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SEASONAL AND INTERANNUAL VARIABILITY IN LAYING DATE, CLUTCH SIZE, EGG VOLUME AND HATCHING ASYNCHRONY OF FOUR LARK SPECIES IN MEDITERRANEAN SPAIN

Francisco SUÁREZ* [1], Jesús HERRANZ*, Miguel YANES*, Ana M. SÁNCHEZ**, Jesús T. GARCÍA* & Juan MANRIQUE***

SUMMARY.—*Seasonal and interannual variability in laying date, clutch size, egg volume and hatching asynchrony of four lark species in Mediterranean Spain*

Aims: To describe the variation in laying date, clutch size, egg volume and hatching asynchrony of four lark species (Skylark *Alauda arvensis*, Short-toed Lark *Calandrella brachydactyla*, Thekla Lark *Galerida theklae* and Lesser Short-toed Lark *Calandrella rufescens*) and at two different time scales: between years (large-scale variation), and within seasons (short-scale variation).

Location: Two climatically contrasting Mediterranean areas: Layna, located in the centre of the Iberian Peninsula and with a continental Mediterranean climate, and Cabo de Gata, located in the south-western Iberian Peninsula and with a semi-arid climate. Breeding Skylarks and Short-toed Larks occur in Layna, whereas breeding Thekla Larks and Lesser Short-toed Larks occur in Cabo de Gata.

Methods: During the study period between 1991-95 in Layna and between 1991-94 and 1996-97 in Cabo de Gata, searches were carried out for nests of the four species and laying date, measured egg-length and width, and hatching asynchrony recorded. Overall, 118 nests of Skylarks, 165 of Short-toed Larks, 334 of Thekla Larks and 259 of Lesser Short-toed Larks were studied. Between-year variations in breeding parameters were analysed with General Linear Models (GLM's). To investigate the presence or absence of asynchronous hatching in relation to year, laying date and clutch size, bi and multinomial logistic regression models were fitted.

Results: The breeding season in Cabo de Gata started earlier (60 days before) and was longer (15-25 days) than in Layna. The frequency distribution of laying dates was unimodal in all cases, with the exception of Lesser Short-toed Larks. Annual mean laying dates did not vary significantly among years in Layna, but the opposite was found in Cabo de Gata. However, mean laying dates of clutches from the 25 percentile show large between-year variations in all cases. Regarding the among-year variation in clutch size, all species studied except the Thekla Lark show a high degree of constancy in this parameter. The seasonal pattern of clutch size variation was similar in all species studied, with maximum clutch sizes on intermediate dates, and smaller early and late clutches. Mean clutch volume appears relatively constant in relation to annual variation in three of the species studied. Nevertheless, in Thekla Larks a significant inter-annual variation was observed in this breeding parameter. Finally, the incidence and/or the extent of hatching asynchrony are similar in all the species studied, increasing with clutch size and laying date.

Conclusions: This study shows that the four lark species have different reproductive strategies which cannot be explained solely in terms of their body mass or biogeographical affinities. More studies are needed to evaluate how these factors could affect breeding success in larks in Mediterranean habitats and the implications on demography and population dynamics.

Key words: *Alauda arvensis*, *Calandrella brachydactyla*, *Galerida theklae*, *Calandrella rufescens*, larks, breeding period, mediterranean habitats, semi-arid climate, Iberian Peninsula.

RESUMEN.—*Variación estacional e interanual en la reproducción de cuatro alondras en España mediterránea: fecha y tamaño de puesta, tamaño de los huevos y asincronía de puesta*

Objetivos: Describir la variación en la fecha de puesta, tamaño de puesta, volumen de los huevos y asincronía de eclosión para cuatro especies de alaúdidos (Alondra Común *Alauda arvensis*, Terrera Común *Calandrella brachydactyla*, Cogujada Montesina *Galerida theklae* y Terrera Marismeña *Calandrella rufescens*) a dos escalas temporales: entre años, y dentro de cada temporada de reproducción.

