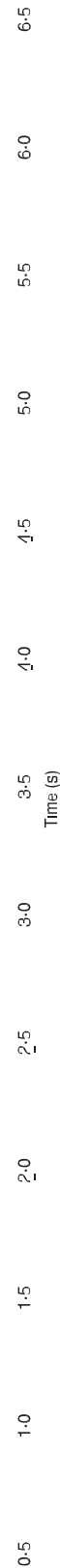


Fig. 1. Spectrogram of the six sequences included in the song repertoire of a male Dupont's lark from locality a. The last sequence is the 'whee-ur-wheeee' (see also Fig. 3).

neighbour, non-neighbour and overall acoustic matching, respectively.

3 and 4. Latitude and longitude, to control for geographical variation.

5. Recording period, to control for temporal variation.

6. An index of male competition. The intensity of male antagonism was expressed as the relative proportion of singing males in each locality, obtained by dividing the number of males that sang a complex song by the total number of males vocalizing in the area (i.e. singing and calling birds). When Dupont's lark males are engaged in parental care, they reduce the intensity of territorial disputes at dawn and singing activities drop (P. Laiolo & J. L. Tella, personal observations), thus a greater proportion of males singing should imply harsher disputes for territories or mates, and greater competition levels within a zone.

Before carrying out analyses, data were log-transformed, and a normal distribution and an identity link function were used in models. By applying Bonferroni correction, a model was considered significant for P -values < 0.008 . Analyses were carried out with the package Statistica 6.1 (StatSoft 2003).

Results

Acoustic similarity

The song repertoire within sites included 11–34 song types. Overall song-type sharing within localities varied between 0.16 and 0.54, whereas spectrotemporal matching comprised between 0.38 and 0.96 (Table 1). Differences among localities were significant (song-type sharing: $F_{19,914} = 61.9, P < 0.001$; spectrotemporal matching: $F_{19,914} = 24.6, P < 0.001$). A significant correlation resulted between the two measures of acoustic similarity ($R_s = 0.54, n = 21, P < 0.05$).

Spatial autocorrelation analyses showed that only four localities out of the 21 sites had no clear patterns of acoustic differentiation with spatial distance among individuals, either in spectrotemporal matching or in song-type sharing. In 12 localities we found song-type dissimilarities, and in 10 localities we found spectrotemporal dissimilarities that were significantly lower than expected by chance for distances shorter than 500 or 1000 m (Table 1). Divergence was never significantly greater than expected by chance for longer distances, implying that a stabilizing profile in dissimilarity patterns was achieved, with song matching occurring within a limited spatial radius (Fig. 3).

Wilcoxon matched pairs tests confirmed that song-type sharing and spectrotemporal matching were greater between neighbours than between non-neighbours (spectrotemporal features: $T = 13, n = 21, P < 0.001$; song type: $T = 6, n = 21, P < 0.001$; Fig. 4).

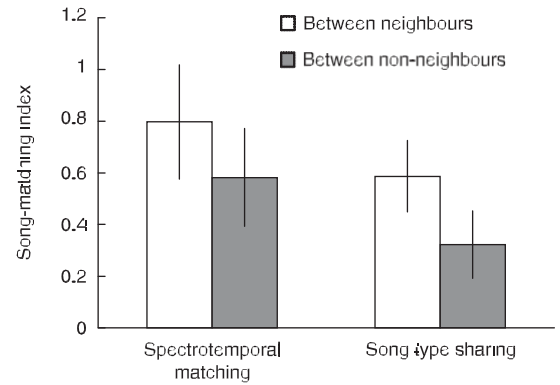


Fig. 4. Mean values (SD) of song spectrotemporal matching and song-type sharing between neighbours and non-neighbours. Values were obtained by averaging the mean values for each locality ($n = 21$).

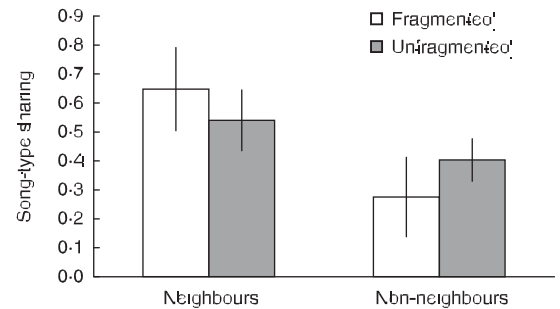


Fig. 5. Mean values (SD) of song-type sharing between neighbours and non-neighbours in fragmented and continuous steppeland. Values were obtained by averaging the mean values for each locality ($n = 21$).

