

HOME RANGE, TERRITORIALITY AND HABITAT SELECTION BY THE DUPONT'S LARK *CHERSOPHILUS DUPONTI* DURING THE BREEDING AND POSTBREEDING PERIODS



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SUMMARY.—*Home range, territoriality and habitat selection by the Dupont's Lark Chersophilus duponti during the breeding and postbreeding periods.*

Aims: Home ranges, habitat use and selection of Dupont's Lark *Chersophilus duponti* during the breeding and postbreeding periods were analysed using radiotagged birds.

Location: Layna, central Spain (Soria, 41°05'N, 1°50'W; 1200 m a.s.l.).

Methods: A total of 32 birds were radiotagged (22 males, 4 females and 6 juveniles) and monitored nearly daily from April 1st to September 1st. The following variables were measured (1) home ranges using the Minimum Convex Polygon, MCP, (2) core areas using the kernel 80 % density estimator, (3) the distance between successive daily locations, and (4) the degree of overlap of between individuals and periods in home ranges and core areas using Cole's Index of Concordance. The use and selection of vegetation formations was studied on an individual basis comparing the percentage of bird locations and random points in each vegetation unit. The selection of habitat structure was measured along transects within the birds' home ranges and compared to that measured along random transects outside home ranges.

Results: Home ranges (mean, 8.1 ha), core areas (3.7 ha) and the distance between successive daily locations (around 120 m) did not differ between age-sex classes, or between periods in either sex. Juveniles showed larger core areas and movements than adults during the post-breeding period. Overlap between neighbouring males, as well as between juveniles and adults during the postbreeding period, was scarce in comparison with the overlap between members of the same pair or the overlap between the periods. Two males (9.1%) changed their home ranges during the breeding period, and the only fledgling captured near its nest stayed within paternal home range until at least 1 month old. The density in the study area was 1.0 males/10ha.

Dupont's Lark positively selected *Genista pumila* shrubs and negatively *Genista scorpius* shrubs, dry pastures and cereal fields. There were no differences between sexes, nor between periods among adults. Selection by juveniles differed from adult selection during the postbreeding period, using dry pastures more frequently than *Genista pumila* shrubs. Birds positively selected areas of high pillow-shape shrub cover at ground level, avoiding those of high tall-shrub cover at ground level. A binary logistic regression model including only pillow-shaped shrub cover at ground level as explanatory variable, correctly predicted 76% of home ranges, as confirmed by jackknife re-sampling estimation.

Conclusions: Three main conclusions can be drawn from a conservation perspective: (1) the species' territorial behaviour and strict habitat selection make it highly vulnerable to habitat changes, imposing careful habitat management; (2) management should also regard the marginal habitats used by juveniles; (3) the low density found in one of the best areas for the species in Iberia supports the low estimates of the Spanish population of the Dupont's Lark made in previous studies.

Key words: Alaudidae, core areas, home range, Mediterranean, radio-tracking, Spain.

RESUMEN.—*Áreas de campeo, territorialidad y selección de hábitat de la Alondra Ricotí Chersophilus duponti durante los periodos reproductor y post-reproductor.*

Objetivo: Se analizan por primera vez el uso del espacio y selección de hábitat de la Alondra de Dupont durante los periodos reproductor y post-reproductor mediante individuos radiomarcados.

Localidad: Layna (Soria, centro de España, 41°05'N, 1°50'W; 1200 m s.n.m.).

Métodos: Se marcaron un total de 32 individuos mediante radio-emisores (22 machos, 4 hembras y 6 jóvenes del año), realizándose un seguimiento casi diario desde principios de abril a principios de septiembre. Se estimaron (1) las áreas de campeo, medidas mediante el Mínimo Polígono Convexo, MPC, (2) los núcleos centrales, utilizando el estimador de densidad Kernel 80%, (3) la distancia del movimiento entre días suce-

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sivos, y (4) el solapamiento entre individuos y periodos en las áreas de campeo y los núcleos centrales utilizando el índice de concordancia de Cole. La utilización y selección de las unidades de vegetación se estimó considerando el individuo como unidad, y comparando los porcentajes de utilización de éstos con los obtenidos de muestreos al azar. La selección de la estructura del hábitat se analizó comparando diversas variables estructurales medidas en transectos situados dentro y fuera de las áreas de campeo.

Resultados: Las áreas de campeo (7,4 ha de media), los núcleos centrales (3,6 ha) y el movimiento entre días sucesivos (unos 120 m) no difirieron entre las clases de sexo-edad consideradas, ni entre periodos para cada uno de los sexos. Los jóvenes mostraron áreas centrales de mayor tamaño y movimientos de más largo alcance que los adultos durante el periodo post-reproductor. El solapamiento entre machos vecinos fue reducido, al igual que entre individuos adultos y jóvenes durante el periodo post-reproductor, mientras que el solapamiento entre miembros de una misma pareja y entre periodos fue elevado. Dos machos (9,1%) cambiaron de área de campeo en el periodo reproductor, y el único pollo marcado cerca del nido se mantuvo en el área de campeo parental hasta al menos 1 mes de edad. La densidad obtenida para esta zona fue de 1,0 machos/10 ha.

