

Interspecific interactions drive cultural coevolution and acoustic convergence in syntopic species

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Summary

1. Antagonistic interactions have been favourite subjects of studies on species coevolution, since coexistence among competing species often results in quantifiable character displacement. A common output for competitive interactions is trait divergence, although the opposite phenomenon, convergence, has been proposed to evolve in some instances, for example in the communication behaviour of species that maintain mutually exclusive territories.
2. I use here experimental and observational evidence to study how species interactions drive heterospecific signal convergence, and analyze how convergence feeds back to the interaction itself, in the form of aggressive behaviour. I recorded the learned territorial signals of two non-hybridizing larks, *Galerida cristata* and *G. theklae*, and used allopatric populations as controls for evaluating acoustic convergence in syntopy. Acoustic variation was analyzed with respect to social conditions controlling for other potential agents of natural selection, habitat and climate.
3. Interspecific convergence of *Galerida* calls peaked in syntopy. Although call acoustic structure was affected by climate and habitat, it matched gradients of density and proximity to congeners even at small local scales. The process of cultural transmission, in which individuals may acquire components of behaviour by copying neighbours, enhances the correlation between call acoustics and the local social milieu.
4. Territories were defended against both species, but playback stimuli of convergent congener calls elicited a stronger aggressive reaction than congener calls from allopatric locations.

5. This study shows that learned behaviours may coevolve as a consequence of antagonistic interactions, determining reciprocal cultural evolution or cultural coevolution. As for (biological) coevolution, the distribution of competing species influence whether a particular area becomes a syntopic environment in which convergence is occurring, or an allopatric environment lacking interactions and reciprocal change. Because of their plastic nature, cultural coadaptations may rapidly shift in response to fluctuating social selection, thus propelling dynamic interactions and fine adjustments to the local environment.

Key-words: Aggressiveness, biotic interactions, interference competition, geographic mosaic of coevolution, social learning.

Introduction

Much research has been devoted to the problem of how particular forms of ecological interactions evolve, and whether interactions drive reciprocal adaptations (Thompson 1994). Antagonistic interactions have been favourite subjects of studies on coevolution, since coexistence among competing animal or plant species often results in quantifiable divergent displacement of morphological or behavioural characters (Caruso 2000; Kirschel, Blumstein & Smith 2009). The magnitude of displacement varies with the patterns of competitive intensity and its ecological context, so that interacting species tend to differ in fewer traits in allopatry than in sympatry (Gray & Robinson 2002; Grether *et al.* 2009).

Among sympatric taxonomically similar species, one common output for competitive interactions is exaggerated ecological or reproductive trait divergence (Schluter 2000; Pfennig & Pfennig 2010). Alternative to divergent displacement, however, coexistence within animal communities may also depend on competitive dominance or antagonistic interactions, which permit species to exploit the same space or resources (Adams 2004). Defence of food supplies, shelters or breeding areas from heterospecifics has indeed been demonstrated in a variety of animal species, especially fishes (Myrberg & Thresher 1974; Genner, Turner & Hawkins 1999) and birds (Catchpole 1978; Cody 1978; Temeles 1990; Robinson & Terborgh 1995). In cases in which interactions are frequent, social selection may drive the evolution of ritualized territorial behaviours, such as signalling (communication) to advertise territorial ownership. Signalling aggressiveness provides information about the antagonistic response an animal is about to perform, avoiding direct physical disputes and the associated fitness costs (Tinbergen 1952; Moynihan 1968). Orians and Wilson (1964) and Cody (1969) first suggested that coexisting species may reciprocally converge, rather than diverge, in signalling because similarities increase the

efficacy of aggressive signals used in interspecific contests. Although interspecific warning signals may result from the failure to discriminate heterospecifics (Murray 1976; Helb *et al.* 1985; Schultz & Switzer 2001), there is evidence of birds and amphibians visually and acoustically signalling to individual receivers of other species. Leary (2001) found that sympatric populations of *Bufo fowleri* Hinckley and *B. terrestris* (Bonnaterre) diverged in their mating signals (advertisement calls) but converged in their release vocalizations, which are used by males to prevent the erroneous approaching and amplexus of conspecific and heterospecific males. In birds, individuals may recognize and react to invading heterospecific competitors by uttering signals to defend territories (Abs 1963; Catchpole 1978; Sæther 1983), and convergence can evolve where interference competition peaks, i.e. in sympatric conditions (Tobias & Seddon 2009).

The convergence in the above mentioned examples is the outcome of coevolutionary processes, as the target signals are innate. In species learning their signal repertoire, convergence can result from cultural processes (social learning), which may lead to the transfer of signal features from one species to another with greater ease and rapidity than expected for signals under exclusive genetic control (Secondi *et al.* 2003). The convergence in learned signals has been poorly explored in a context of reciprocal cultural change in interacting species, although visual forms of convergence, such as visual mimicry, have been crucial for the early development of the theory of (biological) coevolution (Müller 1873).

In this study, I explore how the proximity of interacting species, and their distribution and density, generates convergence in socially transmitted signals used to defend territories. Along with other forms of selection, social selection varies geographically with the patterns of co-occurrence of interacting species and it is thus expected to drive the geographic differentiation of learned features of organisms (van Schaik 2009). I use here

experimental and observational evidence to study how interactions drives heterospecific signal convergence, and analyze how convergence feeds back to the interaction itself, in the form of aggressive behaviour and spacing. The territorial vocalizations of the Crested lark *Galerida cristata* (L.) and Thekla lark *G. theklae* (Brehm) in a wide geographic gradient of co-occurrence within Spain are the models of this study. I disentangle the relative contribution of reciprocal social selection over ecological (habitat -or climate-driven) explanations of signal variation, expecting that acoustic convergence of territorial signals should peak in syntopic conditions if one species is the agent of changes in the other signals and vice versa (Tobias & Seddon 2009). If convergence is due to ecological parallelism, acoustic variation should respond more strongly to gradients in environmental factors such as climate and habitat configuration than to fluctuating social conditions, such as differences in density or distances among territories (Goldberg & Lande 2006). Similarly, if coevolution occurs, congener signals evolved in syntopic conditions are expected to trigger a stronger aggressive reaction than signals that have evolved in a non-competitive, allopatric context (Peiman & Robinson 2010).

