

HABITAT USE OF TWO SIBLING SPECIES, THE SHORT-TOED CALANDRELLA BRACHYDACTYLA AND THE LESSER SHORT-TOED *C. RUFESCENS* LARKS, IN MAINLAND SPAIN

Francisco SUÁREZ*, Vicente GARZA** & Manuel B. MORALES*¹

SUMMARY.—*Habitat use of two sibling species, the Short-toed Calandrella brachydactyla and the Lesser Short-toed C. rufescens Larks in mainland Spain.* This paper makes a comparative analysis of (1) the physical factors and habitat types that determine the spring abundance of the Short-toed Lark and the spring and winter abundances of the Lesser Short-toed Lark at a wide, peninsular scale and (2) the microhabitat use of both species with respect to vegetation structure. In the first analysis we considered 82 localities, while the second was based on presence-absence data for the species along 100 m transect lines (1036 transects in 34 localities). Short-toed Larks were present in 82% of the census localities. Its abundance was primarily linked to habitat type, longitude and bioclimatology. General linear models including these variables explained approximately 40% of the variation in the abundance of this species. Lesser Short-toed Larks displayed a more restricted breeding distribution (33% of localities) and its abundance was linked to the type of habitat (29% of variance explained by the model). In winter, the localities where this lark was contacted were the same as in spring. Annual rainfall was the only predictor variable for abundance in winter (26% of variance). The transect lines where Short-toed Larks were contacted differed in practically every structural parameter of vegetation from those where it was absent. This pattern was similar for Lesser Short-toed Larks in spring, while in winter there were differences in the cover of short shrubs (<40 cm tall) and the mean vegetation height only. The comparison of vegetation structure in localities where one species or the other was present revealed differences in the vegetation parameters in transect lines with either recorded presence or absence. In the sympatric localities, the observed frequencies for transect lines with either one or the other species were lower than expected. In these localities, a discriminant analysis based on vegetation structure traits classified correctly 100% of observations of one lark or the other. Although the mechanisms involved in the segregation of these two larks in the sympatric zones are not clear, the results indicate a spatial segregation at two scales: i) geographic, determined by physical factors as well as habitat type, and ii) local, set by certain parameters of the vegetation structure. Differential microhabitat use by the two species, together with a clumped distribution of Lesser Short-toed Larks, may be the cause of this segregation, although interspecific territoriality should not be ruled out. The range of the vegetation structure parameters selected by the two sibling lark species may prove to be highly useful in designing conservation programmes for them, classified as Vulnerable in Europe.

Key words: habitat segregation, habitat use, Iberian Peninsula, Lesser Short-toed Lark, Short-toed Lark, sibling species, sympatry.

RESUMEN.—*Uso del habitat en dos especies gemelas de aláudidos, la Terrera Común Calandrella brachydactyla y la Terrera Marismeña C. rufescens, en España peninsular.* En el presente artículo se analizan de forma comparada (1) los factores físicos y tipos de hábitat que determinan la abundancia primaveral de Terreras Comunes y la abundancia primaveral e invernal de Terreras Marismeñas a una escala geográfica amplia y (2) el uso del microhábitat en relación con la estructura de la vegetación de ambas especies. En el primer análisis consideramos 82 localidades, mientras que el segundo se basa en datos de presencia/ausencia a lo largo de transectos de 100 m de longitud en 34 localidades ($n = 1036$ transectos). La Terrera Común apareció en el 82% de las localidades censadas. Su abundancia estuvo ligada fundamentalmente al tipo de hábitat, longitud geográfica y piso bioclimático. Los modelos generales lineales que incluyeron estas variables explicaron aproximadamente un 40% de la varianza de las abundancias de esta especie. La Terrera Marismeña mostró una distribución más restringida (33% de las localidades) y su abundancia varió básicamente según tipos de hábitat (29% de la varianza). Los transectos en los que apareció la Terrera Común difirieron prácticamente en todos los parámetros de estructura de la vegetación de aquellos en los que la especie estaba ausente. Este patrón fue similar para la Terrera Marismeña en primavera, mientras que en invierno sólo se encontraron dife-

* Departamento Interuniversitario de Ecología, Facultad de Ciencias, Universidad Autónoma, E-28049 Madrid, Spain.

** C/ Santovenia, 10, E-28008 Madrid, Spain.

¹ Corresponding author. e-mail manuel.morales@uam.es

rencias en la cobertura de matorrales de menos de 40 cm de altura y en la altura media de la vegetación. La comparación de la estructura de la vegetación en localidades donde una u otra especie fue contactada reveló diferencias en los parámetros estructurales analizados entre transectos con presencia y transectos con ausencia. En estas localidades, el análisis discriminante de la presencia/ausencia de estas especies en función de las variables de estructura de la vegetación clasificó el 100% de las observaciones de una u otra Terrera. Aunque los mecanismos implicados en la segregación de las dos especies en zonas simpátricas no están claros, los resultados indican una segregación espacial a dos escalas: i) geográfica, determinada por factores físicos y tipos de hábitat, y ii) local, definida por ciertos parámetros de la estructura de la vegetación. El uso diferencial del microhábitat por ambas especies, junto con una distribución agregada de la Terrera Marismeña, puede ser la causa de dicha segregación, aunque la competencia interespecífica entre las dos especies no puede ser descartada. El rango en los parámetros de estructura de la vegetación que utiliza cada una de ellas puede ser de gran utilidad en el diseño de programas de conservación de estas especies, clasificadas como Vulnerables en Europa.

Palabras clave: especies gemelas, península Ibérica, segregación de hábitat, simpatría, Terrera Común, Terrera Marismeña, uso del hábitat.