La Alondra Ricotí seleccionó positivamente los cambronales, mientras que aulagares, pastizales-tomillares y cultivos fueron seleccionados negativamente. No se observaron diferencias entre machos y hembras adultos, ni en los adultos entre periodos; los jóvenes mostraron diferencias con los adultos en el periodo post-reproductor, utilizando en mayor medida el pastizal-tomillar y en menor el cambronel. La Alondra Ricotí seleccionó positivamente una estructura del hábitat en las áreas de campeo determinada por la cobertura de caméfitos almohadillados de bajo porte a nivel del suelo y negativamente por los matorrales medianos a esta misma altura. El modelo de regresión logística binaria, incluyendo una sola variable, la cobertura de caméfitos almohadillados a nivel del suelo, predijo un 76,5% de las áreas de campeo.

Conclusiones: Desde el punto de vista de su conservación se concluye que (1) el carácter territorial de la especie y su estricta selección de hábitat imponen una gestión específica de sus hábitats, (2) los hábitats considerados como marginales para los adultos, pero seleccionados por los jóvenes, deben ser contemplados en dicha gestión y (3) la baja densidad encontrada en el área de estudio, una de las mejores para la especie en Iberia, es consistente con las bajas estimas poblacionales realizadas para el conjunto de España en estudios recientes.

Palabras clave: Alaudidae, área de campeo, área central, Mediterráneo, radio-seguimiento, España.

INTRODUCTION

The Dupont's Lark *Chersophilus duponti* is one of the scarcest passerine birds in Europe. Its distribution is restricted to the Iberian peninsula where the species occupies flat, short shrub pseudo-steppes from sea-level to 1400 m (Garza *et al.*, 2003a), with a breeding population recently estimated to range between 1300 and 1900 territories (Garza *et al.*, 2003b; Tella *et al.*, 2005). Consequently, the species has been classified as «endangered» in the Red Book of the Birds of Spain (Garza *et al.*, 2004). In spite of its high level of threat, knowledge on the biology of this lark species is incomplete and reduced to some basic reproductive aspects (Cañadas *et al.*, 1988; Herranz *et al.*, 1993; Herranz *et al.*, 1994) and habitat selection during the breeding and wintering periods (Suárez & Garza, 1989; Garza & Suárez, 1990; Martín-Vivaldi *et al.*, 1999). Little is known, however, on the species' territorial behaviour and space use during reproduction and, particularly, during the postbreeding period (De Juana & Suárez, 2004), in spite of their rele-

vance in designing a realistic conservation strategy (Rivera *et al.*, 2003).

This lack of knowledge can be partly attributed to the species' terrestrial habits and secretive behaviour which make visual observation very difficult. Additionally, its monotonic call notably limits precise auditory location (P. Laiolo, *pers. com.*). These facts can become an important source of error, not only in habitat selection studies based on auditory records, but also in those based on direct sighting of larks as birds normally run to hide in the vegetation as the observer approaches, so that the initial location of individuals is unknown and its habitat use may be consequently mis-assigned. Therefore, sampling methods assuring a more accurate location of birds, while avoiding alteration of their normal behaviour, need to be applied in studies of space and habitat use by Dupont's Larks.

In the present study, data from radiotagged Dupont's Larks were used to analyse their space use and habitat selection patterns during the breeding and post-breeding periods. This approach allowed both the obtention of reliable records of bird locations, and the monitoring



of the study population on an individual basis over two different and consecutive periods of the species' annual cycle. More specifically, spatial use was studied in relation to the following questions: (1) Do home ranges of Dupont's Larks vary according to sex, age (adults vs. juveniles) or period? (2) How much do home ranges of neighbouring Dupont's Larks overlap?, and (3) Does this overlap differ between periods? Regarding habitat selection, two main points are addressed: (1) What are the vegetation composition and structure features of habitats preferred by the species?, and (2) Are habitats used by adults different from those occupied by juveniles in terms of vegetation composition and structure?

MATERIAL AND METHODS

Study area

The study area was located in the high plateau (*páramo*) of Layna, central Spain (Soria, 41°05'N, 1°50'W; 1200 m a.s.l.). Landscape is a flat short shrub-steppe dominated by *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Linum suffruticosum* (Suárez *et al.*, 1993). Small cereal cultures are found interspersed in the shrub-steppe. Climate is continental Mediterranean with cold winters and fresh but dry summers (annual rainfall of 500 mm and yearly average temperature of 10.2 °C). The total surface of the study area was 385 ha.

Data collection

Dupont's Larks were captured between April 5th and July 23rd, 2003 using four different methods: net traps with song recording ($n = 10$ males), cage trap with song recording ($n = 12$ males), net traps without song recording ($n = 2$ females), nest traps ($n = 2$ females), and captured at hand ($n = 6$ young). The dominance of males in this sample is attributable to the capture methods used plus the difficulties of capturing females and young. Each individual was provided with a 1.5 g back-mounted harness radio-tag (Rappole & Tipton, 1991) manufactured by Biotrack (Biotrack Inc.). The species is sexually size-dimorphic, and therefore sex was determined biometrically using bill, wing

and weight measurements, and by the presence of the brood patch in the case of females captured at the nest. Fledglings were identified by their back and neck feather pattern. A total of 32 Dupont's Larks was captured and radio-tagged: 22 males, 4 females and 6 juveniles.