Methods

The Crested and Thekla lark constitute two independent non-hybridizing lineages that diverged ~ 3.7 MYA in the Sahara (Guillaumet, Crochet & Godelle 2005). They live in sympatry in most of the Western Palearctic, sharing similar food items and habits, with some habitat divergence: Crested lark densities peak in dry agropastoral or semi-desert habitats, and Thekla lark in bushy sclerophyllous vegetation (Laiolo, Obeso & Roggia 2011). The warning call (hereafter call) is used in territorial defence, and these larks respond aggressively to congener calls within territories (Abs 1963). Although calls may be given by both sexes, only one mate tends to call within territories, the one that also

sings (the male). Calls are learned: Captive juveniles isolated from calls of their own species are unable to perform typical adult calls, and signals in natural conditions pass through several transitional forms before taking on their final structure (Bergmann & Weiss 1974; Cramp 1988). In spite of being given by males, the model vocalization is here defined as a ‘call’ for simplicity, to differentiate it from the ‘song’, the sexual signal males utter in flight during spring (Laiolo, Obeso & Roggia 2011). *Galerida* species utter calls throughout the year in their territories, but also when human intruders enter territories, and during captures for ringing (as aggressive/distress signal; pers. obs.), thus also for non-sexual purposes outside of breeding. Indeed, passerine ‘calls’ reveal a learned component in the families of Alaudidae (Laiolo *et al.* 2008), Troglodytidae (Price 2003), Corvidae (Laiolo *et al.* 2001; Enggist-Dueblin & Pfister 2006; Bluff, Kalcenik & Rutz C. 2010), Paridae (Nowicki 1989; Clemmons & Howitz 1990), Aegithalidae (McGowan, Wood & Hatchwell 2005), Fringillidae (Mundinger 1979; Riebel & Slater 1998; Vicario 2006; Sewall 2011), Emberizidae (Greenlaw, Shackelford & Brown 1998; Liu, Wada & Nottebohm 2009), Ptilonorhynchidae (Kelley & Healy 2011) and Dicruridae (Goodale & Kotagama 2006a). Post-dispersal learning and, possibly, open-ended-learning are the mechanisms through which *Galerida* songs and calls are acquired. The songs include imitations of a variety of bird species, and are finely tuned to the context in which local territories are found, both with respect to the number of species imitated and to the homospecific social environment (Laiolo, Obeso & Roggia 2011). The neighbours engaging territorial disputes share the acoustic features of neighbour calls (Appendix S1), a behavioural matching that is common in species that learn their vocal repertoire after natal dispersal (passerines: Beecher *et al.* 1997; primates: Mitani & Brandt 1994; bats: Boughman 1998).

The calls were compared in a gradient of increasing interspecific distance and habitat segregation in Spain (Fig. 1). The fine scale mosaic of cereal cultivations and steppes of the Ebro Valley, where the minimum distance among recorded congeners was 31 m (average: 1.2 km \pm 0.04SE, range 31 m-4 km), represents a syntopic area (i.e. the species are in close contact in the same geographic area). Larks coexist but their typical habitats (steppes vs. cereal fields) are well separated in another area, Doñana (congeners at 4 -19 km, average distance: 8.6 km \pm 0.07SE). This area is defined as sympatric, since species share the same geographic area but do not coexist in close contact. Thekla larks from Mallorca and Sierra Gador, at 220 and 27 km from the nearest congener populations respectively, and Crested larks from Asturias and Sevilla, at 100 and 20 km from the nearest congener, respectively, represent the allopatric populations.

From 2003 to 2011, I sampled these populations while walking 88 transects, as described by Laiolo, Obeso & Roggia (2011). The length of each transect was 2 km and birds within 50 m from each transect side were recorded, totalling 20 ha surveyed per transect (2 km \times 100 m). Birds call from exposed perches and their territories can be easily mapped during breeding (Suarez, Hervás, & Herranz 2009). The field-work was performed in the morning (from 6 -7 a.m. to 1 p.m.), and in the afternoon (from 5:30 to 7:30 p.m.), when bird acoustic activity peaked during breeding. The birds within the transect area were approached to a distance <20 m to be recorded with Sony TC-D8 DAT and Marantz 660 PMD recorders, and a Sennheiser ME67 microphone.

Each transect was walked only once and was not repeated over years; each study area was visited in only one year (Appendix S2). Individuals were therefore recorded in their territories during a single visit only, thus avoiding the problems of re-sampling the same individual. The position of all lark individuals (including non-vocal ones) was recorded by means of Garmin Navigators, and the species visually identified with Leica 10 x 50

binoculars. By using individual geographical coordinates, I calculated the density of each lark within transects (expressed as n. birds/10 ha) and the distance from the nearest congener, used here as a measure of interspecific competition levels. By inspecting aerial photographs (<http://sigpac.mapa.es/fega/visor/>) and by direct observation, I quantified the composition of the micro-habitat (in plots of 20 m radii from each lark) and habitat (in the 20 ha area of transects) as the percent cover of ploughed land (e.g. bare ground), fallowlands (abandoned cereal fields unploughed in the last 3 years, dominated by *Eruca vesicaria* (L.), *Salsola kali* (L.), *Silybum marianum* (L.)), cereal fields (barley and corn fields), pastures (grasslands of prevailing Poaceae), steppelands (*Lygeum*, *Genista*, *Stipa*, *Helianthemum*, *Artemisia* spp.) and pine plantations (in order of increasing vegetation height and density). Ultimately, for each lark plot of a 20 m radius, I derived an estimate of mean annual temperature and mean annual precipitation from climatic digital layers of the Iberian Peninsula (meteorological data spatially modelled at a resolution of 1 km²; Seoane *et al.* 2003; Laiolo & Tella 2006).

Variation in call acoustic properties and environmental parameters

Calls of different syllable length (2-7 syllables) are alternated during territorial defence and have a similar syntactic structure in *Galerida* larks (Appendix S1). The calls in these species are normally uttered in bouts, in which calls of different syllable length are alternated without a specific order. I focused here on calls with 2, 3 and 4 syllables, which constitute > 80 % of the calls uttered. A complete call train is hereafter defined as a sequence of the three call types, and is the unit of the following analyses.

The sound analyses were carried out with Avisoft SASLab Pro (Version 3.91) Software by Raimund Specht (Berlin), performing a Fast Fourier Transform (sampling frequency 22050 Hz, FFT length 512, time resolution 8.9 msec, frequency resolution 43 Hz, Window Function: Bartlett). To capture variation in temporal and spectral call properties, I

measured 9, 12, and 15 acoustic parameters in calls of 2, 3 and 4 syllables, respectively. The acoustic characteristics were measured in the time domain on envelopes and in frequency domain on fast Fourier transform mean spectra, and summarize variation in syllable duration and frequencies (Appendix S3). Acoustic features that have been shown to vary seasonally or daily in birds, such as vocalization rate or the proportion of different acoustic structures (McNamara, Mace & Houston 1987), were not considered in this study. Notably, this kind of seasonal or daily acoustic variation is well known for bird song, a vocalization involved in the defence or attraction of seasonal resources (breeding territories, receptive females, etc.) (Kunc, Amrhein & Naguib 2005; Laiolo *et al.* 2008), but has not been described in vocalizations used to defend permanent resources (Laiolo *et al.* 2007).

Overall, I analyzed 2,015 calls (from 3 to 21 per individuals) and calculated mean values per individual of the 36 acoustic features mentioned above. The sample of individuals giving the complete train of call types corresponds to 132 Crested and 131 Thekla larks. Overall, I measured 934 calls of 2, 3 and 4 syllables in the Crested lark, and 1081 calls of 2, 3 and 4 syllables in the Thekla lark (sample sizes per population per species are given in Appendix S2).