INTRODUCTION

Pairs of species with highly similar morphology, partially coinciding in distribution and habitat type and with rare cases of hybridisation (sibling species), are a relatively common phenomenon in regional faunas (see Stepanyan, 1983; Blondel, 1995). In mainland Spain, clear cases of sibling species include Melodious *Hippolais polyglotta* and Olivaceous *H. pallida* Warblers, Short-toed *Calandrella brachydactyla* and Lesser Short-toed *C. rufescens* Larks, Crested *Galerida cristata* and Thekla *G. theklae* Larks and Common *Certhia familiaris* and Short-toed *C. brachydactyla* Treecreepers, among others. The majority of sibling species display spatial segregation (parapatry) at different spatial scales (see Barlow & McGillivray, 1983; Osiejuk & Kuczynsky, 2000; Baumann, 2001). First, at a wide geographic scale, differences between sibling species in physical and vegetation requirements usually determine differences in their distribution and abundance, although with wide areas of coexistence (sympatric areas). Second, in these sympatric areas there tends to be a differential selection at the microhabitat scale, often related to vegetation structure and, in some cases, to interspecific agonistic behaviours. However, there also tends to be some degree of coexistence at this scale, which varies in intensity between pairs of sibling species.

There has been little research into differences between Short-toed and Lesser Short-toed Larks, and habitat distinctions between both species are far from clear-cut (Cramp, 1988). They have quite different distributions in the Iberian Peninsula during the breeding season.

While the former species occupies almost the entire Mediterranean zone, the latter is primarily located in the coastal belt of the arid south-east, the Ebro valley and certain brackish wetlands in Castilla-La Mancha and Doñana (Purroy, 1997). These differences have been interpreted in terms of bioclimatology (Tellería *et al.*, 1988a, 1999; Martínez & Purroy, 1993), considering that Short-toed Larks are most abundant in the meso- and supra-Mediterranean levels while the largest abundances of Lesser Short-toed Larks are found in the thermo- and meso-Mediterranean. Many of the areas occupied by Lesser Short-toed Larks are also occupied by Short-toed Larks, although the parameters of the vegetation structure which define their microhabitat segregation are yet to be defined beyond the fact that Short-toed Larks prefer zones with lower vegetation cover (Sampietro *et al.*, 1998).

In the Iberian Peninsula, the Short-toed Lark is a trans-saharan migrant while the Lesser Short-toed Lark is regarded as a resident (Tellería *et al.*, 1999). Both are currently classified in Europe as "vulnerable", given that their populations in this area are clearly declining (Hagemeijer & Blair, 1997). There is also evidence that the Spanish populations have undergone a considerable decline in recent decades as a consequence of agricultural intensification (Purroy *et al.*, 1997; Bota, 2002), following trends similar to those experienced by other steppe and farmland bird species both in Iberia and the rest of Europe (Suárez *et al.*, 1999; Krebs *et al.*, 1999).

The present paper analyses, on the one hand, the geographic factors that determine the abun-

dance of the two sibling Short-toed Larks in steppe areas with natural vegetation cover (camphyte and grassland steppes as defined by Suárez *et al.*, 1992) and extensive cereal croplands in mainland Spain during the breeding season and winter, and, on the other, their microhabitat use in terms of vegetation structure. The study is based on the following hypotheses: (1) the geographic factors that determine the abundance of each species at a wide scale are different and (2) at those points where the two species coexist, there are certain parameters of the vegetation structure that are differentially selected by the two species at the microhabitat scale. If these hypotheses are correct, the predictive models describing habitat and microhabitat preferences of these two larks may be highly useful in the development of management guidelines for steppe habitats with a view to the conservation of these two species.

MATERIAL AND METHODS

Relative densities and geographic, climatic and habitat type variables

Censuses of both lark species were carried out in 34 localities with a predominance of shrub-steppes and dry pastures, distributed across the Mediterranean region of the Iberian Peninsula (Fig. 1). These localities were selected on the basis of the following criteria: (1) representation of all Iberian steppe types and (2) inclusion of the broadest possible range of geographic, climatic and vegetation conditions, from sea level to 1350 m a.s.l. (see Table 1 and Garza & Suárez, 1990, for details on the main features of these localities).

Relative lark densities were estimated in spring (May and June) and winter (January and February) 1988 by means of transect lines (Järvinen & Väisänen, 1975), separating data collected in the inner belt (50 m, 25 m on each side of the transect line) from those outside this belt (see Table 1 for size of areas censused in each zone and season). These data were used to calculate the proportion of contacts within the inner belt for each of the two species and periods. Relative densities for each locality were calculated by transformation of the total data by means of linear models fitted to the proportion of contacts in each census period (see Bibby *et al.*, 1992).

In order to ensure a wide range of geographical and climatic situations, results from other studies and our own unpublished data, all of which were the latest data collected using the above-mentioned methodology, were also included in the analyses, as long as they met the following conditions: (1) studies carried out in the Iberian Mediterranean region (Fig. 1), (2) data corresponding to either natural vegetation or extensive cereal pseudo-steppes, and (3) larks censused using transect lines. Relative densities were therefore comparable with our own data. In order to avoid pseudoreplication, only our own data were considered in localities with more than one study. For studies that included a full annual cycle, winter densities were defined as the mean values recorded in January and February and spring densities as the means for April and May. A total of 82 localities were considered, 76 of which were censused in spring, 43 in winter and 38 in both periods. Other authors' studies taken into account and their main features are presented in the Appendix.

For each locality we considered the abundance of each species and an initial set of variables that included habitat type, geographic longitude and latitude, mean temperature of the hottest and coldest months, annual and relative thermal amplitude and spring, summer, autumn, winter and annual average rainfall. Weather data were provided by the stations of the Spanish National Meteorological Institute closest to each study locality. These data were included in the analyses only when the series of records was longer than 10 years and the difference in altitude between the station and the study locality was not greater than 100 m.