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

** Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/ Tulipán s/n. E-28933 Móstoles, Madrid, Spain.

*** C/ Zaragoza 12, E-04001 Almería, Spain.

[1] Corresponding author: E-mail: francisco.suarez@uam.es

Localidades: Dos zonas de clima contrastado: Layna (Soria) en el centro de la península Ibérica y con un clima mediterráneo continental, y Cabo de Gata (Almería), en el sureste de la península y con un clima semiárido. En la primera zona se reproducen la Alondra Común y la Terrera Común, mientras que en la segunda zona se reproducen la Cogujada Montesina y la Terrera Marismeña.
Métodos: Se han prospectado ambas zonas y buscado los nidos de las cuatro especies durante los años 1991 a 1995 en Layna y durante 1991-94 y 1996-97 en Cabo de Gata. Se ha establecido la fecha de puesta, medido la anchura y longitud de los huevos y anotado si hubo eclosiones asincrónicas. En total se han estudiado 118 nidos de Alondra Común, 165 de Terrera Común, 334 de Cogujada Montesina y 259 de Terrera Marismeña. La variación interanual y estacional en los parámetros reproductivos se ha analizado mediante modelos lineales generales (GLM). Para investigar sobre la presencia o ausencia de eclosiones asincrónicas dependiendo del año, fecha de puesta y tamaño de puesta se han utilizado regresiones logísticas bi y multinomiales
Resultados: La temporada reproductiva en Cabo de Gata empezó primero (60 días antes) y duró más (15-25 días) que en Layna. La distribución de frecuencias de la fecha de puesta de todas las especies resultó unimodal, excepto en el caso de la Terrera Marismeña (bimodal).La media anual de la fecha de puesta no se relacionó de forma significativa con el año en Layna, pero sí en Cabo de Gata. No obstante, la fecha media de las puestas del percentil 25 mostró una gran variación con el año en todos los casos. Respecto a la variación interanual del tamaño de las puestas, todas las especies, excepto la Cogujada montesina, mostraron una escasa variación anual. El patrón temporal en el tamaño de puesta resultó similar en las cuatro especies, siendo las mayores puestas las intermedias, mientras que las puestas tempranas y tardías resultaron ser más pequeñas. El volumen medio de la puesta mostró escasa variación interanual en tres de las cuatro especies estudiadas. Sin embargo en la Cogujada Montesina observamos una variación interanual significativa. Por último, la frecuencia de nidos de eclosión asincrónica, así como el grado de asincronía fue similar en todas las especies estudiadas, aumentando éste con el tamaño de puesta y con la fecha de puesta.
Conclusiones: Este estudio muestra que las cuatro especies presentan diferentes estrategias de reproducción que no se deben exclusivamente al tamaño corporal o a aspectos biogeográficos. Son necesarios estudios más específicos para evaluar cómo dichos factores pueden influir sobre el éxito reproductor de estas especies en hábitat mediterráneos y cuáles son las implicaciones sobre la demografía y la dinámica poblacional de estas especies.

Palabras clave: *Alauda arvensis*, *Calandrella brachydactyla*, *Galerida theklae, Calandrella rufescens*, Alaúdidos, época de reproducción, hábitat mediterráneo, clima semiárido, península Ibérica.

INTRODUCTION

Most studies on reproduction in passerines have focused on species subject to low rates of predation, generally cavity-nesters (Martin, 1992), which allow working with large data sets. Accordingly, studies of species with high rates of nest predation are relatively scarce. Such studies are limited by the difficulty to obtain large data sets in order to establish, for example, evolutionary tendencies (Møller & Jennions, 2002). Because of the great difficulty of studying reproduction of these species, several aspects of the breeding biology of some groups of birds have received little attention, resulting in scarce information about these species. For example, larks are a ground nesting family with high levels of nest predation (De Juana *et al.*, 2004; Donald, 2004), and for which studies of reproduction involving large data samples are scarce. This also applies for temperate species, despite the interest which has recently been aroused by the drastic declines experienced by many lark species in Europe (Donald *et al.*, 2001; De Juana, 2004). This decline seems related to a low reproductive success, at least in Skylarks *Alauda arvensis* (Donald, 2004).

Long-term studies of lark reproduction in the Mediterranean region are practically non-existent (see Cramp, 1988). Although some aspects have been studied in certain Mediterranean species, mainly Dupont's Lark *Chersophilus duponti,* Thekla Lark *Galerida theklae* and Lesser Short-toed Lark *Calandrella rufescens* (*e.g.*, Herranz *et al.*, 1994; Yanes, 2000), the general knowledge about these species remains poor. The absence of knowledge is specially marked in the case of reproduction of Eurosiberian larks (*e.g.*, Skylark) within the Mediterranean region, for which the information is necessary to establish biogeographical patterns at a European scale (Barbier, 2001).

In the Iberian Peninsula, located in the southwestern part of the Palearctic, the climate varies according to region from the wetter and temperate conditions typical of the Eurosiberian region of central Europe, to the xeric and hot conditions characteristic of the southernmost areas of the Mediterranean region. This geographic scenario provides an ideal framework to study the reproduction of species in different climatic conditions and the extent to which different species respond to variation in the seasonality of different habitats.

The aim of this study is to describe the variation in some reproductive parameters (laying date, clutch size, egg volume and hatching asynchrony) of four lark species in two areas in Spain (central and south-western Spain) and at two different time scales: between years (large-scale variation), and within seasons (short-scale variation). As far as is known, there are no multi-annual studies on this topic in Spain.