Effects of fragmentation on sharing patterns

Two-way ANOVA showed significant differences in song sharing between neighbours and non-neighbours ($F_{1,34} = 27.4, P < 0.001$) and highlighted the effects of fragmentation on neighbour–non-neighbour sharing patterns (neighbour–non-neighbour fragmentation: $F_{1,34} = 10.5, P = 0.0027$). This implied that the existing differences in sharing between neighbours and non-neighbours were significantly affected by the presence of elements of fragmentation in the steppe (Fig. 5). In the case of spectrotemporal matching, differences were no more significant.

The proportion of steppeland cover varied from 31% to 100% (average 83.2%) in the study localities. Fragmentation at the local scale was the result of agriculture (cereal fields, orchards), forestry (pine plantations) and, to a lesser extent, urbanization (highways, buildings, railways, etc.) and woodland encroachment. The index of male competition (relative proportion of singing males) comprised between 1 (all birds singing) and 0.4 (40% of birds singing).

Latitude, longitude, interindividual distances, index of male competition, steppe cover and recording period were uncorrelated (all $R_s < 0.35, n = 21, NS$), thus they

Table 1. Average song-type sharing and spectrotemporal matching (overall, between neighbours and between non-neighbours) in the 21 study localities. Distance classes at which observed dissimilarities in song-type pool and spectrotemporal features were significantly lower or greater than expected by chance are also shown, as derived from spatial autocorrelation analyses

Locality	Song-type sharing			Spectrotemporal matching			Song-type dissimilarities		Spectrotemporal dissimilarities	
	Overall	Neighbours	Non-neighbours	Overall	Neighbours	Non-neighbours	Distances at which dissimilarities are significantly lower than expected by chance ($P < 0.05$)	Distances at which dissimilarities are significantly greater than expected by chance ($P < 0.05$)	Distances at which dissimilarities are significantly greater than expected by chance ($P < 0.05$)	Distances at which dissimilarities are significantly greater than expected by chance ($P < 0.05$)
a	0.35	0.55	0.27	0.81	0.87	0.78	< 500	–	< 1000	–
b	0.26	0.76	0.12	0.45	1.10	0.42	< 1000	–	–	–
c	0.43	0.81	0.34	0.40	0.56	0.37	–	–	–	–
d	0.32	0.68	0.20	0.43	0.66	0.42	–	–	< 500	–
e	0.34	0.51	0.18	0.48	0.54	0.37	< 500	–	< 500	–
f	0.16	0.67	0.08	0.54	0.79	0.51	–	–	< 1000	–
g	0.38	0.50	0.43	0.48	0.96	0.62	< 1000	–	–	–
h	0.38	0.63	0.35	0.64	1.05	0.89	< 500	–	< 500	–
i	0.43	0.70	0.43	0.55	0.98	0.75	–	–	–	–
j	0.45	0.60	0.42	0.75	1.03	0.65	–	–	< 1000	–
k	0.37	0.77	0.26	0.96	1.18	0.40	–	–	–	–
l	0.37	0.44	0.30	0.52	1.01	0.91	< 500	–	< 1000	–
m	0.47	0.45	0.32	0.63	0.49	0.55	< 500	–	–	–
n	0.41	0.43	0.58	0.49	0.65	0.62	< 1000	–	< 1000	–
o	0.34	0.51	0.51	0.38	0.79	0.32	–	–	–	–
p	0.50	0.60	0.37	0.93	0.69	0.44	< 500	–	–	–
q	0.53	0.40	0.38	0.83	0.56	0.61	< 500	–	–	–
r	0.46	0.65	0.42	0.72	0.89	0.92	< 500	–	< 500	–
s	0.48	0.48	0.30	0.91	0.65	0.62	< 1000	–	–	–
t	0.29	0.91	0.20	0.59	0.49	0.47	–	–	–	–
u	0.54	0.58	0.49	0.62	1.05	0.51	–	–	< 500	–

Table 2. Results of generalized linear models carried out to highlight predictors of acoustic matching. Only ecological and ethological predictors that significantly entered in the models, and acoustic variables significantly affected, are shown. Significance levels were Bonferroni corrected. Sample size corresponds to 21 localities