Since the study was performed in different years, I tested for the magnitude of variation between years as compared with variation between species and recording site in two localities of northern Ebro Valley located at 25 km from each other in 2004 (14 birds recorded) and 2007 (22 birds). Factorial ANOVA performed entering all acoustic variables highlighted almost significant differences between the two species ($F_{3,30} = 8.18$; $P = 0.054$) and localities ($F_{3,30} = 5.86$; $P = 0.085$) but no difference between years ($F_{3,30} = 1.7$; $P = 0.371$). This limited variation over short time periods is therefore unlikely to bias the results of the study, also taking into account that habitat and social determinants were

estimated during each recording session, and thus described the actual ecological context in which each call was given.

To quantify the extent to which the 263 individuals recorded for this study could be assigned to the correct species or populations on the basis of the 36 acoustic features of their calls, a discriminant function analysis (DFA) was performed. A DFA was also performed to test for habitat use divergence among species and populations, entering the 6 habitat and 6 microhabitat variables. The predictive power of the databases was tested by cross-validation: half (131) of the individuals were randomly extracted from the data set of their populations and treated as test subjects, the rest were held out for the cross validation. With this procedure, discriminant functions were constructed with different individuals from those used to derive the percentages of correct classification.

To analyze the social, climatic and habitat determinants of call variation throughout Spain, I first reduced the dimensionality of call and habitat datasets by means of a principal component analyses (PCA). I retained four independent components to summarize the 36 acoustic parameters (Appendix S4) and four components to summarize 6 habitat and 6 microhabitat variables (Appendix S5). Then, I performed generalized linear mixed models (GLMM) with a Gaussian distribution of errors to analyze variation in PCA acoustic scores with respect to predictors of climate (mean annual temperature and rainfall), habitat (four PCA scores), and social environment (density and distance to the nearest congener). Location and transect identity were entered as random factors (transects nested within locations), to control for spatial autocorrelation. Model selection was based on Akaike's Information Criterion (AIC).

Interspecific interactions and playback experiments

In none of the 21 transects walked in the sympatric area of Doñana did I detect the co-occurrence of the two species, while in Ebro Valley they coexisted in 55 % of transects. In

Ebro Valley I observed 51 antagonistic interactions (chasing, fights, and threat postures against close intruders) in 110 km walked, 49 between conspecifics and 5 between congeners. The proportion of interspecific interactions (9%) may appear to be low as compared to intraspecific ones, but does not include intrasexual (male-male) disputes, which inflate the proportion of intraspecific interactions in the breeding period, when they naturally peak.

In April 2011, I analyzed species reaction to the playback of allopatric and sympatric, conspecific and congeneric calls in the northern Ebro Valley (Navarra). Here the individuals of each species are in contact with congeners (distance 20-1500 m) and territories have been monitored since 2004 (Laiolo *et al.* 2005; Laiolo, Obeso & Roggia 2011). Prior to playback experiments in 2011, I repeated transects to locate individuals and note their movements and posts, in order to approximate territorial borders. Taking into account the large area of the experimental site (ca 20 000 ha) and *Galerida* site fidelity (Suarez, Hervás & Herranz 2009), I am quite confident that birds were tested only once although most were unbanded.

The calls used for playback stimuli were from Ebro Valley (syntopic Crested and Thekla larks, 15 and 16 individuals respectively), Asturias and Sevilla (allopatric Crested larks, 15 individuals), Mallorca and Gador (allopatric Thekla larks, 17 individuals). As controls, I used the songs of 15 Dupont's larks (*Chersophilus duponti* (Vieillot); Appendix S6) and the calls of 10 House sparrows (*Passer domesticus* (L.); Appendix S6), two species that coexist but do not interact with *Galerida* larks in Ebro Valley. The song is the vocalization type that the Dupont's lark uses to communicate aggressiveness and shares with neighbours (Laiolo & Tella 2005), whereas the sparrow call is a communal vocalization given in roosts (Summers-Smith 1954). *Chersophilus* songs, therefore, resemble *Galerida* vocalizations in some functional aspects (territoriality and acoustic

matching), whereas no functional similarity occurs in the case of *Passer* calls. With respect to the acoustic structure, *Passer* calls are formed by one syllable only, and thus are simpler than *Galerida* calls, whereas *Chersophilus* song strophes are made up of syllables as *Galerida* calls (Appendix S6).

The stimuli were created with Avisoft-SasLab Pro using complete call trains (one call of 2 syllables, followed by calls of 3 and 4 syllables) of *Galerida* species, and vocalizations of control species (song and call bouts of Dupont's lark and House sparrow), filtered with a high pass filter at 0.8 kHz and normalized to an amplitude of 80% of a volt. Call trains and vocalizations of control species were copied and appended several times to create a 4-minute broadcast. The playback experiments lasted 10 minutes, comprising 3 minutes of silence followed by 4 minutes of playback and then 3 minutes of silence again. Experiments were performed from 7:00 a.m. to 1:00 p.m. and from 6:00 to 7:00 p.m., in good weather conditions, after territory owners were located. The vocalizations were broadcasted with a Marantz PMD660 recorder and Philips SBA1500/37 loudspeaker hidden in shrub vegetation close to individual posts. In total, 85 Crested lark and 87 Thekla lark territories were tested with the call playback of 30 Crested lark and 33 Thekla lark subjects, 15 *Chersophilus* subjects, and 10 *Passer* subjects. During 7 minute observations starting at the beginning of playback, all movements and vocal activity of larks were recorded. Pre-playback observations (the 3 minutes previous to broadcasting) were not considered for data collection: the birds' daily routine was not affected by the silent equipment in this time lag. Six behavioural variables were noted as indices of aggressive response: the closest distance approached to the speaker and the latency to the closest approach, the latency to call and call bout duration, the latency to sing and song bout duration. Since territorial mates often approached the speaker together while only one vocalized, times and distances refer to the vocalizing individual and the mate that

approached the speaker. The playback experiment was aborted and repeated the next day on eight occasions, when territorial individuals approached the playback area prior to broadcasting, or the playback stimulus attracted non-target neighbours. In all the other cases, each territory owner heard only one species playback. To summarize variation in behavioural parameters, a PCA was performed and two principal components were extracted, the first capturing variation in approach distance and call activity, the second in singing behaviour. PC1 was positively related with approaching distance and time to approach and call, and negatively associated with call duration; PC2 was negatively related with singing duration and positively with time to sing (Appendix S7).

To analyze whether PC1 and PC2 of behavioural responses varied when individuals were presented to conspecific calls, congener calls and the vocalizations of the other genera (controls), and between the species tested (Thekla or Crested lark territory), a GLMM was performed. The time the experiment was carried out (to the closest hour, from 7 to 19) was also entered in models, to control for daily variation in some of the recorded behaviours (such as singing; McNamara, Mace & Houston 1987). The playback subject identity was entered as a random factor, since each *Galerida* stimulus was presented in $1.9 \pm 0.06\text{SE}$ territories, one per individual per species (in keeping with Kroodsma *et al.* 2001). A Gaussian distribution of errors was used.