Individuals were daily located during daytime from early April to early September by means of bi- or triangulations from a mean estimated distance of 201 m ($SD = 120$ m), thus avoiding interference with their normal behaviour. For radio-tracking, AOR-AR8200 multi-band receptors (AOR Inc.) and three element Yagi antennas were used. In order to minimise location error, bi- or triangulations were made from positions at 80-100° with respect each other (White & Garrot, 1990). The exact position of the bird was determined through the maximum probability estimate (Lenth, 1981) using the LOAS 3.0 software (Ecological Software Solutions, Inc.). The mean error polygon estimated from triple triangulations (Kenward, 2000) was 295 m² ($SD = 212$ m²), while the mean angle error was 0.3° ($SD = 1.87$). A total of 1201 radio-locations were obtained. Mean and maximum time individuals were monitored was 51 and 106 days, respectively. Since the exploration of data using a bootstrapping procedure showed that the size of home ranges stabilized at 20 locations, analyses included only birds with more than 20 radio-tracking locations.

Habitat use and selection were studied under two different approaches. First, at a landscape scale, existing vegetation units were determined and mapped through photo-interpretation (ortho-photograph resolution = 0.6 m) and later confirmation in the field. Four vegetation units were defined: (1) short shrub dominated by *Genista pumila*, (2) tall shrub with dominance of *G. scorpius*, (3) pasture dominated by different grasses (*Stipa* spp., *Poa* spp.) and short-tall thyme (*Thymus* spp.), (4) and cereal cultures. The use of the different vegetation types made by radio-tagged Dupont's Larks was determined after the frequency of locations of each individual in each vegetation unit, obtained by plotting locations on a geo-referenced digitalised ortho-photograph using a vector based Geographical Information System (Arcview 3.2 software, ESRI, Inc.).

Second, during August 2003 habitat structure was measured along transects within the birds' home ranges (defined by their minimum convex

polygons, MCP, $n = 16$) and compared to that measured along random transects outside home ranges ($n = 17$). Transects were 20 m long and one m wide, and their starting point and direction were randomly determined. They were divided into 2 m long units within which the following variables were measured at ground, 20 and 40 cm height: (1) bare ground cover, (2) rock cover, (3) pasture cover, (4) cover of pillow-shaped, short shrub, (5) cover of non pillow-shaped short-shrub, and (6) tall shrub (40-60 cm high) cover. Maximum vegetation height was also measured, and a mean value was calculated for all maximum heights in each two meters unit. Slope was not considered since, in all the study area, it was always under 15%, which is the upper limit determining the species' presence (Garza & Suárez, 1990; V. Garza, *pers. obs.*).

Home range analysis

The study was divided into two consecutive periods, coincident with the corresponding phases of the species' annual cycle: reproductive (up to June 30th, when the last of controlled nest was abandoned by fledgings), and post-reproductive (July 1st to August 31st). Two different estimates of individual home ranges were used, both calculated using the Animal Movement Analysis extension for Arcview software (Hooge & Eichenlaub, 1997): the minimum convex polygon (MCP; Hayne, 1949), and the kernel density estimator (Worton, 1989; 1995). The first one reflects the whole area used by individuals, but it closely depends on the number of locations recorded and may include areas used only punctually or accidentally, thus overestimating real territory size (White & Garrot, 1990). The second method is more robust to a potential effect of the number of locations (Jiguet *et al.*, 2000), and a good estimator of core areas, since it minimises the influence of isolated points, thus being a reliable approach to territory size in territorial species (Worton, 1995; Powell *et al.*, 1997; Jiguet *et al.*, 2000). The 80% isopleth to define kernel areas (IK80) was used since they did not sensibly increase for higher probability values when estimated at 5% intervals (Harris *et al.*, 1990). Therefore, MCPs are appropriate for studying variation within the complete range used by individuals and kernel areas are espe-

cially suitable when studying territories or territorial behaviour.

The degree of overlap between each individual's reproductive and post-reproductive home ranges was calculated using Cole's Index of Concordance (C; Cole, 1949), defined as

$$C = 100 \cdot 2 \cdot A_{12} / (A_1 + A_2)$$

where A_{12} is the area of overlap, and A_1 and A_2 are, respectively, the areas corresponding to the reproductive and post-reproductive home ranges. The overlap between neighbouring home ranges was also calculated, considering only those radio-tracked males between which we had the certainty that no other untagged male existed. Cole's index was calculated both for MCPs and IK80s. The distance between each bird's two consecutive locations was measured using also Arcview 3.2 software.

Three age-sex classes were considered in the analyses: adult males, adult females and juveniles. Differences in MCP and IK80 between age-sex classes within each temporal period were analysed by means of a General Linear Model (GLM) using the number of observations as a covariate in order to control its effect. Home range overlap and distance differences between age-sex classes were analysed by means of one-way ANOVAs, considering in the latter case the mean distance for each individual in order to avoid pseudo-replication. The potential influence of the period was studied in all cases using a repeated measures ANOVA test. Those individuals with less than 10 observations per category were excluded from the analyses.

Habitat use and selection analysis

The use of vegetation formations was studied on an individual basis estimating the percentage of locations in each of the above defined vegetation units for each radio-tagged bird (mean number of observations per individual $\pm SD = 30.9 \pm 17.4$, $n = 32$). The effect of age-sex on this variable was analysed by means of one way ANOVA, while that of the period effect was assessed by means of a paired *t* test. Selection of vegetation unit was analysed comparing the total frequencies of use by radio-tracked Dupont's Larks with the frequencies obtained from 100 points sample at random in



the study area. This comparison was made by means of a χ^2 test. Ivlev's index (Ivlev, 1961) was calculated for each vegetation unit in order to estimate the intensity and sign of selection.