MATERIAL AND METHODS

Study areas

The study was conducted in two different locations in Spain. The first site was in central Spain, in Layna, Soria province (41°05' N, 01°50' W), at an altitude of 1,200 m a.s.l. The climate is continental Mediterranean (Peinado & Rivas Martínez, 1987), with an annual rainfall of 500 mm and a mean annual temperature of 10.2 °C. The landscape is flat or gently undulating and the vegetation is a shrub-steppe dominated by *Genista pumila*, *G. scorpius*, *Thymus* spp., *Poa* spp. and *Stipa* spp. The study in Layna took place over five consecutive years (1991-95). The second site was in the south-western part of the Iberian peninsula, at Cabo de Gata, Almería province (36°50' N, 02°25' W), at an altitude of 50 m a.s.l. The climate is semi-arid Mediterranean, with an annual rainfall of 220 mm and a mean annual temperature of 18.0 °C. This xeric region is characterised by high spring and summer temperatures and a marked summer drought (Mooney, 1981). The landscape is also flat and the vegetation a shrub-steppe dominated by *Stipa tenacissima*, *Fagonia cretica*, *Thymus* spp. and *Crucianella maritima*. At this site, the study was conducted over a total of six years, although these were not all consecutive (1991-94 and 1996-97). A more detailed description of the vegetation and bird communities is given by Yanes & Suárez (1996a) and Tellería *et al.* (1988).

Study species

All of the four larks studied are multibrooded (at least 2-3 broods/year; *own data*), ground nesting species. Two of them, the Thekla and Lesser Short-toed Larks, have a typically Mediterranean distribution. The other two, the Skylark and the Short-toed Lark *Calandrella brachydactyla* have a wider distribution extending into temperate areas of Europe. The four species differ in body size, the Skylark and the Thekla Lark being considerably larger (females, 33 g and 36 g, respectively) than the Short-toed and Lesser Short-toed Larks (21 g and 19 g, respectively) (Suárez *et al.*, 2005; Herranz *et al.*, 2005). Furthermore, the Skylark and the Thekla Lark are closely-related species (Sibley & Ahlquist, 1990), while the other two species are congeneric. Nest predation rates were high in both areas (between 70 and 90%, Suárez *et al.*, 1993; Yanes & Suárez, 1996a).

Reproductive data

Nests of the four species were searched for throughout the breeding season at each study site. Search effort was similar among years and study sites. Nests were found both by daily surveys and by observing adult behaviour during the nestling period (March-June in Cabo de Gata; May-July in Layna). The nests were visited daily to determine reproductive parameters, including laying date and clutch size, hatching success, and brood size. Laying date was estimated directly for some nests which were visited before laying had finished. Otherwise, first egg date was determined by backdating from hatching date, which was known directly from visits at hatching time in some nests, or estimated from nestlings´ body growth curves in other cases (*e.g.*, Shkedy & Safriel, 1992). A 12-day incubation period and a 1 egg per day laying rate were assumed (Cramp, 1988). Laying date varied frequently between years. Thus, relative laying dates were calculated (as the difference in days to the first laying date recorded for each year) to standardise data from different years and areas. The mean laying dates of the 25 percentile was also used, i.e. the mean date for the first 25% of the clutches for each species and year. This measure allowed a partial control for biases due to the second clutches.

Clutch size was considered as being the maximum number of eggs found in the nest. As partial losses of chicks due to starvation are very rare in these lark species (*e.g.*, Yanes & Suárez, 1996b; Yanes, 2000), for nests found during brooding a minimum clutch size equal to the maximum number of chicks recorded was assumed. To analyse the temporal pattern of clutch size in each breeding season clutches of each species were classed in three categories in relation to the first laying date recorded each year (early clutches: those belonging to the lower 25 percentile; intermediate clutches: the 50% of clutches excluding the lower and upper 25 percentiles; late clutches: those belonging to the upper 25 percentile). Overall, clutch size was recorded for 114 Skylark nests and 159 Short-toed Lark nests in Layna and for 334 Thekla Lark nests and 249 Lesser Short-toed Lark nests in Cabo de Gata.

Egg-length and width were measured with a digital calliper to the nearest 0.1 mm. Egg volume was calculated from Hoyt's (1979) equation: volume (mm^3) = 0.51 × length nmm) × width^2. A total of 275 eggs from 81 Skylark nests, 356 eggs from 106 Short-toed Lark nests, 968 eggs from 282 Thekla Lark nests and 695 eggs from 213 Lesser Short-toed Lark nests were included in the analyses for this paper, using a mean egg volume of clutches as an unit.