In order to reduce multicollinearity, the matrix of Pearson correlation coefficients among independent variables was examined. The final set of variables was composed by longitude (LON, in degrees), habitat type (HAB; 1: cereal crops $-n = 24-$, including ploughed fields, sown fields, fallow land and stubble fields; 2: dry pastures $-n = 7-$, including dry pastures and long-term fallow lands; and 3: shrublands $-n = 51-$, of any plant species composition and including esparto *Stipa tenacissima* grasslands), annual average rainfall (AAR) and bioclimatic level (BCL, following the Rivas-Martínez classification; Rivas-Martínez *et al.*, 1990). These are synthetic variables that summarise the glo-

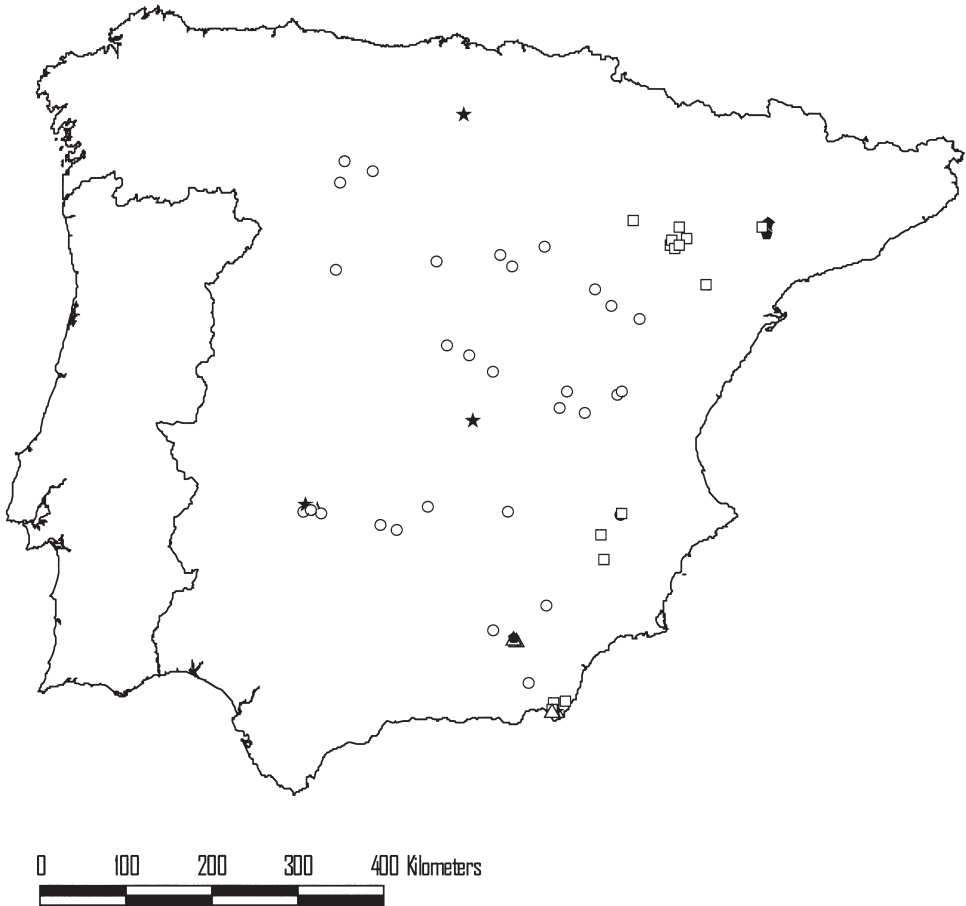


FIG. 1.—Map of the Iberian Peninsula showing the census localities for Short-toed and Lesser Short-toed Larks. Circles: localities with presence of Short-toed Larks only; squares: localities with presence of both Short-toed and Lesser Short-Toed Larks; triangles: localities with presence of Lesser Short-toed Larks only (spring and winter); pentagons: localities with presence of Lesser-Short-toed Larks only (spring); stars: localities where neither species was found.

[Mapa de la península Ibérica con las localidades en las que se realizaron censos de *Terrera Común* y *Marismeña*. Círculos: localidades con presencia exclusivamente de *Terrera Común*; cuadrados: localidades con presencia de *Terrera Común* y *Marismeña*; triángulos: localidades con presencia exclusivamente de *Terrera Marismeña* (primavera e invierno); pentágonos: localidades con presencia exclusivamente de *Terrera Marismeña* (primavera); estrellas: localidades en las que no se detectó ninguna de las dos especies.]

bal geographic, climatic and habitat differences between all the study localities.

Habitat use

Vegetation use by the two species of Short-toed Larks was studied by analysing their pre-

sence or absence every 100 m along each transect in the first 34 localities mentioned above. From the mid-point of each of these sections, vegetation structure was estimated within a circle of 10 m radius, recording the percentage cover of each vegetation type, estimated after Prodon & Lebreton (1981), and vegetation height (maximum, MVH, and average, AVH).

TABLE I

Main characteristics of the study localities, Short-toed (CB) and Lesser Short-toed (CR) Lark densities, and area censused in spring and winter.

[*Características principales de las localidades estudiadas, densidades de Terrera Común (CB) y Terrera Marismña (CR) y área censada en primavera e invierno.*]