In order to analyse the effect of habitat structure, the variables measured were compared by means of a one way ANOVA in which inclusion or not in an individual's home range was used as a single factor. A binary logistic regression model was built to predict territory presence from habitat structure. For this purpose, a first model was generated using all variables to study their relative significance. Using this information, a second reduced model was produced to which new variables were sequentially added. The statistic G^2 was used as a criterion to evaluate whether each successive model was more significant than the previous one (Quinn & Keough, 2002; Malo *et al.*, 2004).

The significance of the model variables and coefficients was assessed using a Wald- χ^2 test. Model reliability was evaluated by means of a Jackknife re-sampling. All analyses were performed with the SPSS 12.0 statistical package (LEAD Technologies Inc.).

RESULTS

Space use

Dupont's Lark male density in the study area, considering radio-tagged birds, as well as those confirmed by song in at least two or three different simultaneous contacts and geo-referred using a GPS (Garza *et al.*, 2003a), was 1 male/10 ha. Total home ranges, estimated as MCPs (Fig. 1), varied considerably between

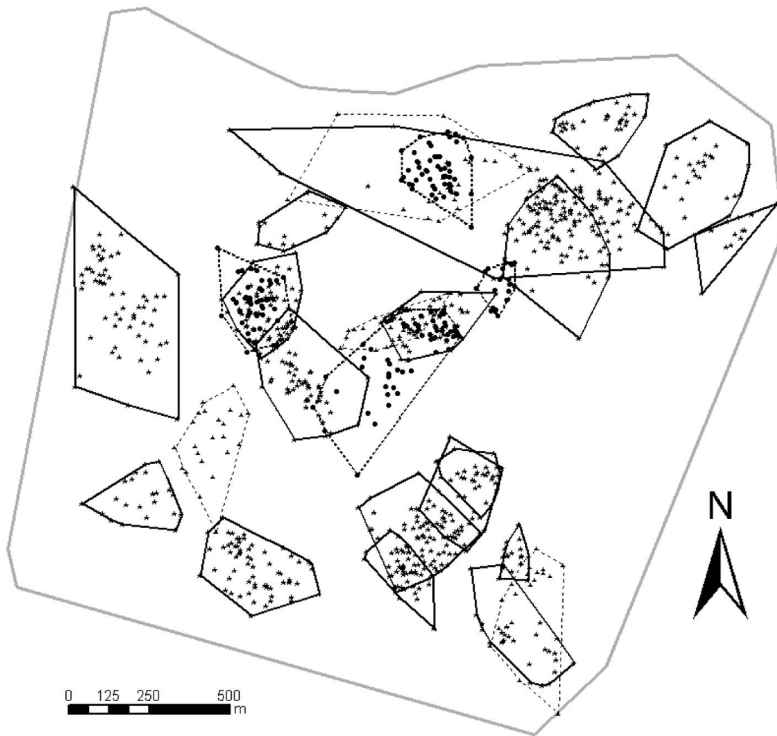


FIG. 1.—Radio-tracking locations and corresponding Minimum Convex Polygons (MCPs) of the radio-tagged Dupont's Larks monitored. Males: asterisks and solid lines; females: dots and thick broken lines; juveniles: triangles and thin broken lines. The grey line represents the limits of the study area.

[Localizaciones de las Alondras Ricotí radiomarcadas y controladas, junto con los Mínimos Polígonos Convexos (MPC) correspondientes. Machos: asteriscos y líneas continuas; hembras: círculos y líneas discontinuas gruesas; juveniles: triángulos y líneas discontinuas finas. La línea gris señala el límite de la zona de estudio.]

individuals, ranging from 1.0 to 37.3 ha, with a mean value of 8.08 ha (Table 1). No significant differences were found between the three age-sex classes considered (Table 1). Among adults, no difference was found either between the reproductive and post-reproductive home ranges (mean \pm SD = 6.80 \pm 8.76 ha and 5.13 \pm 2.72 ha, respectively; repeated measures ANOVA test; $F = 0.669$, $df = 1$, $P = 0.434$).

Variation between individuals was also important among IK80s (Fig. 2), with a minimum of 0.3 ha, a maximum of 7.9 ha, and an average of 3.6 ha. This variation was statistically significant between age-sex classes, the larger corresponding to juveniles, followed by adult males; the average size of adult female IK80s was less than half that of adult males, and one third that of juveniles (Table 1). As with MCPs, adult IK80s did not show significant differences between the reproductive and post-reproductive periods (mean \pm SD = 3.42 \pm 2.40 ha and 3.80 \pm 2.08 ha, respectively; repeated measures ANOVA test; $F = 0.070$, $df = 1$, $P = 0.797$).

Overlap between home ranges was in general small, both for MCPs and IK80s (Table 2), and even null in a relatively high percentage of

cases (45%). The value of Cole's Concordance Index between members of the same pair was around six times higher and showed significant differences in relation to overlap between neighbouring males (MCPs: $F = 14.453$, $df = 1$, $P = 0.003$; IK80: $F = 25.662$, $df = 1$, $P < 0.001$). During the post-reproductive period, the overlap between juveniles and either male or female neighbouring adults was small (Table 2), being null in 60% of cases for MCPs and 70% for IK80s.