For the study of hatching asynchrony, eggs were tagged and small chicks were marked at hatching with indelible ink and weigthed daily using a 0.01 g precision digital balance. Hatching asynchrony was assumed when: 1) there wasdirect evidence either of a female incubating before the clutch was complete or of one or more eggs hatching at least one day after the others (92.3% of the nests), and 2) if one or more chicks was one or two days behind in mass compared to the rest of the brood (for nests that were found with nestlings less than 4-days old, 7.7% of the nests). In all species, the high growth rate of the nestlings causes that, during this age, the intrabrood variation of chicks´ weights, is lower than the daily variation. Nests found when containing nestlings older than 4-days were excluded from the analysis of hatching asynchrony. Consideration was made of 45 Skylark nests for which it was uncertain whether or not asynchrony had occurred, as well as 92 Short-toed Lark nests, 152 Thekla Lark nests and 98 Lesser Short-toed Lark nests.

Data analysis

Between-year variations in clutch size and egg volumes were analysed with General Linear Models (GLM's), using year as a random factor and laying date as continuous variable. The quadratic term of laying date was also included in the analysis since a quadratic pattern is expected in multibrooded species (Crick *et al.*, 1993; Soler *et al.*, 1995; Gil-Delgado *et al.*, 2005). For all species, extreme clutch categories with sample sizes smaller than five were combined with adjacent ones. Second order interactions were rejected when they were not significant. Paired Student's t-tests were used to compare within clutches the volume of the first and last eggs with the remainder.

Binomial or multinomial logistic regression models were fitted to investigate the presence or absence of asynchronous hatching in relation to year, laying date and clutch size, considering: 1) presence or absence of asynchronous nests, and 2) the extent of asynchrony (three classes: 0, 1, or 2 days). Clutch size was included in the model as a fixed factor, laying date as a continuous variable, and year as a random factor (to control for annual differences due to variables other breeding parameters). All means are expressed ± S.D. Analyses were made with SPSS statistical package (SPSS Inc., 2001).

RESULTS

Laying date

First laying date of each year and mean laying dates for the lower 25 percentile were not significantly correlated with the number of nests for any species (Pearson correlation test, $P > 0.1$). The frequency distribution of laying dates was unimodal in all cases, with the exception of the Lesser Short-toed Lark (Fig. 1). Overall, females of Thekla and Lesser Short-toed Larks start to lay in southern Spain (Cabo de Gata) 60 days before Skylark and Short-toed Lark females in central Spain (Layna, see

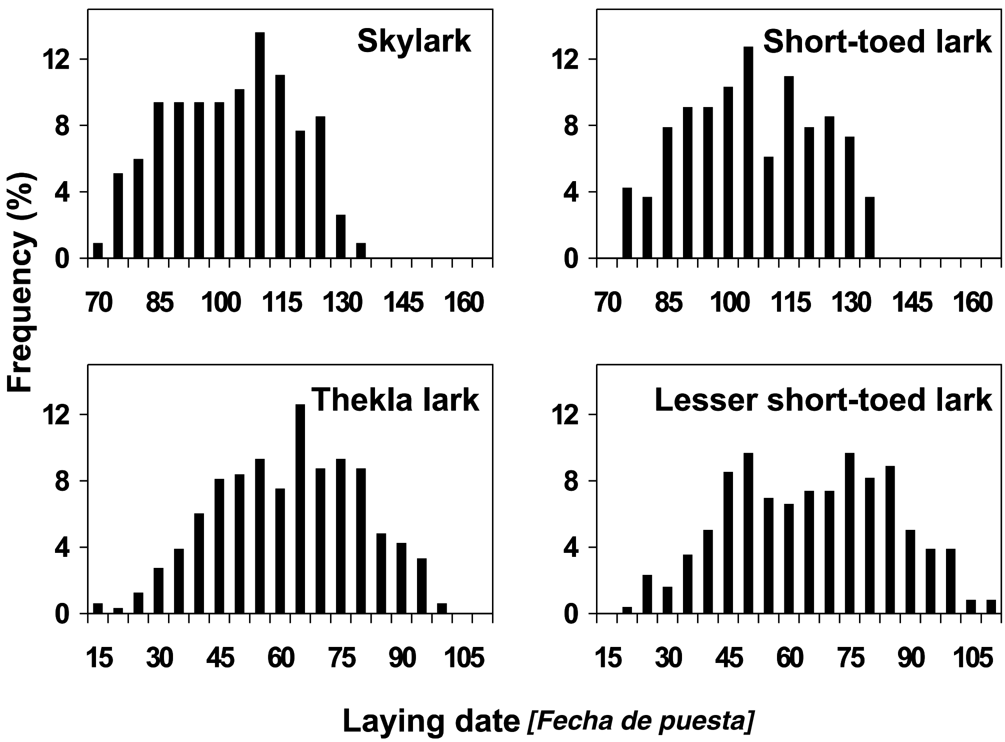

FIG. 1.—Frequency distributions of laying dates in the four species (day 1 = March 1st).
[Distribución de frecuencias de las fechas de puesta en las cuatro especies estudiadas (día 1 = 1 de Marzo).]