Locality [localidad]	Lat.	Long.	Alt. (m)	Abundance (birds/10 ha) [abundancia (aves/10 ha)]			Surface (ha) [superficie (ha)]		Main habitat [hábitat principal]
				CB		Winter [invierno]	Spring [primavera]	Winter [invierno]	
				Spring [primavera]	Spring [primavera]				
Perales de Alfambra	40°41'	1°05'	1150	52.7	0.0	—	6.0	—	Shrubland [matorral]
Valeria	30°49'	2°09'	1025	22.5	0.0	0.0	5.7	4.2	Shrubland [matorral]
Layna	41°24'	2°22'	1150	17.8	0.0	0.0	6.3	6.3	Shrubland [matorral]
Barcones	41°12'	2°49'	1100	12.6	0.0	0.0	3.9	5.1	Shrubland [matorral]
Retortillo	41°19'	2°58'	1240	5.8	0.0	0.0	4.2	6.0	Shrubland [matorral]
Blancas	40°49'	1°28'	1050	28.6	0.0	0.0	6.0	6.6	Shrubland [matorral]
Embid	40°59'	1°41'	1100	22.4	0.0	0.0	4.5	—	Shrubland [matorral]
Olmedilla	39°56'	1°23'	1100	0.9	0.0	0.0	3.0	—	Shrubland [matorral]
Pedro Izquierdo	39°58'	1°20'	1100	13.4	0.0	0.0	6.3	—	Shrubland [matorral]
Hoya Cerrada	39°46'	1°49'	1050	24.8	0.0	0.0	5.4	—	Shrubland [matorral]
El Hoyazo	39°58'	2°03'	1100	20.3	0.0	0.0	3.9	—	Shrubland [matorral]
Osera	41°35'	0°35'	270	4.3	19.4	85.3	5.7	4.8	Semiarid shrubland [matorral semiárido]
Belchite	41°24'	0°42'	450	2.9	34.1	9.7	5.7	4.5	Semiarid shrubland [matorral semiárido]
Urrea de Gaen	41°39'	1°12'	400	6.8	31.1	26.4	3.6	3.3	Semiarid shrubland [matorral semiárido]
Cordovilla	38°33'	1°37'	500	0.0	47.1	50.3	4.5	4.5	Shrubland [matorral]
Calasparra	38°18'	1°34'	350	3.6	5.8	0.0	4.5	4.5	Shrubland [matorral]
Lillo	39°42'	3°19'	690	0.0	0.0	0.0	2.4	—	Saline shrubland [matorral salino]
Montiel	38°47'	2°50'	950	18.2	0.0	0.0	5.4	4.8	Shrubland [matorral]
Castuera	38°47'	5°33'	390	4.0	0.0	0.0	7.5	7.5	Dry pastures [pastizales secos]
Castuera	39°49'	5°22'	450	0.0	0.0	0.0	7.5	6.6	Dry pastures [pastizales secos]
Castuera	38°46'	5°19'	450	2.4	0.0	0.0	8.1	7.5	Dry pastures [pastizales secos]
Castuera	38°48'	5°27'	400	0.3	0.0	0.0	9.6	7.5	Dry pastures [pastizales secos]
Castuera	38°52'	5°32'	370	0.0	0.0	0.0	7.2	9.0	Dry pastures [pastizales secos]
Alcudia Valley	38°39'	4°31'	630	7.4	0.0	0.0	8.1	7.5	Dry pastures [pastizales secos]
Alcudia Valley	38°37'	4°19'	730	5.5	0.0	0.0	7.5	8.1	Dry pastures [pastizales secos]
Guadix	37°37'	3°01'	670	6.8	0.0	0.0	3.6	—	Semiarid shrubland [matorral semiárido]
Baza	37°31'	2°43'	780	0.0	89.1	62.9	0.3	3.6	Semiarid shrubland [matorral semiárido]
Baza	37°32'	2°45'	770	0.0	34.4	145.1	3.0	2.7	Semiarid shrubland [matorral semiárido]
El Alquíán	36°50'	2°15'	75	0.0	19.6	96.1	4.2	4.8	Esparto grassland [espartal]
El Alquíán	36°50'	2°11'	90	0.0	22.7	51.4	5.1	3.9	Esparto grassland [espartal]
Nijar	36°55'	2°04'	180	3.9	10.4	32.7	4.2	4.5	Esparto grassland [espartal]
Nijar	36°54'	2°13'	180	3.7	4.8	54.2	5.1	4.8	Esparto grassland [espartal]
Alfés	41°31'	0°37'	220	—	—	0.0	—	3.6	Semiarid shrubland [matorral semiárido]
Baza	37°32'	2°45'	770	—	—	0.0	—	3.6	Semiarid shrubland [matorral semiárido]

Vegetation types were dry pasture (PC), shrubs shorter than 40 cm (SC <40 cm), shrubs taller than 40 cm (SC >40 cm), all shrubs (TSC) and all vegetation (TVC). Presence of crops within the transect band was also recorded. Subsequently, this variable was deleted from the analyses due to the very low frequency of crop presence in transects (only 5.6% out of 1036 transects), and also because a preliminary analysis revealed a lack of influence on the results.

Statistical analyses

The relationships between lark densities and the geographic, climatic and habitat type variables was analysed using General Linear Models (GLM), considering habitat type (HAB) and bioclimatic level (BCL) as dummy variables (codes for HAB: cereal crops, 1,0; dry pastures, 0,1; shrublands, 1,1; codes for BCL: thermomediterranean, 1,0; mesomediterranean, 0,1; supramediterranean, 1,1). Density was normalised by means of log-transformation, and analyses were performed on two different data sets: (1) all localities considered, including those in which the species were not detected in either period ($n=82$), and (2) the subset of localities in which either Lark was detected in the breeding season (Short-toed Lark, $n=25$; Lesser Short-toed Lark, $n=26$) or in winter (Lesser Short-toed Lark, $n=40$). The aim of the first analysis was to study the general patterns governing the relative density of the species in the pseudo-steppes of Mediterranean Iberia as a whole, while the purpose of the second was to model the factors which determine the relative densities of both species of Short-toed Larks in the localities where the species were present. Density differences between periods and between species in the same locality were analysed by means of paired Student-t tests.

The relationship between vegetation structure and the presence of each species of Short-toed Larks in either spring or winter was analysed using logistic regression models, only considering data from localities where the species was present during either the breeding season or in winter. For this analysis, all records, i.e., both within and outside the survey belt, were taken into account. We also used a stepwise discriminant analysis to study the degree

of prediction of the habitat segregation models in terms of vegetation structure in localities with a potential presence of the species. In this analysis, only two classes were considered: (1) presence in any given transect of Short-toed Larks and absence of Lesser Short-toed Larks and (2) the reciprocal absence of Short-toed Larks and presence of Lesser Short-toed Larks. The SPSS 10.0 statistical package was used in all analyses, with error intervals provided as mean \pm SD and significance thresholds at $P = 0.05$.