By focusing on data of *Galerida* playbacks only (i.e. excluding controls), I tested for differences in PC1 and PC2 of behavioural responses with respect to ‘kinship’ (congener *vs.* conspecific) and ‘population structure’ (allopatric *vs.* syntopic), and the interaction of the two terms, by means of GLMMs. The test species and the time of the day were entered as fixed factors and playback subject identity as a random factor. A Gaussian distribution of errors was used.

All statistical analyses were performed with SPSS 13.0 and R (R Development Core Team 2009; packages lme4, languageR, zipfR). Markov Chain Monte Carlo (MCMC) algorithms were used for Maximum Likelihood estimation of parameters with GLMM approximation in R (Bates & Maechler 2009; Bolker *et al.* 2009).

Results

Acoustic and habitat differences among species and populations

DFA significantly discriminated the calls of the two larks (Wilks' Lambda = 0.32, $\chi^2 = 280$, $P < 0.001$), and the first three discriminant functions explained 82% of the variability in the data set. The percent of successful classification of an individual to its species on the basis of its calls, however, varied among populations: All allopatric larks and sympatric larks at Doñana held out for cross-validation were successfully assigned to their own species, whereas in Ebro Valley 39% of Thekla larks and 27% of Crested larks were improperly classified as the congener (Fig. 2; Appendix S8a). In the syntopic Ebro Valley, the probability of call misclassification by DFA significantly decreased when the distance from the nearest congener increased (generalized-linear models, distance: $t = -2.23$, $n = 141$, $P = 0.028$; no significant effects of the species and its interaction with distance), and increased when the density of the congener increased ($t = 6.46$, $n = 141$, $P < 0.001$, species: $t = 1.99$, $n = 141$, $P = 0.049$; species \times density: n.s.). When considering habitat use, the two species again differed significantly (Wilks' Lambda = 0.43, $\chi^2 = 215$, $P < 0.001$), but 55% of Thekla larks and 36% of Crested larks from Ebro Valley were found in the typical congener habitat (Fig. 3; Appendix S8b).

Acoustic variation with respect to climatic, habitat, and social predictors

PC1 acoustic scores, indicating the maximum frequency of first call syllables, differed between species, increased with bare ground cover and annual rainfall, and were significantly affected by the distance from, and the density of, the congener (Tab. 1).

Social predictors affected larks in opposite ways: When the congener was abundant or close, the Thekla lark, whose signals had the lowest pitch, increased the PCA score associated with call frequency, whereas the Crested lark, which uttered the highest frequency calls, decreased it (Tab. 1). The effect of congener density was also found within the syntopic area (Fig. 4; GLMM, congener density: $t = 2.6$, $n = 141$, $P = 0.01$; species \times congener density: $t = 3.8$, $n = 141$, $P = 0.002$), and variation within species appears to be independent of proximity (and thus kinship): individuals from the same local population (individuals located < 10 km from each-other) may cover the whole range of variation of PC1 values to match the local social condition (Fig. 4). PC2 scores, associated with frequency range, were also significantly affected by rainfall and social parameters, and responses differed between species as well (Tab. 1). The congener distance also influenced the score related with call and syllable durations (PC4), whereas temperature only affected the score associated with overall maximum call frequencies (PC3) (Tab. 1).

Experimental evidence of antagonistic interactions

Approaching and calling behaviours in reaction to playback (PC1) were significantly less intense when territorial individuals were tested with control vocalizations than when tested with *Galerida* calls (GLMM, $t = 9.51$, $n = 122$, $P < 0.001$). The response, however, was similar when individuals were presented with congener or conspecific calls ($t = 0.34$, $n = 122$, $P = 0.73$), and in the two species territories ($t = 0.08$, $n = 122$, $P = 0.93$). PC1 decreased with time of the day ($t = 3.34$, $n = 122$, $P = 0.001$). Singing behaviour (PC2) also was more intense early in the day ($t = 2.14$, $n = 122$, $P = 0.034$), it was more pronounced in the Thekla lark ($t = 2.07$, $n = 122$, $P = 0.040$), and when individuals were faced with playbacks of conspecific calls compared to congener calls ($t = 4.79$, $n = 122$, $P < 0.001$) or control vocalizations ($t = 6.59$, $n = 122$, $P < 0.001$). When testing for differences in individual responses to allopatric and sympatric populations, PC1 was significantly lower

(i.e. shorter approach distances and longer calling times) for the birds exposed to sympatric than to allopatric calls (Fig. 5; Tab.2). A significant interaction between ‘kinship’ and ‘population structure’ emerged, with territorial individuals responding more strongly to congener calls recorded in sympatry than to those recorded in allopatry (Fig. 5; Tab.2). The singing response (PC2) was more marked towards conspecific and sympatric calls (Fig. 5; Tab. 2). The responses to the six playback treatments (*Chersophilus* control, *Passer* control, sympatric congener, sympatric conspecific, allopatric conspecific and allopatric congener) and pair-wise comparisons are detailed in Appendices S9 and S10.

Discussion

This study shows that ecologically and taxonomically similar species converged in their social behaviours and reciprocally evolved characteristics of signals important to interactions. The properties of territorial signals varied with interaction strength, depending on the degree of spatial coexistence and encounter probability and ultimately resulting in a mosaic of covariation across geographic regions. The convergence of congener calls increased when moving from allopatry to syntopy, territories were defended against both species but convergent congener calls from sympatric regions elicited a stronger aggressive reaction than calls from allopatric congeners.

In *Galerida* species, variation due to social predictors mainly affected PCA scores associated with call frequencies, with symmetric shifts but in opposite directions. The Crested lark, characterized by the highest pitched calls, uttered calls with lower maximum frequencies when Thekla larks were close or abundant, whereas the latter species, which normally gave the lowest pitched calls, uttered calls with higher maximum frequencies in areas where the congener was abundant (Fig. 4); a similar pattern was found for PCA scores associated with call frequency range and duration variables. Social factors also influenced the posterior call classification by discriminant function analysis, with

misclassifications (i.e. Thekla larks incorrectly classified as Crested lark and vice versa) becoming more probable in conditions of closer coexistence or greater congener density.

Reciprocal call variation matched gradients of density and distance to congeners even at small local scales within the syntopic area, suggesting that convergence can quickly evolve in response to shifting social conditions. When territories did not overlap in sympatry, as in Doñana site, each species was clearly distinguished by its call, and variation within each species appeared to be independent of relatedness or proximity, since individuals from the same population (i.e. those most probably sharing a common ancestor) gave signals that differed greatly in their acoustic structure (Fig. 4). This figure, and the fact that young birds are unable to develop adult vocalizations in the absence of tutors (Bergmann & Weiss 1974), suggest that the correlation between *Galerida* behavioural responses (call output) and the local social milieu is due to cultural processes, in which individuals acquire components of behaviour by copying territorial neighbours. Animal culture is in fact a behaviour or information transmitted by social learning (Rendell & Whitehead 2001). Its evolution requires the capacity for observational learning and results in behaviours that no individual could invent on their own (Boyd & Richerson 1985), as in the case of complex vocalizations transmitted from one neighbor to the other. In the syntopic study area, traditional agricultural practices have maintained a dynamic rotation system that promotes regular territorial turnover between the two species, which share a long history of local range contractions and expansions also due to natural successional events (Guillaumet *et al.* 2006; Suarez, Hervás & Herranz 2009). Socially transmitted adaptations may in these cases evolve or disappear faster than matching between genes and the social environment in response to fluctuating interactions (West-Eberhard 1983), especially when species turnover is speeded up by human activities (Laiolo 2010).