	Estimate	SE	Wald statistics	Exact <i>P</i>
Overall spectrotemporal matching				
Steppeland cover	0.21	0.06	11.8	0.00058
Index of male competition	0.20	0.04	19.4	0.00001
Non-neighbours spectrotemporal matching				
Steppeland cover	0.19	0.06	9.2	0.0024
Index of male competition	0.22	0.05	22.9	0.000002
Non-neighbour song-type sharing				
Steppeland cover	0.19	0.06	9.5	0.0020
Neighbour song-type sharing				
Steppeland cover	-0.17	0.06	8.8	0.0029

were entered in generalized linear models as independent predictors. Dupont's lark males shared significantly more song types with non-neighbours and less with neighbours in areas with a larger proportion of continuous steppeland (Table 2). Spectrotemporal similarities between non-neighbours were also significantly correlated with steppeland cover and increased with the level of competition in the site (Table 2). Overall spectrotemporal matching significantly increased with the intensity of male competition and with steppeland cover (Table 2). Recording period, distance and geographical location had no effect on the degree of song-type sharing and spectrotemporal matching, either between neighbours or non-neighbours (range of *P*-values 0.054–0.99). Distances between counter-singing neighbours were significantly shorter in fragmented than in continuous steppes (171 ± 33 m vs. 221 ± 47 m, Mann–Whitney $U = 23$, $n = 21$, $P = 0.027$), whereas distances between clusters of individuals were not affected by fragmentation.

Discussion

σ₀ϕN- \bar{v} MϕηN \bar{n} ϕN $\bar{\sigma}$ Mϕη $\bar{\sigma}$ ϕ

Male Dupont's larks from nearby territories shared more song types and matched the physical features of songs better than non-adjacent birds. Spatial autocorrelation analyses confirmed that in most localities song type or spectrotemporal similarities were highest within clusters of adjacent territories, and declined with distance. While short-distance dissimilarities tended to be significantly lower than expected by chance, long-distance dissimilarities were never greater. This suggests that vocal units within localities tended to show a discrete (or patchy) spatial distribution, and that acoustic sequences only diffused over very short distances.

The resulting patterns of song variation in Dupont's lark might derive either from the combination of innate behaviour and extreme philopatry or from learning processes occurring after dispersal. In most animal taxa vocal signals develop without significant environmental input, but in songbirds they are known to be learned

(Beecher & Brenowitz 2005). Many species learn their song from their neighbours after dispersal, during their first breeding season (Kroodsma 1982). These learning mechanisms would determine the static nature of song variants, which may remain spatially localized even when singing individuals are actually moving. In the light of this, a higher degree of song spectrotemporal matching and type sharing between neighbours than between non-neighbours can be interpreted as the outcome of song-learning processes (Beecher 1996). According to the acoustic mimicry hypothesis, young males or floaters may take advantage of song learning and matching from territorial adult males (Craig & Jenkins 1982). Floaters of song sparrow have been shown to match perfectly the songs of adult males, and obtain their first territories by inserting themselves between the territories of their tutors (Beecher, Campbell & Stoddard 1994). These new birds might be mistaken initially by each neighbour for the other, and this may reduce aggression. Stoddard (1996) pointed out that this mimicry could function particularly well when adult males are otherwise occupied in caring the young. Dispersing young males of Nuttall's white-crowned sparrow *Zonotrichia leucophrys nuttalli* Forster better matched the frequency and temporal characteristics of their neighbours' rather than their fathers' songs, supporting the idea that song matching of neighbours is an integral component of territory settlement by juveniles (Bell, Trail & Baptista 1998). Song sharing may also provide advantages to young birds when co-operative interactions with neighbours occur, because sharing songs might increase familiarity between group members, which in turn could bring fitness advantages (Beletsky & Orians 1989). Sharing songs to increase familiarity can also be beneficial when neighbours do not co-operate, and might serve as a signal of respect of territory boundaries among old neighbours (Dear Enemy Hypothesis; Beecher & Brenowitz 2005).

In Dupont's lark, a high number of floater males occurs because of the limited availability of suitable habitat (Garza, Suárez & Tella 2003), strongly male-biased sex ratio among adults (Tella *et al.* 2004) and

Acknowledgements

We wish to thank V. Garza, F. Suárez, M. Vögeli, D. Serrano, M. Carrete, E. Pelayo, F. J. Sampietro, G. Bota, J. Román, J. Hernandez, J. Manrique, P. Arratibel, and S. Mazzoletti for generously providing us information on Dupont's lark localizations. D. Serrano, D. Blumstein, J. Jokimaki and S. Thirgood usefully commented on a first draft of the manuscript, and G. Kerby helped in editing. Corine digital maps were kindly provided by R. Diaz-Delgado and the LAST laboratory of the Estación Biológica de Doñana. This research was supported by a Marie Curie Intra-European Fellowship within the 6th European Framework Programme to P. Laiolo and by ECODOCA (European Community-Access to Research in Doñana Biological Station).

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Received 22 April 2005; final copy received 15 July 2005
Editor: Simon Thirgood

Supplementary material

The following supplementary material is available for this article online.

Appendix S1. Spanish and Moroccan localities where Dupont's lark songs were recorded and known distribution of the species.

This material is available as part of the online article from <http://www.blackwell-synergy.com>