The distances covered by individuals daily were relatively short and varied significantly among radio-tracked birds (range = 2-990 m, mean \pm SD = 118 \pm 90 m, $F = 3.604$, $df = 25$, $P < 0.001$). The average distance covered by each individual varied significantly between the sex-age classes considered (adult males: mean \pm SD = 111 \pm 26, $n = 18$; adult females: mean \pm SD = 101 \pm 20, $n = 4$; juveniles: mean \pm SD = 148 \pm 24, $n = 4$; $F = 4.279$, $df = 2$, $P = 0.026$), although variation was not significant between sexes either for the whole period of study ($F = 0.566$, $df = 1$, $P = 0.461$) or separately for each period (reproductive: $F = 3.480$, $df = 1$, $P = 0.082$; post-reproductive $F = 2.310$, $df = 1$, $P = 0.151$). On average, juveniles daily

TABLE 1

Mean (\pm SD of home range estimates (ha) of radio-tracked adult male, adult female and juvenile Dupont's larks, and results of the GLM analysis of the differences between those groups. The number of locations per individual was included as a covariate, and only those birds with more than 20 locations were considered. [*Media \pm DT de las áreas de campeo (ha) de machos adultos, hembras adultas y juveniles de Alondra Ricotí estimadas mediante Mínimo Polígono Convexo (MPC) y áreas kernel definidas por la isolínea de probabilidad del 80% (IK80), y resultados del GLM en el tamaño de las áreas de campeo entre dichos grupos de edad-sexo. El número de localizaciones por individuo se incluyó como covariante en los análisis, y sólo se consideraron individuos con más de 20 localizaciones*]

	Adult males [Machos adultos] $n = 18$	Adult females [Hembras adultas] $n = 4$	Juveniles [Jóvenes] $n = 4$	Total [Total] $n = 26$	F	P
MCP [MPC]	8.80 \pm 8.68	5.49 \pm 4.27	9.00 \pm 6.06	8.08 \pm 7.55	2.290	0.128
Covariate [Covariable]					12.071	0.003
IK80 % [IK80 %]	3.99 \pm 1.68	1.54 \pm 1.30	4.66 \pm 1.61	3.68 \pm 1.86	7.270	0.005
Covariate [Covariable]					4.560	0.046

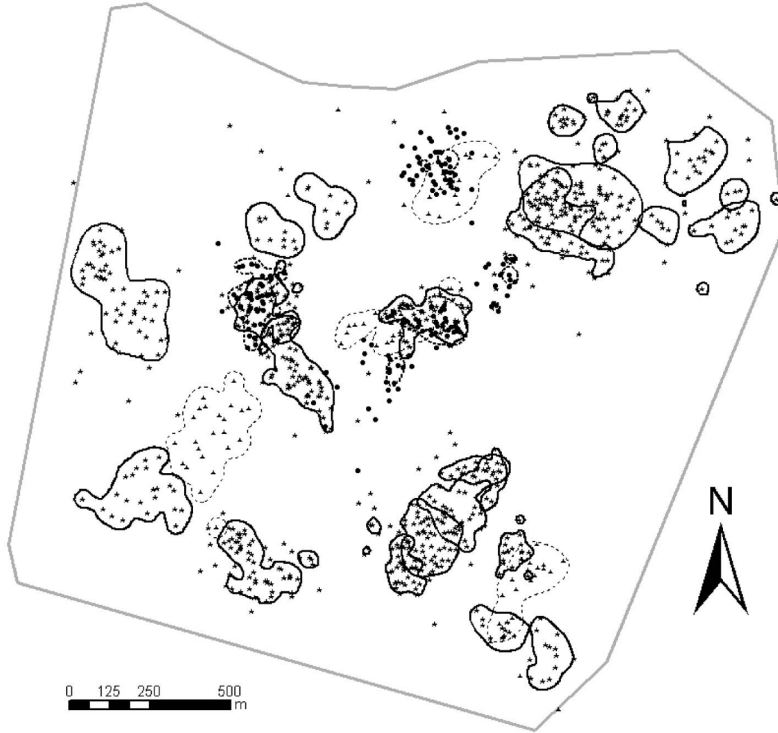


FIG. 2.—Radio-tracking locations and corresponding kernel areas defined by the 80% isopleths (IK80) of the radio-tagged Dupont's Larks monitored. Males: asterisks and solid lines; females: dots and thick broken lines; juveniles: triangles and thin broken lines.

[Localizaciones de las Alondras Ricotí radiomarcadas y controladas, junto con las correspondientes áreas kernel definidas por la isolénea de probabilidad del 80% (IK80). Machos: asteriscos y líneas continuas; hembras: círculos y líneas discontinuas gruesas; juveniles: triángulos y líneas discontinuas finas.]

TABLE 2

Mean \pm SD of the degree of home range overlap, measured by means of Cole's Index (%), between neighbouring males, pair members, periods (reproductive and post-reproductive) and age classes. Data from juveniles correspond only to the post-reproductive period.

[Media \pm DT del grado de solapamiento entre áreas de campeo de machos vecinos, miembros de una misma pareja reproductora, periodos reproductivo y postreproductivo de un mismo individuo, y clases de edad-sexo, medido con el índice de Cole. Los datos de juveniles corresponden sólo al periodo postreproductivo.]