Simulations of congener intrusion primarily elicited approach and calling in both species, and interspecific aggression peaked for signals that were recorded in conditions of greatest spatial and resource overlap, in line with results obtained in other animal groups (reviewed in Peiman & Robinson 2010). On the other hand, singing behaviour was most often induced by playbacks of local conspecific calls, suggesting that territorial calls carry information to both homo- and heterospecific receivers, differently eliciting intrasexual antagonism and responses via sexual signals (songs). Indeed, calls maintained some species-specific acoustic features (Tab. 1) that may serve in homospecific discrimination.

Alternative explanations to competition-driven convergence may explain convergence in animal signals (Grant 1972). For instance, habitat-driven parallelism may occur, i.e. convergence resulting from acoustic adaptations to the physical properties of a shared habitat (Ryan & Brenowitz 1985). In *Galerida* species, climate and habitat did contribute along with social factors to shaping acoustic signals, resulting in a certain degree of habitat-driven variation that accompanies competition-driven convergence. In both larks, low PCA scores associated with maximum frequencies are found in environments with the highest temperature, whereas frequency range and the maximum frequencies of the first syllables were highest in the wettest areas, partly in line with predictions of adaptive acoustic transmission. Low frequency sounds are in fact suited to transmission in hot and dry climates, since attenuation of high frequencies is exacerbated by temperature (Wiley & Richards 1982; Ruegg *et al.* 2006). High-pitched vocalizations are also given where interference by vegetation is low (Ryan & Brenowitz 1985), and larks inhabiting bare, ploughed land uttered calls with the highest pitched syllables.

Alternative to deterministic explanations, learning mistakes could be evoked to explain convergence among neighbour species (Murray 1976). However, differences between song and call response to playback dismiss this idea, since sexual signals (songs)

are more intensely given in response to conspecific stimuli. Another alternative hypothesis for convergence is phylogenetic conservatism, due to common ancestry. Nevertheless, there is no evidence that syntopic populations share a recent common ancestor: *Galerida* larks have speciated in the Sahara range and independently colonized Spain from Eastern Europe (the Crested lark) and Northern Africa (the Thekla lark) (Suarez, Hervás & Herranz 2009; Guillaumet *et al.* 2006). Evidence of hybridization between *Galerida* species has not been obtained in Ebro Valley (Mendez *et al.* 2011), thus dismissing another potential explanation, convergence due to hybridization (Qvarnström *et al.* 2006).

Cultural coevolution

This study presents a case of coevolution in learned characters, in which information reciprocally acquired from heterospecifics serve to maintain exclusive territories. If heterospecific communication has been documented in species sharing predators and resources, no reciprocal heterospecific social learning has been detected in these cases. The “seet”-hawk-call, an anti-predator signal shared by woodland birds, is transmitted among conspecifics (Marler 2004, Magrath, Pitcher & Gardner 2009). Similarly, the imitation of heterospecific flock-members for resource exploitation (Gorissen, Gorissen & Eens 2005; Goodale & Kotagama 2006a, b) represents a case of copying heterospecifics in the absence of reciprocity. In the scientific arena, the term cultural coevolution is presently restricted to the synergy between vertebrates with great cognitive skills and humans, the latter being the coevolving counterpart. The interactions between fishermen and dolphins, farmers and maize-stealing crows, tourists and bears or corvids, are examples of this concept (Marzluff & Angel 2005; Jimenez *et al.* 2011). This study widens this narrow definition to embrace those forms of heterospecific communication that involve reciprocal selective copying of signals important to the interaction. ‘Context-dependent’ acoustic mimicry, in which individuals copy the signals of other species with the aim of maintaining mutually

exclusive territories or defending resources, may be considered a special case of this phenomenon if variation is reciprocal (Baylis 1982). Similarly, divergence of learned mating signals in contact zones may represent special cases of cultural coevolution between taxonomically similar species, leading to divergence rather than to convergence (Irwin, Bensch & Price 2001).

From an ecological point of view, social learning and social selection can ultimately feedback to community dynamics, given that coevolving syntopic species functionally behave as a single species with respect to resource use (space, breeding sites, food, etc.), interactions and the ecological contribution to the community. On the other hand, this cultural process may have evolutionary implications if innate learning predispositions coevolve with cultural components (Byers, Belinsky & Bentley 2010). Social selection on cultural traits may shape the evolution of these genetic components, if individuals whose calls do not match those of congener neighbours are unable to hold territories and are excluded from the reproductive portion, and thus from the gene pool, of local populations.

Some similarity may be envisaged between cultural and biological coevolution in their geographic patterns of variation: In both evolutionary processes, a mosaic of different phenotypes (learned traits in cultural coevolution, innate ones in biological coevolution) results from local differences in interactions between species. Similarly, species distribution and population dynamics influence whether a particular area becomes a syntopic environment in which reciprocal selection is actually occurring, or an environment of loose interactions and no reciprocal change (Thompson 1999). On the other hand, the geographic mosaic theory of coevolution predicts partial character mismatches as a result of gene flow, which can spread coadapted alleles in populations where interaction strength is low or vice versa (Thompson, Nuismer & Gomulkiewicz 2002). However, if the cultural process is based on horizontal or oblique transmission, i.e.

migrating individuals match their behaviour to that of neighbours irrespective of their genetic identity, cultural coevolution may lead to fewer fitness drawbacks ('maladaptations') and sharper gradients of character variation than biological coevolution and, to a certain extent, propel the evolution of more dynamic adjustments to environmental conditions.

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The following Supporting Information is available for this article online:

Appendix S1. Waveforms and spectrograms of the territorial calls of the Crested and Thekla lark, and call matching behaviour between neighbour larks.

Appendix S2. Sample size per study location.

Appendix S3. Acoustic variables measured in *Galerida* calls.

Appendix S4. Factor loadings of Principal Component Analysis performed on acoustic data.

Appendix S5. Factor loadings of Principal Component Analysis performed on habitat data.

Appendix S6. Spectrograms of control vocalizations used in playback experiments.

Appendix S7. Factor loadings of Principal Component Analysis performed on behavioural indices of aggression in playback experiments.

Appendix S8. Performance of Discriminant Function Analysis in classifying *Galerida* calls and habitat use to the proper species and populations.

Appendix S9. Differences in the responses to congener and conspecific calls and to control vocalizations in playback experiments.

Appendix S10. Aggressive response to playbacks of control, congener and conspecific, syntopic and allopatric vocalizations

Figure captions

Figure 1. Distribution of the Crested lark *Galerida cristata* and Thekla lark *G. theklae* in Spain and the location of the study areas. Modified from Suarez, Hervás & Herranz 2009.