Fig. 1), the breeding season being 15-25 days longer in Cabo de Gata than in Layna (Fig. 1). The annual dates of first clutches and those of the lower 25 percentile for the two species at Layna were approximately 40-45 days later than for the two species at Cabo de Gata in the four shared years of the study periods (Table 1). The mean annual date of first clutches of each species-pair was: May 15 ± 5 days at Layna against March 27 ± 8 days at Cabo de Gata. The mean date of the lower 25 percentile of each species-pair was May 27 ± 5 days at Layna against April 17 ± 9 days at Cabo de Gata. The dates of first clutches did not differ between the two species at Layna nor between those at Cabo de Gata (Student's t-test for paired samples, $P > 0.05$ in all cases). At Layna the mean laying dates of the lower 25 percentile of clutches for Skylarks were not significantly correlated with those for Short-toed Larks ($r = 0.49$, $P = 0.402$, $n = 5$). However, at Cabo de Gata they were significantly correlated between Thekla and Lesser Short-toed Larks ($r = 0.92$, $P = 0.009$, $n = 6$).

Annual laying dates did not vary significantly among years for both species at Layna (GLM; year: $F_{4,273} = 0.27$, $P = 0.89$), and no significant differences between species were found (species: $F_{1,273} = 1.36$, $P = 0.24$). In the southern study area, Thekla and Lesser Short-toed Larks did not differ significantly with respect to laying date (species: $F_{1,581} = 1.08$; $P = 0.30$), but significant between-year differences were found for both species (year: $F_{5,581} = 15.96$, $P < 0.001$; interaction year x species: $F_{5,581} = 0.87$, $P = 0.50$). However, when only the early clutches were taken into account (mean laying date of clutches from lower 25 percentile), there was large between-year variation in all cases, both in Layna (year: $F_{4,118} = 7.91$, $P < 0.001$; interaction year x species: $F_{4,118} = 2.65$, $P = 0.036$), as well as in Cabo de Gata (year: $F_{5,239} = 51.46$, $P < 0.001$; interaction year x species: $F_{5,239} = 8.85$, $P < 0.001$).

TABLE 1

Annual dates of the first and last clutches laid and of the lower 25 percentile of all clutches. All data expressed as means ± *SD*.
[Datos anuales de fecha de la primera y última puesta en cada especie, así como las fechas medias de las puestas correspondientes al percentil 25. Los datos muestran medias ± DT.*]*

Species *[Especie]*	Variable	Year *[Año]*							Mean ± *SD* *[Media* ± DT*]*
		1991	1992	1993	1994	1995	1996	1997	
Skylark *[Alondra Común]*	Date of first clutch *[Fecha de la primera puesta]*	79	69	78	73	76	—	—	75.0 ± 4.1
	25th percentile *[Percentil 25]*	87	78	95	91,5	86	—	—	87.5 ± 6.4
	Date of last clutch *[Fecha de la última puesta]*	131	134	129	113	123	—	—	126.0 ± 8.3
	n	38	31	21	13	15	—	—	—
Short-toed Lark *[Terrera Común]*	Date of first clutch	83	72	71	85	74	—	—	77.0 ± 6.5
	25th percentile	90	95	91	82	85	—	—	88.8 ± 4.9
	Date of last clutch	131	134	131	115	130	—	—	128.2 ± 7.5
	n	30	53	32	17	33	—	—	—
Thekla Lark *[Cogujada Montesina]*	Date of first clutch	38	22	13	26	—	27	16	23.7 ± 8.9
	25th percentile	63	51	45	44	—	48	38	48.3 ± 8.6
	Date of last clutch	94	96	99	89	—	92	80	91.7 ± 6.7
	n	40	84	70	61	—	38	40	—
Lesser Short-toed Lark *[Terrera Marismeña]*	Date of first clutch	43	40	21	31	—	24	20	29.8 ± 9.9
	25th percentile	62	52	37	45	—	44	38	46.2 ± 9.5
	Date of last clutch	108	102	95	92	—	93	83	95.5 ± 8.6
	n	51	81	48	22	—	31	61	—

Clutch size

Clutch size in the four species ranged from two to five eggs (Table 2). The modal clutch size in all cases was four, except for Lesser Short-toed Larks (3 eggs). Clutches were higher in Layna than in Cabo de Gata (GLM nested design; between-subject effects: $F_{1,855} = 10.03$, $P = 0.001$), and there were significant differences among species at the same site (within-subject effects: $F_{2,855} = 19.85$, $P < 0.001$). Clutch size was larger at each site for the larger member of the pair (Table 2). When species of similar size were compared, the frequencies differed significantly between the two largest species (Skylark *vs.* Thekla Lark, $\chi^2 = 9.608$, $df = 3$, $P = 0.022$; see Table 2), but not between the two smallest species (Short-toed *vs.* Lesser Short-toed Larks, $\chi^2 = 6.240$, $df = 3$, $P = 0.101$).