Measure of home range [Medida del área de campeo]	Neighbouring males [Machos vecinos] n = 11	Pairs [Parejas] n = 2	Periods [Periodos]		Juveniles-adults [Jóvenes-adultos] n = 10
			Reproductive [Reproductivo] n = 6	Post-reproductive [Post-reproductivo] n = 2	
MCP [MPC]	9.14 \pm 13.30	54.34 \pm 29.50	51.80 \pm 18.00	32.74 \pm 12.22	8.02 \pm 19.21
IK80 [IK80]	9.00 \pm 14.18	62.54 \pm 8.16	48.54 \pm 5.60	35.74 \pm 29.46	5.80 \pm 9.43

moved longer distances than adults during the post reproductive period (adults: mean \pm SD = 110 \pm 29, n = 16; juveniles: mean \pm SD = 148 \pm 24, n = 4; F = 5.930, df = 1, P = 0.012). No differences were found in the distances covered by adults in the two periods (repeated measures ANOVA test; F = 0.177, df = 1, P = 0.683). The average distance covered by radio-tracked birds was closely correlated to their home range size (GLM using the number of locations as covariate; MCPs: F = 27.40, df = 1, P < 0.001; IK80s: F = 33.69, df = 1, P < 0.001).

Only two males (9.1% of the total sample) significantly changed the location of their home ranges during the reproductive period. One of them moved to a new site 700 m apart from the previous one where a second core area was generated in which the distance covered daily was significantly shorter (mean \pm SD = 272.0 \pm 255.1 m, n = 22 days, and 137.4 \pm 81.1 m, n = 65 days, respectively; F = 14.317, df = 1, P < 0.001). The second bird shifted to a new core area at 250 m from his previous site, performing similar displacements in both of them (mean \pm SD = 141.1 \pm 83.2 m, n = 13 days, and 153.3 \pm 110.4 m, n = 47 days, respectively; F = 0.137, df = 1, P < 0.713).

Habitat use and selection

Most radio-tacking locations of Dupont's Larks occurred in the short shrub dominated by *Genista pumila*, while pastures and tall shrubs dominated by *G. scorpius* were scarcely used. Cereal cultures were not used at all (Table 3). Use frequencies of vegetation units significantly differed from those obtained by random sampling (χ^2 = 106.9, df = 3, P < 0.001; Table 3). Selection turned out to be positive in the case of *G. pumila* shrubs (Ivlev's index = +0.17) and negative in the case of all other vegetation units (pastures = -0.31; *G. scorpius* shrubs = -0.46, cereal cultures = -1.00).

The use frequency of these vegetation units by adult Dupont's Larks did not varied either between sexes (global data, one way ANOVA, P > 0.05 for all vegetation units) or periods (paired t test, P > 0.1). The use of vegetation units by juvenile birds during the post-reproductive period differed from that of adults during the same period: juveniles used more the pastures than adults (F = 9.699, df = 1, P = 0.006, n = 5 juveniles and 16 adults, Table 3), and less *G. pumila* shrubs (F = 9.798, df = 1, P = 0.017). The tall shrub dominated by *G. scorpius* was equally used by both age classes (F = 0.503,

TABLE 3

Mean \pm SD of the frequency (%) of location of radio-tracked individuals grouped by age classes in each vegetation unit, for all birds during the entire period, and the corresponding values from points randomly sampled outside home ranges.

[Media \pm DT de la frecuencia porcentual de localizaciones de individuos radio-marcados, agrupados por clases de edad, en las distintas unidades de vegetación consideradas, así como del total de individuos durante el periodo de estudio y los puntos muestreados al azar.]

	<i>Genista pumila</i> shrub [Matorrales de <i>Genista pumila</i>]	Pastures [Pastizales]	<i>G. scorpius</i> shrub [Matorrales de <i>G. scorpius</i>]	Cereal cultures [Cultivos de cereal]	n
Adults post-reproductive [Adultos post-reproductor]	83.8 \pm 14.5	12.3 \pm 12.3	3.9 \pm 6.5	0.0	16
Juveniles post-reproductor [Jóvenes post-reproductor]	63.5 \pm 17.7	34.7 \pm 19.3	1.7 \pm 3.9	0.0	5
Total average for the entire period [Media total para todo el periodo]	82.7 \pm 15.6	15.1 \pm 15.0	2.2 \pm 3.1	0.0	32
Random sample [Muestreo al azar]	58.0	29.0	6.0	7.0	100



$df = 1$, $P = 0.487$). As for adults, frequencies of use of the vegetation units by juveniles significantly differed from those sampled at random ($X^2 = 47.0$, $df = 3$, $P < 0.001$; Table 3).

Ground and 20 cm height cover of pillow-shaped short shrubs were significantly higher within home ranges than outside them, while the cover of tall shrubs for the same heights behaved inversely (Table 4). None of the remaining vegetation structure variables showed significant differences. The adjusted logistic regression model including all variables was statistically significant ($G^2 = 32.23$, $df = 12$, $P = 0.001$, Cox & Snell $R^2 = 62.3$), correctly classifying 87 % of all cases (94.1 % within home ranges, 81.4 % outside them). The simplified logistic regression model (Table 5) included only one variable: ground cover of short shrubs. This model was also statistically significant ($G^2 = 6.33$, $df = 1$, $P = 0.012$, Cox & Snell $R^2 = 17.5$) and correctly classified 76.0% of all cases (75.0% within ranges, 75.8% outsi-

de them). The jackknife procedure ($n = 17$) correctly classified 75.8% of all cases (75.0% within ranges, 76.5% outside them).

DISCUSSION

The results here presented can be considered an important and novel contribution to the knowledge of Dupont's Lark general biology. Moreover, they contribute notably to the species' conservation by examining three critical aspects: (1) its use of space, revealing a strong territorial behaviour, (2) its strict habitat selection, and (3) the existing differences between adults and juveniles in relation with the first two issues.