Figure 2. Plot representing the first two axes (DC) of Discriminant Function Analyses performed with call variables of the eight study populations (all recorded individuals are shown). The bottom diagrams depict Euclidean distances among centroids (of DC with eigenvalues >1) of allopatric and sympatric populations with respect to acoustic variables. The acoustic features of recorded calls were averaged for each individual before performing DFA, and thus each point represents an individual bird in DFA plot.

Figure 3. Plot representing the first two axes (DC) of Discriminant Function Analyses performed with habitat variables of the eight study populations (all recorded individuals are shown). The bottom diagrams depict Euclidean distances among centroids (of DC with eigenvalues >1) of allopatric and sympatric populations with respect to habitat variables. Each point in DFA plot represents an individual bird.

Figure 4. Relationship between the first principal component (PC1) of acoustic variation with respect to congener density in the syntopic populations of Ebro Valley. PC1 was associated with syllable maximum frequency. Points represent average value per transect, as several individuals were recorded per transect. Letters indicate individuals from two populations of the Thekla lark (A and D) and three of the Crested Lark (B, C, and E) in which several individuals were recorded, to show that acoustic features (y-axis) can vary independently of individual proximity (and supposed relatedness).

Figure 5. Aggressive response of Ebro Valley *Galerida* larks to playbacks of control vocalizations and to playbacks of calls from syntopic and allopatric, congener and conspecific populations. The response was quantified by two principal components associated with distance and time to approach and calling behaviour (PC1), and with singing behaviour (PC2). Mean values and standard errors are shown.

Fig. 1

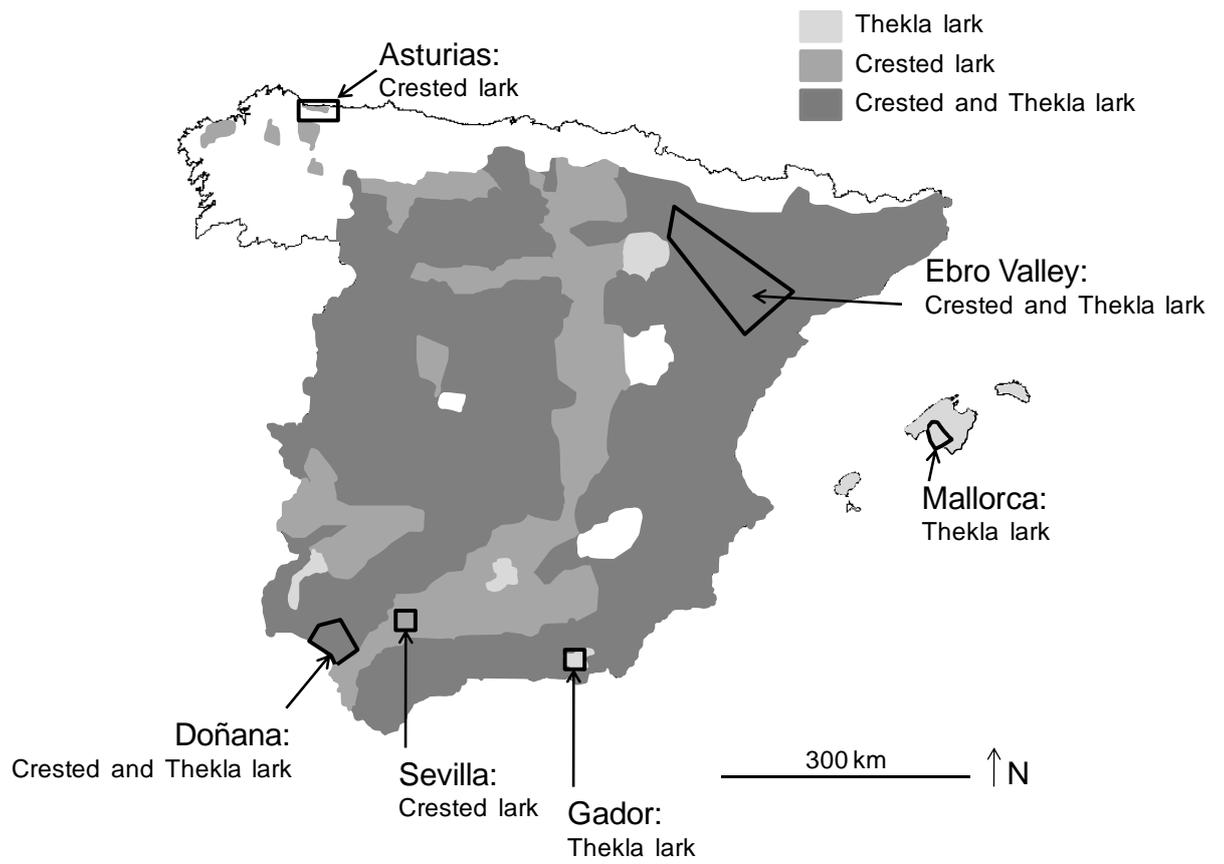


Fig. 2.