RESULTS

Relationships of relative densities of Short-toed and Lesser Short-toed Larks with geographic, climatic and habitat type variables

The distribution of the two species during the breeding season followed clearly distinct patterns. Short-toed Larks were present in practically all localities with the exception of certain areas of Almería and Badajoz provinces (Fig. 1), and occupied the entire altitudinal range sampled, from sea level to 1350 m a.s.l. In contrast, Lesser Short-toed Larks only appeared in the Ebro River valley and the semi-arid south-east, at altitudes below 500 m a.s.l. (88% of localities). The only exceptions were three inland salt lakes in the Castilla-La Mancha region located at altitudes of 700 - 800 m a.s.l. In the majority of localities where Lesser Short-toed Larks were present ($n=25$), Short-toed Larks were also found (64%), while Lesser Short-toed Larks were found in 26% of the localities with presence of Short-toed Larks ($n=62$) only. On the other hand, Lesser Short-toed Larks generally displayed a more clumped distribution than Short-toed larks (mean \pm SD values for the coefficient of variation of the number of contacts per transect in localities where each species was present: 228.15 ± 103.60 and 156.77 ± 78.19 for Lesser Short-toed and Short-toed Larks, respectively; $t=2.099$, $P=0.045$).

The relationships between the abundance of the two species and the climatic, geographic and habitat type variables were also different (Table 2). Short-toed Lark abundance in shrublands was more than twice its abundance in dry pastures and croplands (shrublands: $8.64 \pm$

TABLE 2

General linear models relating spring densities of Short-toed Larks and spring and winter densities of Lesser Short-toed Larks to habitat variables. LONG: geographic longitude; AAR: annual rainfall; HAB: habitat type; BCL: bioclimatic level.

[Modelos generales lineales que relacionan las densidades primaverales de Terrera Común y las densidades primaverales e invernales de Terrera Marismeña con variables de hábitat. LONG: longitud geográfica; AAR: precipitación invernal; HAB: tipo de hábitat; BCL: piso bioclimático.]

Species [especie]	Dependent variable [variable dependiente]	Data set [base de datos]	R ²	Parameters [parámetros del modelo]	df	Mean Square [media cuadrática]	F	P		
<i>Calandrella brachydactyla</i>	Spring density [densidad primavera]	All localities [todas las localidades]	0.35	Intersection	1	1.95	11.18	<0.001		
				HAB	2	0.05	0.29	0.75		
				BCL	2	1.41	8.10	<0.001		
				LONG	1	2.22	12.75	<0.001		
				AAR	1	0.14	0.79	0.38		
	Localities with presence [localidades con presencia]	0.41	Intersection	1	1.51	11.78	<0.001			
			HAB	2	0.42	3.29	<0.05			
			BCL	2	0.47	3.67	<0.05			
			LONG	1	0.72	5.61	<0.05			
			AAR	1	0.03	0.22	0.64			
<i>Calandrella rufescens</i>	Spring density [densidad primavera]	All localities [todas las localidades]	0.53	Intersection	1	2.70	15.42	<0.001		
				HAB	2	0.57	3.27	<0.05		
				BCL	2	0.90	5.13	<0.01		
				LONG	1	1.07	6.10	<0.05		
				AAR	1	1.34	7.63	<0.01		
				Localities with presence in spring [localidades con presencia en primavera]	0.29	Intersection	1	0.54	2.70	0.12
						HAB	0	—	—	—
	BCL	1	0.49			2.45	0.13			
	Winter density [densidad invernal]	All localities [todas las localidades]	0.38	Intersection	1	0.15	0.36	0.55		
				HAB	2	1.60	3.72	<0.05		
				BCL	2	0.83	1.93	0.16		
				LONG	1	0.11	0.26	0.61		
				AAR	1	0.05	0.106	0.75		
				Localities with presence in winter [localidades con presencia en invierno]	0.26	Intersection	1	0.002	0.004	0.95
HAB						0	—	—	—	
BCL	1	0.14	0.33			0.58				
				LONG	1	0.14	0.33	0.57		
				AAR	1	171	3.91	0.07		

10.87 birds/10 ha, $n=35$; dry pastures: 3.90 ± 2.75 , $n=5$; croplands: 3.06 ± 4.21 birds/10 ha, $n=22$). Overall, however, Short-toed Lark abundances were higher in the supra- and mesomediterranean levels in localities where it was present (thermomediterranean: 3.31 ± 3.55 birds/10 ha, $n=11$; mesomediterranean: 7.69 ± 9.84 birds/10 ha, $n=34$; supramediterranean: 13.97 ± 13.84 bird/10 ha, $n=17$). In this species,

geographic longitude and bioclimatic level were significantly associated to bird density when considering the full set of study localities, whereas for the sub-set of those where it was present, habitat type was also significantly associated to density. The percentage of variance explained by the models was similar in both cases (35% and 41%). These figures were relatively high considering the types of variables

employed and both models were significant ($P < 0.001$).