Home range

Most lark species show a more or less marked territorial behaviour, whose intensity ap-

TABLE 4

Mean \pm SD of percentage cover of the different vegetation types considered at ground level and at 20 cm height, and results of the ANOVA analysing potential differences in those variables within and outside individual home ranges. Only significant results ($P < 0.05$) are included.

[Media \pm DT de los porcentajes de cobertura de los diferentes tipos de vegetación a nivel de suelo y a 20 cm de altura, así como resultados del ANOVA que analiza las diferencias en dichas variables dentro y fuera de las áreas de campeo individuales. Sólo se muestran los resultados significativos ($P < 0.05$).]

	Within home ranges [Dentro de las áreas de campeo]	Outside home ranges [Fuera de las áreas de campeo]	SS [SC]	df [g]	F	P
Pillow-shaped shrubs at ground level [Matorrales almohadillados a la altura del suelo]	19.0 \pm 10.8	7.9 \pm 13.2	1017.299	1	6.955	0.013
Tall shrubs at ground level [Matorrales de altura media a la altura del suelo]	1.0 \pm 2.3	8.2 \pm 13.6	434.518	1	4.430	0.044
Pillow-shaped shrubs at 20 cm height [Matorrales almohadillados a 20 cm de altura]	4.7 \pm 5.4	1.1 \pm 2.2	108.640	1	6.654	0.015
Tall shrubs at 20 cm height [Matorrales de altura media a 20 cm de altura]	0.4 \pm 0.8	5.1 \pm 9.0	187.701	1	4.421	0.044

TABLE 5

Results of the reduced binary logistic regression model predicting the presence of Dupont's Lark home ranges after vegetation structure variables. Model coefficients $\pm SE$ and the corresponding Wald's significance tests are included.

[Resultados del modelo reducido de regresión logística binaria que predice la presencia de territorios de *Alondra Ricotí* en función de la estructura de la vegetación. Se incluyen los coeficientes del modelo $\pm ET$ y las correspondientes pruebas de significación de Wald.]

	Coefficient [Coeficiente]	Wald [Wald]	df [gl]	P
Cover of pillow-shaped shrubs at ground level [Cobertura de <i>Matorrales almohadillados a la altura del suelo</i>]	0.073 \pm 0.031	5.464	1	0.019
Constant [Constante]	-1.017 \pm 0.556	3.352	1	0.067

pears to be correlated with diet composition and seems to be higher in insectivorous species, which tend to remain territorial over the entire annual cycle and show a less aggregated pattern of spatial distribution of their reproductive territories (Willoughby, 1971; Dean & Hockey, 1989). The Dupont's Lark, a markedly insectivorous species as revealed by its bill's shape and dimensions (Cramp, 1988), seems to follow that pattern. On one hand, the overlap between ranges found in this study is small, not only for MCPs, but also for IK80s which better approach real territories. This is especially true when the overlap between ranges of neighbouring males is compared with that between ranges of members of the same reproductive pair. On the other hand, the high overlap between one individual's two consecutive ranges (reproductive and post-reproductive), which is of the same order of magnitude as that found between members of the same pair, suggests a continuity of territories over time, at least during the entire period considered in this study. Additionally, individual home range areas measured using MCPs are around two-fold those estimated by means of IK80s, for all sex and age classes considered, which points out to the existence of highly used core areas representative of real territories and much more extended total home ranges including points visited only occasionally or accidentally. Nevertheless, males appear to make incursions into the core areas of neighbouring males and total home ranges with a

similar frequency, as suggested by the similar values of the corresponding overlap indices. This incursion behaviour has been described in other territorial passerines (Naguib *et al.*, 2001), although the different methodologies used make results hardly comparable (Mills-paugh *et al.*, 2004).

Female spatial behaviour appears to be similar to that of most males. Although these results should be taken with caution due to small sample size, the fact that females show total home ranges and core areas similar in size and time continuity to those of their reproductive partners suggests the existence of spatial fidelity to reproductive territories, not only among males, but also among females, which can be interpreted as female territorial behaviour.

In a context of generalised territorial stability, the existence of two males that completely changed their home ranges makes this behaviour especially remarkable. For one of the males, the mean distance between consecutive locations was greater before shifting home range, while no significant difference was found for the other male. In both cases, the cover of low pillow-shaped shrub seemed smaller in their first home ranges. These data suggest that those males could initially have marginal territories or be unpaired, and therefore that a non reproductive fraction of the adult population could exist. This fact is consistent with the clearly male-biased sex ratio found in some lark species (De Juana *et al.*,



2004), where the presence of non-reproductive adults has been reported (Guerrieri *et al.*, 1997; Donald, 2004).

Garza *et al.* (2003b) have suggested that the spatial distribution of Dupont's Lark home ranges in a nearby study area (Barahona plateau, central Spain) was aggregated. These authors, however, did not establish whether that distribution pattern was a consequence of a selective use of the different vegetation formations or the result of a potential colonial or semi-colonial behaviour. In our study area, the spatial distribution of both MCPs and IK80s, was also aggregated (Fig. 1). Nevertheless, these habitat selection results suggest that this pattern is a consequence of the spatial heterogeneity of preferred vegetation (see below) rather than result of gregarious behaviour.

Juvenile dispersal during the first month after fledging seems to occur within parental territories, as suggested by the only radio-tagged young tracked for at least one month, which seems to be the dominant pattern among lark species (De Juana *et al.*, 2004). However, the young seem to later establish their own territories and, although the origin of tagged juveniles was unknown, it is reasonable to assume that they came from within the population studied (see, for example, Rivera *et al.*, 1998). In this line of evidence, radio-tracking in late September showed that some juveniles still maintained home ranges located in the same area as those held late July.