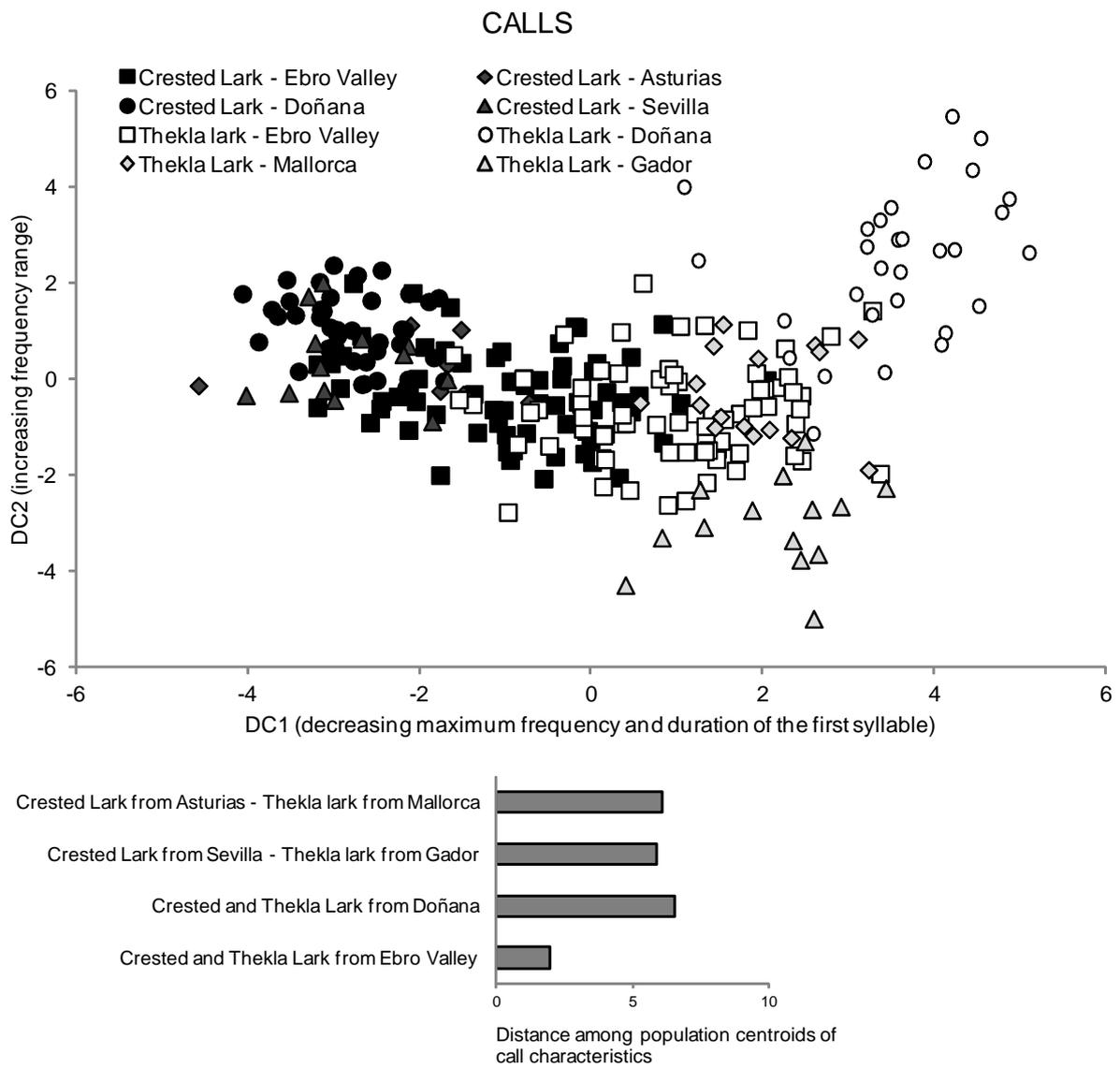


Fig. 3

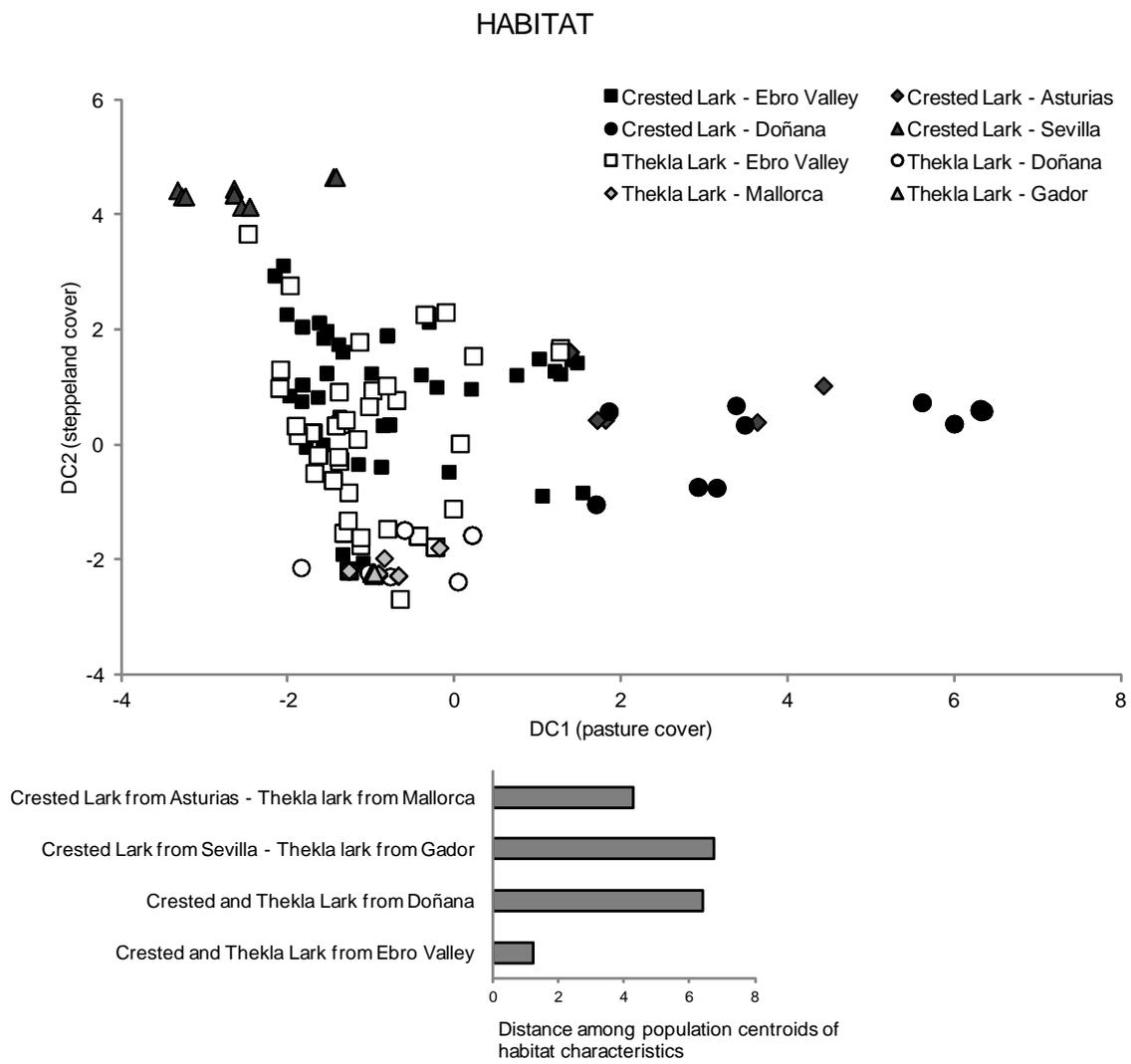


Fig.4.

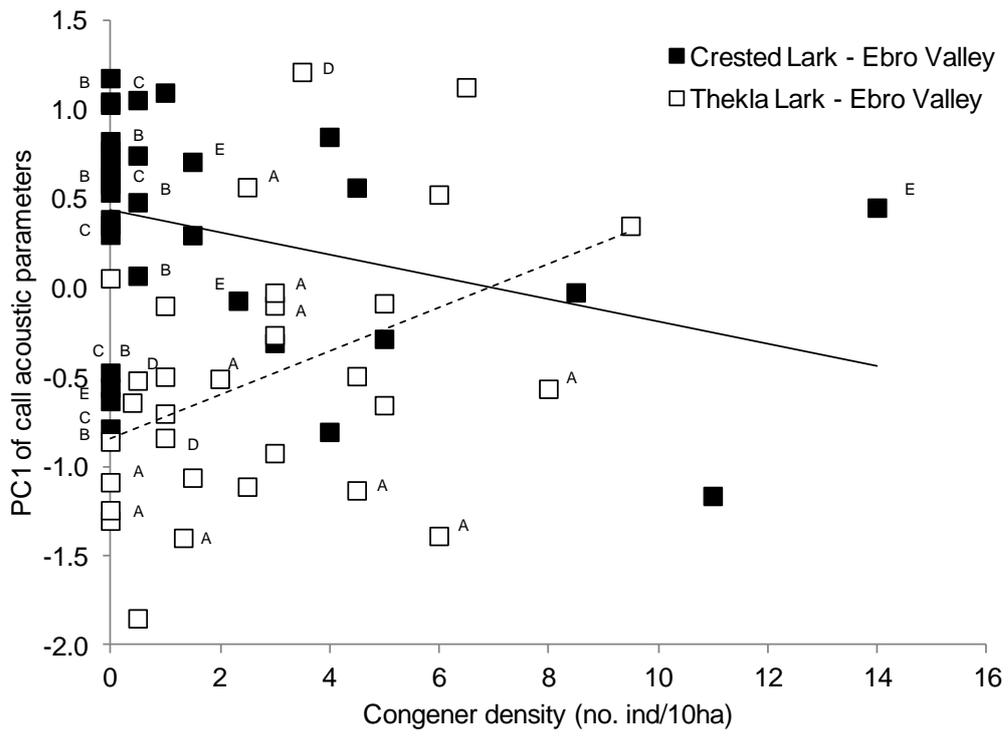


Fig. 5.