Clutch size did not vary significantly in relation to year and mean laying date in Skylarks (GLM, year: $F_{4,108} = 1.68$, $P = 0.16$; laying date: $F_{1,108} = 1.71$, $P = 0.19$), Short-toed Larks (year: $F_{4,153} = 0.44$, $P = 0.77$; laying date: $F_{1,153} = 1.42$, $P = 0.23$) and Lesser Short-toed Larks (year: $F_{5,243} = 1.58$, $P = 0.17$; laying date: $F_{1,243} = 0.99$, $P = 0.32$). The clutch size of Thekla Larks varied significantly in relation to year (being considerably smaller in 1991, see Fig. 2) but not to laying date (year: $F_{5,318} = 3.10$, P = 0.009; laying date: $F_{1,318} = 0.88$, $P = 0.35$). The significance level of the results was unaltered when the quadratic term of laying date was used.

The observed pattern of seasonal distributions of clutch size for all species studied suggests that this parameter did not remain constant throughout the breeding season (Fig. 3). Clutch size increased to mid season and then decreased at the end of the season. Thus, intermediate clutches were larger than early and late clutches in all species studied and in both study areas (Fig. 3). The General Linear Model shows that clutch sizes vary significantly between different laying periods (early, intermediate and late clutches; $F_{2,842} = 6.72$, $P = 0.0012$). The lack of significance of the interaction species x clutch ($F_{6,842} = 1.10$, $P = 0.36$) means that the temporal pattern was the same for the four species studied. It is thus concluded that intrinsic between-species differences in clutch size exist and that the temporal pattern was similar in all of the four species studied.

Egg volume

Mean egg volume of clutches varied significantly between species (Table 3; ANOVA, volume, $F_{3,623} = 1243.41$, $P < 0.001$). The results suggest that mean egg volume of clutches was related to body mass, with larger mean volume of clutches being found in larger species. Mean egg volume of clutches of Skylarks and Short-toed Larks are larger than for Thekla Larks and Lesser Short-toed Larks (Fig. 4). Mean egg volume of clutches did not vary significantly with clutch size, laying date or year for any species (GLM, $P > 0.10$

TABLE 2

Clutch size frequencies and mean clutch sizes for each species (all years combined). *n* = number of nests considered.
[Frecuencias de tamaño de puesta y tamaño de puesta medio para cada especie (datos combinados de todos los años de estudio). n = *número de nidos.]*

Species *[Especie]*	Clutch size *[Tamaño de puesta]*				Mean ± *SD* *[Media* ± DT*]*	*n*
	2	3	4	5		
Skylark *[Alondra Común]*	2.6	28.1	62.3	7.0	3.74 ± 0.63	114
Short-toed Lark *[Terrera Común]*	6.3	45.9	47.2	0.6	3.42 ± 0.62	159
Thekla Lark *[Cogujada Montesina]*	4.8	41.9	46.1	7.2	3.56 ± 0.70	334
Lesser Short-toed Lark *[Terrera Marismeña]*	5.2	57.1	36.1	1.6	3.34 ± 0.60	252

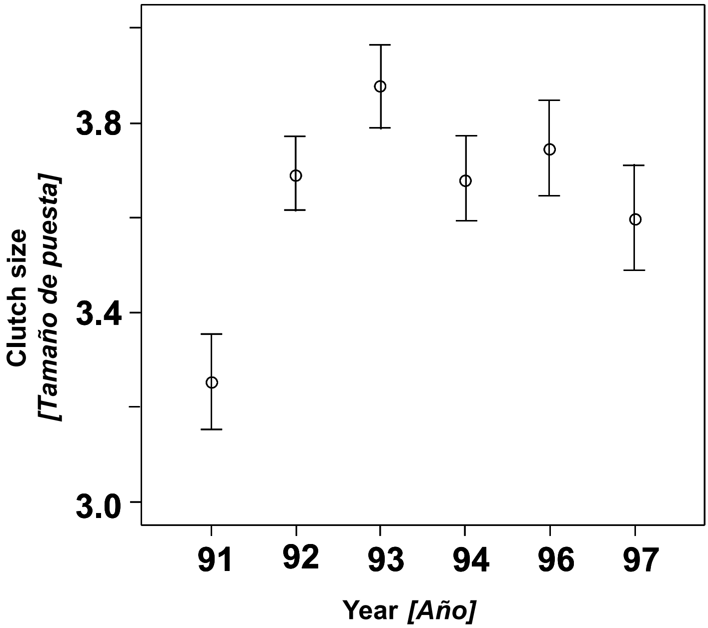

FIG. 2.—Between year variation in clutch size in Thekla Lark at Cabo de Gata (Almería, Spain).
[Variación interanual del tamaño de puesta en la Cogujada Montesina en Cabo de Gata (Almería).]