Habitat use and selection

At a landscape scale the species makes an exclusive use of short shrubs dominated by *Genista pumila*. In fact, 86% of locations occurred in this vegetation unit, slightly increasing to 88% when only adults are considered. These values are much higher than those sampled at random out of the known home ranges. Since radio-tracking provides reliable locations and does not artificially modify the birds' real position, we can conclude that *G. pumila* shrub is nearly the only habitat used by Dupont's Larks in the study area. As consequence, that vegetation unit was the only one positively selected by the species. It is thus clear that *G. pumila* shrubs should be regarded as the priority habitat for the Dupont's Lark in the area studied, at

least during the period considered. This conclusion could be extended to other areas with presence of pillow-shaped camephyte formations on flat relief, which hold the great majority of the European populations of the species. This is especially true when one considers that the Layna plateau, where the study area is located, houses one of the largest known populations of Dupont's Lark (Garza & Suárez, 1990). Nevertheless, Garza & Suárez (1990) also showed that, at a peninsular scale, the species uses a considerable range of short to medium height vegetation formations. In this context, the avoidance of pastures and cultures during the breeding and postbreeding periods seems to be a clear pattern, easier to extrapolate to other geographical regions.

The results of habitat structure selection analysis are consistent with those obtained at the landscape scale. Cover of pillow-shaped, low shrub was significantly higher within ranges, while tall shrub (40-60 cm high) cover turned out to be significantly lower. Contrarily, vegetation height, which is usually determinant in habitat selection by other lark species (De Juana *et al.*, 2004; Donald, 2004), and bare ground cover, which is normally relevant in cursor species, were not significant. This is probably due to the fact that vegetation height in the study area is predominantly low, while bare ground percentage is generally high. In other study areas with greater vegetation cover and height, these factors could be determinant (Garza & Suárez, 1990). The presence of home ranges is correctly predicted both by the adjusted and simplified binary regression models based on vegetation structure, with ground cover of short shrubs as the main predictor variable. Although this model was not validated using an independent set of data, the results of the jackknifing re-estimation, the high percentage of variance explained, and the consistency with the landscape results, indicates that this is a robust analysis.

Comparison of adult vs. juvenile birds

The results of space use and habitat selection by juvenile Dupont's Larks presented here are a novel contribution to the knowledge on the species' general biology and point to what may be the pattern in other sedentary, mainly insecti-

vorous larks. Young Dupont's Larks seem to disperse rather short distances, although they move longer distances between consecutive days than adults, holding also larger home ranges. Additionally, they make a significantly greater use of those vegetation units avoided by adults, such as the thyme and grass dominated pastures. This evidence indicates that juveniles move to marginal habitats where they can defend their own territories which tend to be larger than those of adults due to their comparatively lower quality.

Conservation implications

The results given here may have important consequences for the conservation of Dupont's Lark. On one hand, the low population density found in one of the best known areas for the species in Iberia supports the conclusion by Garza *et al.* (2003a) and Tella *et al.* (2005) that the former estimate of 13000 birds (Garza & Suárez, 1990) largely overestimated the real population size which is now considered to be 1300-1900 reproductive pairs (Garza *et al.*, 2003a; Tella *et al.*, 2005). Such a small population size and the generalised decline in the Ebro valley (Tella *et al.*, 2005), Andalucía and Castilla-La Mancha (Garza *et al.*, 2004), makes the Dupont's Lark one of the most threatened passerines in Europe. Additionally, the close dependence of territories, at least during the reproductive and post-reproductive periods, on vegetation structure makes the species highly vulnerable to any human-use changes modifying such structure, which could seriously menace its survival in Europe. In fact, most Dupont's Lark populations in Spain are in unprotected areas where drastic changes in land-use (*e.g.*, afforestation, ploughing of natural vegetation or wind farms) have occurred or are likely to do so. A protection plan for this lark which includes habitat management and conservation measures are therefore urgently needed, since the expected changes promoted by the Common Agriculture Policy may profoundly affect the species' habitat structure and composition, especially with regard to afforestation and sheep rearing.

On the other hand, the fact that two adult birds changed their territories during the reproductive period, along with the establishment of

juveniles in marginal habitats, suggests population saturation, at least for reproductive males. Such saturation could be due to two different causes: (1) a high breeding success combined with a lack of empty areas suitable for reproduction, and (2) the loss of nearby habitats suitable for the species as a consequence of different factors, ranging from changes in vegetation structure to drastic land-use modifications. Current data are still insufficient to distinguish between these two possibilities, although nest predation rates are known to be high (over 80%, Herranz *et al.*, 1994), suggesting a low breeding success. This population saturation should not be extrapolated to other Iberian areas (*e.g.*, Cabo de Gata, Almería), where a strong population regression of the species has been detected and Dupont's Larks have disappeared from certain sites that have remained fairly unchanged in terms of habitat composition and structure. Finally, it is important to remind that any conservation plan for the species should regard not only shrub areas selected by adult birds, but also the marginal habitats occupied by juveniles during the post-reproductive period, thus increasing their survival probabilities (see a similar case in Rivera *et al.*, 1999).

As pointed out by Garza *et al.* (2003a, 2004) and Tella *et al.* (2005), the status of Dupont's Lark in Europe may be critical in a near future. The results presented here can contribute to a correct management of Dupont's Lark populations and their habitat, which should be urgently accomplished, given their small size and current threats.

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