Lesser Short-toed Larks were found in practically the same number of localities ($n=19$) in both the breeding season and winter (95% presence in winter out of the 19 localities where it was contacted in spring and 100% presence in spring out of the 18 localities where it was contacted in winter). Winter abundances tended to be higher than spring abundances (34.93 ± 40.28 vs. 19.10 ± 21.60 birds/10 ha), although these differences were only marginally significant (Student-t test for paired samples, $t_{18}=1.926$, $P = 0.070$). In spring, this species was only present in shrublands, and its abundance was three times higher in the localities of the mesomediterranean level than in those of the thermomediterranean (27.57 ± 23.21 birds/10 ha, $n=14$, and 8.47 ± 7.56 birds/10 ha, $n=11$, respectively). In localities where both lark species were present, the abundance of Lesser Short-toed Larks tended to be higher than that of Short-toed Larks (15.98 ± 13.24 vs. 10.73 ± 12.53 birds/10 ha), although this difference was not significant (Student-t test for paired samples, $t_{15}=1.041$, $P=0.314$). In winter, as in spring, Lesser Short-toed Larks were present only in shrublands, where its abundance at the mesomediterranean level was almost double than at the thermomediterranean, although this difference was not significant due to high variance (mesomediterranean: 50.39 ± 47.57 birds/10 ha; $n=8$; thermomediterranean: 28.13 ± 31.49 birds/10 ha; $n=11$). In this species, for the full set of localities, all four variables were significant in spring. The overall GLM explained 53% of the variance ($P < 0.001$). In localities with spring presence of the species, the model did not estimate the significance of habitat type, since only one type of habitat, namely shrublands, was used by the species. None of the remaining variables, however, turned out to be significant. The percentage of variance explained was 29% and the model only approached significance ($P=0.06$). A similar result was logically obtained with the model analysing the subset of localities with winter presence (26% of variance explained, $P=0.19$), whereas in the model analysing the full set of localities, habitat type turned out to be the only significant variable (38% of variance explained, $P < 0.01$).

Habitat use

The habitat use of the two species in the localities where they were present displayed several well-defined patterns. The transect line sections where Short-toed Larks were present differed from those where it was absent in the majority of the vegetation structure variables. Logistic regression models explaining presence and absence of each lark species in transect line sections as a function of vegetation variables were all significant (Table 3). The included variables differed between species and periods, however. For Short-toed Larks, the model included the cover of short shrubs, the cover of dry pastures and total shrub cover, and predicted correctly 67% of observations. For Lesser Short-toed Larks, the variables that best predicted its spring presence were the cover of short shrubs, the cover of dry pastures and the average vegetation height, with a much higher proportion of correct classifications (82%). In winter the predictor variables for the presence of Lesser Short-toed Larks were total shrub cover and maximum vegetation height. In this case, the total percentage of observations classified correctly was similar to that of Short-toed Larks in spring (66%).

Considering all transect lines, there were differences in all the parameters of vegetation structure between localities where only Short-toed Larks were present and those where only Lesser Short-toed Larks were found during breeding (Student-t test, $P < 0.05$), with the exception of total vegetation cover. These differences between the two sets of localities were maintained considering either the transect lines with presence of one of the species only or those where they were absent, although, in the latter case, non-significant factors not only included total cover but also the cover of short shrubs ($P=0.280$). At this scale, Short-toed Larks were present in transect line sections with more cover of short shrubs, lower cover of dry pastures and lower total cover of shrubs than where they were absent (Table 3).

In most of the transect lines in localities where both species could be present in accordance with their distribution areas, only Lesser Short-toed Larks were present (76.5% out of the total of transect line sections with one species or the other, $n=149$), while percentages for the presence of Short-toed Larks only and pre-

sence of both species were considerably lower (9.4% and 14.1%, respectively). The predicted frequencies in transect line sections where only one species or the other was contacted were higher than those actually observed ($\chi^2_1 = 4.55$, $P=0.033$; total number of transect line sections =182).

The majority of the vegetation structure parameters yielded differences between transect lines where one species or the other was present, although the sign and magnitude of the differences were different from those obtained when considering localities where only Short-toed Larks were present and those where only Lesser Short-toed Larks were found during breeding (Table 3). Cover of tall shrubs and total shrub cover, average and maximum height were higher in the case of Short-toed Lark, while cover of short shrubs was almost three times lower, as was the case for herbaceous plants.

The discriminant analysis of habitat use by the two species in localities where their distribution area suggested that both might be present yielded a correct classification of 100% of cases by means of a single function whose contrast was significant ($\chi^2_5 = 31.83$, $P < 0.001$; Table 4).

DISCUSSION

Segregation and overlap between species

Differences in distribution and habitat use between sibling species are usually interpreted as a result of the competition between them, although differential predation has also been found to contribute to such differences in sympatric zones (Gourbiere *et al.*, 1999). The result of these two types of interaction may give rise to their spatial segregation, albeit with a degree of overlap, and to joint changes in the sympatric areas (Gourbiere *et al.*, 1997). Current data on the two sibling species of Short-toed Larks in their sympatric zones of mainland Spain are insufficient to define temporal changes in their distribution areas in terms of speed and direction due to the lack of historic records. Using data from the breeding atlas of Catalonia of 1998 and 2000 (Muntaner *et al.*, 1982; Institut Català d'Ornitologia, 2002), the distributions of both species at the atlas scale (10 × 10

km quadrats) in this region appear to have been relatively stable, with a slight decline in Short-toed Larks that has been interpreted in terms of changes in farm management patterns rather than interactions with Lesser Short-toed Larks.

Our analyses showed a clear segregation of both species on both a wide and a microhabitat scale. On the geographic scale, habitat type appears to have a decisive influence on the abundance of Short-toed Larks in areas with presence of this species, as suggested by Delgado & Moreira (2000) for different agricultural vegetation types in an area of southern Portugal. In addition, there was a declining trend in abundance with longitude and an increasing trend with bioclimatic level, which in turn was associated in our range of sampling localities with altitude and continentality. However, the abundance of Lesser Short-toed Larks, which is absent from croplands and grasslands, was affected by the bioclimatic level and was negatively associated in the total set of localities with longitude. In general terms, these factors confirm Cramp's (1988) affirmation that Lesser Short-toed Larks are found in more arid areas than Short-toed Larks.