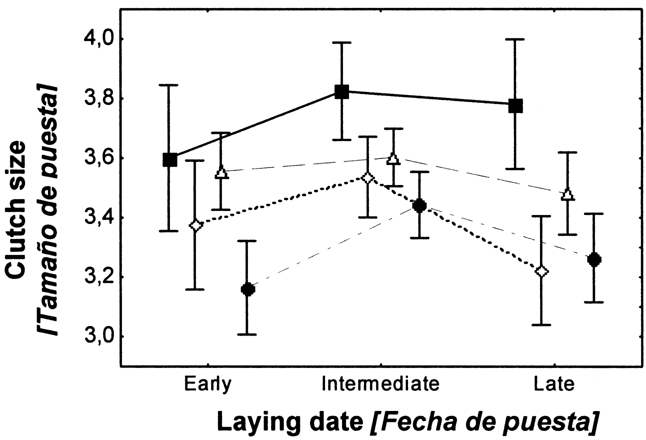

FIG. 3.—Within-season variation in clutch size in the four lark species. Skylark, squares, solid line; Short-toed Lark, triangles, dotted line; Thekla Lark, unfilled polygons, dashed line; Lesser Short-toed Lark, circles, dots and dashes. Early clutches corresponding to the first quartile of laying dates; Intermediate clutches of second and third quartile; Late clutches of fourth quartile.
[Variación estacional en el tamaño de puesta de las cuatro especies. Alondra Común: cuadrados y línea continua; Terrera Común: triángulos y línea rayada; Cogujada Montesina: rombos y línea punteada; Terrera Marismeña: círculos y línea mixta. Puestas tempranas = correspondientes a las del percentil 25%; intermedias = 25% - 75%; tardías = mayor del 75%.]

TABLE 3

Mean, maximum and minimum lengths, widths and volumes of all eggs measured for each species. *n* = number of nests considered.
[Datos medios, máximos y mínimos de las medidas de los huevos de las cuatro especies. Se muestran los valores para la anchura del huevo, la longitud y el volumen. n = *número de nidos con medidas.]*

Species *[Especie]*	Parameter *[Parámetro]*	Length (mm) *[Longitud (mm)]*	Width (mm) *[Ancho (mm)]*	Volume (mm^3) *[Volumen (mm^3)]*
Skylark *[Alondra Común]*	Mean ± *SD* *[Media ±* DT*]*	22.9 ± 1.24	16.6 ± 0.65	3246 ± 335
	Minimum *[Mínimo]*	14.0	11.0	864
	Maximum *[Máximo]*	25.9	19.9	4443
	n	275	275	275
Short-toed Lark *[Terrera Común]*	Mean ± SD	19.8 ± 0.89	14.5 ± 0.54	2119 ± 204
	Minimum	17.4	12.9	1551
	Maximum	22.8	16.0	2820
	n	356	356	353
Thekla Lark *[Cogujada Montesina]*	Mean ± SD	23.0 ± 1.02	16.9 ± 0.54	3354 ± 288
	Minimum	17.3	13.7	1656
	Maximum	26.2	19.9	4716
	n	968	851	851
Lesser Short-toed Lark *[Terrera Marismeña]*	Mean ± SD	20.0 ± 0.96	14.6 ± 0.49	2196 ± 193
	Minimum	14.3	13.3	1528
	Maximum	23.9	16.0	2853
	n	695	607	607

in all cases) except for Thekla Lark, in which year had a significant effect (GLM, year: $F_{3,215}$ = 6.54, $P < 0.001$), as well as the interaction between clutch size and year ($F_{11,215}$ = 2.18, $P = 0.01$).

Within clutches, egg volume differed significantly only for Thekla Larks, in which the first egg was smaller than the remainder (3270 ± 365 mm^3 *vs.* 3413 ± 319 mm^3, Student's test for paired samples: $t = 5.16$, df = 37, $P < 0.01$) and the last eggs was larger (3411 ± 274 mm^3 *vs.* 3343 ± 309 mm^3, $t = 2.93$, $df = 51$, $P = 0.005$). All tests are non significant for the rest of the species (p > 0.10 in all cases; sample sizes: Skylark, *n* = 11 nests, Short-toed Lara, *n* = 12 nests; Thekla Lark, *n* = 53 nests and Lesser Short-toed Lark, *n* = 43 nests).