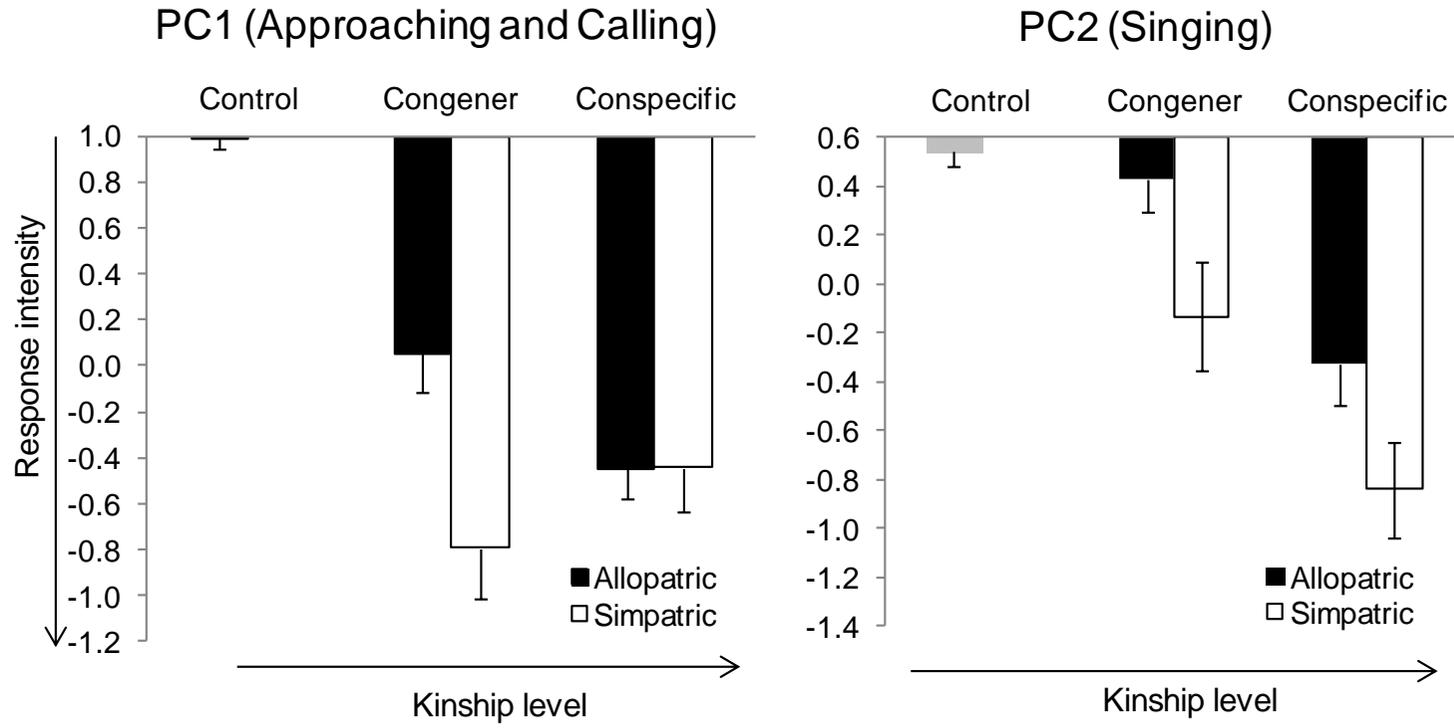


Table 1. Relationships between the PCA factors of call variation and the environmental, climatic, social descriptors. GLMM were performed (sample size: 263 individuals, two nested random effects: 88 transects within 6 sites). Only models separated by < 2 AIC points from models with the lowest AICs are shown.

	<i>Estimate</i>	<i>t</i>	<i>P</i>
PC1 of acoustic variables: AIC: 740.6 (3.9 AIC points from the next most probable model)			
Species	-1.5	12.7	<0.001
Mean annual rainfall	0.005	5.0	<0.001
PC3 of habitat variables			
Distance to the nearest congener	-0.003	4.3	<0.001
Congener Density	-0.08	3.0	0.004
Species x Distance to the nearest congener	0.003	4.6	<0.001
Species x Congener Density	0.23	5.5	<0.001
PC2 of acoustic variables: AIC: 740.6 (3.2 AIC points from the next most probable model)			
Species	0.8	5.7	<0.001
Mean annual rainfall	0.007	8.0	<0.001
Distance to the nearest congener	-0.0004	6.3	<0.001
Congener Density	0.05	1.4	0.16
Species x Distance to the nearest congener	0.0004	5.7	<0.001
Species x Congener Density	-0.1	2.8	0.006
PC3 of acoustic variables: AIC: 752.6 (>5 AIC points from the next most probable model)			
Temperature	0.1	3.5	<0.001
PC4 of acoustic variables: AIC: 734.9 (2.2 AIC points from the next most probable model)			
Species	-0.2	1.2	0.24
Distance to the nearest congener	-0.001	1.5	0.14
Species x Distance to the nearest congener	0.001	2.3	0.02

Table 2. Relationships between the PCA factors of the behavioural response to *Galerida* calls and kinship, population structure and species. GLMM were performed (sample size: 122 individuals, number of groups for the random effect (individual identity) = 61).

	<i>Estimate</i>	<i>t</i>	<i>P</i>
<u>PC1 of behavioural response to playback</u>			
Species (Crested vs. Thekla lark territory)	-0.04	0.03	0.784
Kinship (Congener vs. Conspecific)	-0.40	1.91	0.058
Population structure (Allopatric vs. Sympatric)	-0.66	2.94	0.004
Time of the day (hour)	0.08	3.20	0.008
Kinship x Population structure	0.71	2.41	0.017
<u>PC2 of behavioural response to playback</u>			
Species (Crested vs. Thekla lark territory)	-0.22	1.34	0.193
Kinship (Congener vs. Conspecific)	-0.82	3.40	<0.001
Population structure (Allopatric vs. Sympatric)	-0.74	2.91	0.004
Time of the day (hour)	-0.10	3.34	0.001
Kinship x Population structure	0.14	0.41	0.682