The geographic differences between the two species may be due not only to the above-mentioned physical factors and habitat types, but also to vegetation structure. The majority of the vegetation structure parameters under consideration were different in the localities where only one species or the other was present. These differences were maintained in analyses considering the transect lines in which the species were present, and also those where they were absent, with the exception in the latter case of total vegetation cover and cover of short shrubs. At this scale, Short-toed Larks appeared to select localities with less cover of camephytes and total shrubs, more cover of herbaceous plants and lower vegetation height. This also coincides with the habitat use by that species broadly described by Sampietro *et al.* (1998) in Aragón. On the other hand, our results on Lesser Short-toed Larks seem to partly contradict the general observations made by those authors, who pointed out the important use that Lesser Short-toed Larks make of tall and dense shrubland such as *Rosmarinus officinalis* and *Ononis tridentata* formations. Many of these records correspond, however, to slope areas where Lesser Short-toed Larks are especially

TABLE 3

Logistic regression models explaining spring Short-toed Lark and spring and winter Lesser Short-toed Lark presence as a function of vegetation structure variables. SC < 40 cm: cover of shrubs shorter than 40 cm; TSC: total shrub cover; AVH: average vegetation height; MVH: maximum vegetation height.

[Modelos de regresión logística que explican la presencia primaveral de *Terrera Común* y la presencia primaveral e invernal de la *Terrera Marismaña* en función de variables de estructura de la vegetación. SC < 40 cm: cobertura de matorral de menos de 40 cm de altura; TSC: cobertura total de matorral; PC: cobertura de pastizal; AVH: altura media de la vegetación; MVH: altura máxima de la vegetación.]

Species and season [especie y época del año]	Model [modelo]	χ^2	-2 log (max. likelihood) [-2 log (probabilidad máxima)]	df	P
<i>C. brachydactyla</i>	0.562 · SC < 40 cm - 0.188 · PC - 0.204 · TSC ± 0.060	75.491	599.317	3	< 0.001
<i>C. rufescens</i> , spring [primavera]	-0.302 · TSC - 0.374 · PC - 0.579 · AVH + 6.071	34.324	112.021	3	< 0.001
<i>C. rufescens</i> , winter [invierno]	-0.413 · TSC + 0.224 · MVH - 1.035	14.091	176.957	2	0.001

TABLE 4

Fisher linear discriminant functions using vegetation structure variables as the independent variables and the presence of either Short-toed Larks or Lesser Short-toed Larks as the discriminant factor. SC < 40 cm: cover of shrub shorter than 40 cm; SC > 40 cm: cover of shrub taller than 40 cm; TSC: total shrub cover; PC: Pasture cover; AVH: average vegetation height; MVH: maximum vegetation height.

[Funciones discriminantes lineales de Fisher para presencia de *Terrera Común* o *Terrera Marismaña* en función de la estructura de la vegetación. SC < 40 cm: cobertura de matorral de menos de 40 cm de altura; SC > 40 cm: cobertura de matorral de más de 40 cm de altura; TSC: cobertura total de matorral; PC: cobertura de pasto; AVH: altura media de la vegetación; MVH: altura máxima de la vegetación.]

Discriminant function [función discriminante]	
Presence of <i>C. brachydactyla</i> [presencia de <i>C. brachydactyla</i>]	0.212 · SC > 40 cm + 1.814 · SC < 40 cm + 0.615 · PC + 1.079 · AVH + 2.229 · MVH - 16.605
Presence of <i>C. rufescens</i> [presencia de <i>C. rufescens</i>]	-0.118 · SC > 40 cm + 2.318 · SC < 40 cm + 1.173 · PC + 1.114 · AVH + 1.638 · MVH - 11.590

abundant and Short-toed Larks are absent, whereas our census sites are all located on flat steppe, showing generally more bare ground surface, less shrub cover and lower shrub height. These differences suggest that Lesser Short-toed Larks probably make a different use of microhabitat in flat localities, where they inhabit less densely covered and shorter shrubland areas. Nevertheless, the discriminant function for this species, though presenting a negative influence of the cover of tall shrubs, showed a heavier effect of the cover of short shrubs, the cover of pastures and the mean vegetation height than the function for Short-toed Larks, which broadly agrees with the general observation that Lesser Short-toed Larks use habitats with more vegetation cover and height than Short-toed Larks. The differences between the abundance of these two larks therefore seem to be linked to certain physical and bioclimatic variables and their presence was determined by vegetation structure, which is obviously conditioned to a large extent by these physical variables, as well as by land use.

There are, however, several localities where the two species are sympatric. In these zones, the abundance of Short-toed Larks tended to be considerably lower than that of Lesser Short-toed Larks, although these differences were not significant. As a result, Lesser Short-toed Larks were found to be present alone for the vast majority of the transect lines, while lines where only Short-toed Larks were contacted were few and of the same order of magnitude as those where both species were present (9.4 and 14.1%). The fact that the predicted frequencies of presence of one species or the other were higher than those actually found (percent of predicted and recorded presence of Short-toed Larks and absence of Lesser Short-toed Larks with respect to total data: 7.7 vs. 4.9%; presence of Lesser Short-toed Larks and absence of Short-toed Larks: 62.9 vs. 59.9%), and that the percentage of transect lines in which both species were present was lower (18.1 vs. 20.9%), suggests a degree of segregation between the two species, although there was still a percentage of transect lines in which both species were found (11.5% of total).

The process by which this segregation arises is difficult to define on the basis of currently available data. There are no records of interspecific hybridisation (Cramp, 1988), although

facultative nest parasitism of Short-toed Larks by Lesser Short-toed Larks has been observed, with chicks of the parasite species developing well amongst the host species (Yanes *et al.*, 1996). There is also a lack of data on interspecific territoriality. Lesser Short-toed Lark's nest distribution in Almería appears to be clustered (Manrique *et al.*, 1983), and Short-toed Larks have also been found to breed in loose colonies (Simms, 1992). Nevertheless, the distribution of contacts along the transect lines clearly indicates a contagious distribution of Lesser Short-toed Larks, while Short-toed Larks appeared to show a more random distribution. The diet of the two species in their sympatric areas is unknown (see Herranz *et al.*, 1997 for data on the diet of Lesser Short-toed Lark chicks), although there is evidence that predation does not appear to differ between the two species when they are in the same locality and varies considerably between localities (M. Yanes and J. Herranz, unpublished data). On the basis of the above evidence, it seems clear that habitat use is quite different between the two species under sympatric conditions, as proven by the high percentage of variance explained by the discriminant analysis. Short-toed Larks were preferentially found along transect lines with higher cover of tall shrubs and higher average and maximum vegetation height. This pattern of habitat use in sympatric areas has a different sign from that found with data considering all localities with presence of one or the other species. This suggests a possible displacement of Short-toed Larks by Lesser Short-toed Larks, as the differences in the selected vegetation structure occur primarily for Short-toed Larks.

In summary, the available data indicate a considerable segregation between the two sibling species of Short-toed Larks at two scales. At the geographic scale, the differences are established in terms of certain climatic variables as well as habitat types, while at the local scale in the sympatric zones, the differences were related to vegetation structure. The mechanisms producing the latter differences are still unknown. There is possibly either a differential habitat use between the two species or a displacement of Short-toed Larks by Lesser Short-toed Larks, although the mechanisms potentially involved are difficult to establish (e.g. both species are very close in body mass and body measurements, and no differences in ag-

gressive behaviour have been reported; Cramp 1988), so we cannot hypothesize the dominance of one species over the other.

Habitat use of both species and conservation

Although habitat use by these two larks concurs, overall, with the patterns described in the literature (Cramp, 1998; Sampietro *et al.*, 1998), its quantification on the basis of the structural parameters of vegetation facilitates a refinement of potential conservation measures. In general, the two Short-toed Larks used areas with low cover of tall shrubs and a variable cover of low camephytes, although the average values are generally small. Lesser Short-toed Larks were associated positively with areas of low average vegetation height and low cover of tall shrubs both in spring and winter, although the importance of average vegetation height and of cover of low camephytes and pastures seemed to be greater. This vegetation structure essentially matches grazed wasteland with a predominance of camephytes and a large percentage of bare soil, and long-term fallow land without high stocking rates which causes a tendency towards annual and therophyte-dominated grasslands. These types of environments have undergone a sharp decline in recent decades, including a drastic 800000 ha reduction in fallow land over the 1990-2000 period in the whole distribution area of the Short-toed Lark (see Suárez *et al.*, 1999). This reduction has been cited as one of the possible causes of the decline of the Short-toed Lark in mainland Spain (de Juana & Suárez, 2002) and other bird species in agricultural areas in the rest of Europe (Fuller *et al.*, 1995; Gregory & Baillie, 1998; Suárez *et al.*, 1998). If we wish to preserve these species, this regression of fallow land and low scrub cover in flat areas must be reversed. The measures promoted by the agri-environmental programmes under R. 1257/99/CE allow the maintenance of such types of environments (Peco *et al.*, 2000), as well as the use of sheep grazing to encourage vegetation types with similar structural characteristics to the ones selected by these two species.

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APPENDIX

Additional studies and habitats included in the analyses. The number of localities corresponding to each habitat is shown in brackets. In the case of authors' own unpublished data, locality, year of census, altitude (m a.s.l.), spring Short-toed Lark and spring and winter Lesser Short-toed Lark densities (birds/10 ha), spring and winter censused area (ha) and main habitat, respectively, are given.

[Estudios y habitats adicionales incluidos en los análisis. El número de localidades correspondientes a cada hábitat (cereal crops: cultivos cerealistas; shrubland: matorrales; fallow: barbechos; stubble: rastros; crops: cultivos; ploughed: labrados) se muestra entre paréntesis. En el caso de datos no publicados, se indican, por este orden, la localidad, el año de censo, la altitud en m s.n.m., la densidad primaveral de Terreras Comunes y las densidades primaverales e invernales de Terreras Marismeñas en aves/10 ha, el área censada en ha en primavera y en invierno y el tipo principal de hábitat.]

Hódar (1996), cereal crops (2); Nevado *et al.* (1997), cereal crops (1) and shrubland (1); Canut *et al.* (1987), cereal crops (1), fallow (1) and shrubland (2); Potti & Garrido (1986), cereal crops (1); Tellería *et al.* (1988b), shrubland (4); Tellería *et al.* (1988a), cereal crops (1) and shrubland (1); Campos & Ortuño (1991), cereal crops (1) and shrubland (1); Díaz *et al.* (1993), cereal crops (3); Hernández & Pelayo (1987), shrubland (5); Suárez & Sáez-Royuela (1983), shrubland (1); Pescador & Peris (2001), crops (2); Manrique *et al.* (1992), shrubland (5).

Own data: La Serena, 1991-1992, 400, spring and winter, 1.3, 0.0, 0.0, 15.0, 15.0, crops; La Serena, 1991-1992, 400, spring, 14.7, 0.0, 15.0, stubble; La Serena, 1991-1992, 400, spring and winter, 3.0, 0.0, 0.0, 15.0, 15.0; ploughed; La Serena, 1991-1992, 400, spring and winter, 4.7, 0.0, 0.0, 15.0, 15.0, fallow; Alcobendas, 1991-1992, 670, spring and winter, 0.01, 0.0, 0.0, 15.0, 15.0, crops; Alcobendas, 1991-1992, 670, spring and winter, 3.0, 0.0, 0.0, 15.0, 15.0, shrubland; Alcobendas, 1991-1992, 670, spring, 2.7, 0.0, 15.0, 15.0, stubble; Layna, 1991-1992, 1150, spring and winter, 0.01, 0.0, 0.0, 15.0, 15.0, crops; Layna, 1991-1992, 1150, spring and winter, 0.001, 0.0, 0.0, 15.0, 15.0, ploughed; Layna, 1991-1992, 1150, spring and winter, 2.0, 0.0, 0.0, 15.0, 15.0, fallow; Layna, 1991-1992, 1150, spring, 2.0, 0.0, 15.0, stubble; Layna, 1991-1992, 1150, spring and winter, 13.3, 0.0, 0.0, 15.0, 15.0, shrubland; Calatrava, 2000, 630, spring, 1.9, 0.0, 163.0, cereal crops; Campo Real, 2001, 750, spring, 0.4, 0.0, 200.0, cereal crops.