Hatching asynchrony

Hatching asynchrony of one or two days was common in all species. However, the frequency of asynchronous nests differed between them, being more frequent in species at Layna than in those at Cabo de Gata (Skylark, 72% of nests asynchronous; Short-toed Lark 57%; Thekla Lark 51%; Lesser Short-toed Lark 40%; $F_{3,399}$ = 3.88, $P = 0.009$). Furthermore, the nested-ANOVA design (species nested into study site) show that between-site differences remain significant ($F_{1,399}$ = 9.58; $P = 0.002$), but between-species differences within sites disappear ($F_{2,399}$ = 2.36; $P = 0.10$). These results suggest that more asynchronous nests occur at Layna,

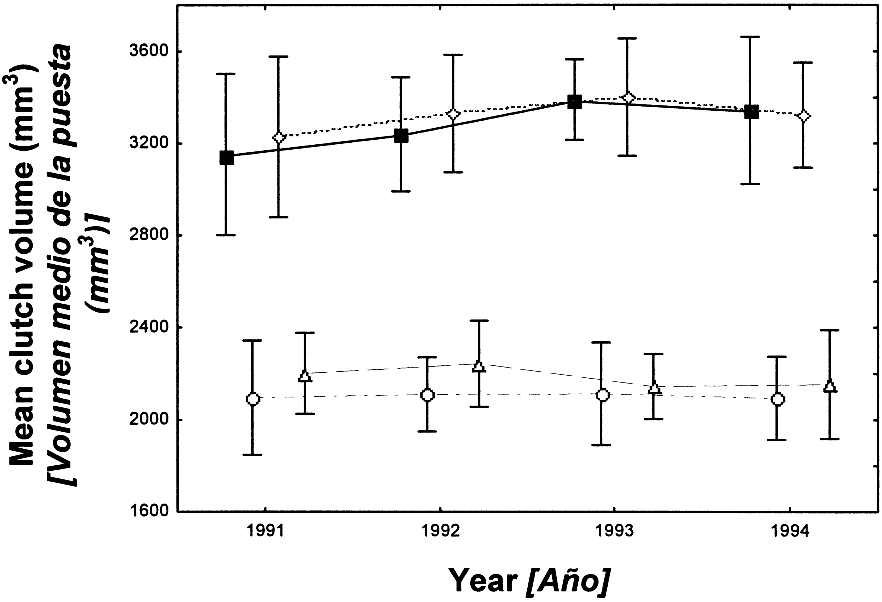

FIG. 4.—Between-year variation in the mean clutch volume (mm^3) in the four lark species in the period 1991-1994 (comparable data set for both study areas). Skylark, squares; Short-toed Lark, circles; Thekla Lark, triangles; Lesser Short-toed Lark, unfilled polygons. All means ± *SD*.
[Variación interanual en la media del volumen de las puestas en las cuatro especies para el periodo 1991 a 1994 (datos anuales disponibles en ambas zonas de estudio]. Alondra Común, cuadrados negros; Terrera Común, círculos; Cogujada Montesina: triángulos; Terrera Marismeña, círculos. Datos expresados como medias ± DT.*]*

and that this difference was independent of the body mass of the species involved.

In Skylarks the occurrence of asynchrony was significantly related to laying date (Table 4, Fig. 5), although clutch size had a near-significant influence (Table 4). In Short-toed Larks hatching asynchrony varied significantly in relation to year, while clutch size had a near-significant influence (Table 4). The occurrence of asynchrony in Thekla and Lesser Short-toed Larks was significantly related to laying date and clutch size (Table 4). Year did not have a significant effect although its influence was almost significant in the latter two species (Table 4).

The results of the analyses of the degree of asynchrony (0, 1 or 2 days) were similar to those regarding the occurrence of asynchrony, with the exception of the influence of clutch size, which was significant for Short-toed Larks, and of year, which was significant for Lesser Short-toed Larks (maximum likelihood χ^2 = 11.590 and 20.597, df = 4 and 10, and P = 0.021 and 0.024, respectively).

DISCUSSION

Laying date

The distribution of laying dates across the breeding season shows a quadratic response in other lark species of temperate areas (Delius, 1965; Guerrieri *et al.*, 1997), indicating the laying of multiple clutches per season. In this study, three of the four species studied show also a quadratic response to laying dates (Fig. 1), with a peak during mid-season, and only Lesser Short-toed Larks shows a pattern resembling a bimodal distribution. This difference from previous studies may be due to the high rates of nest predation in the study areas. In the former, nest predation rates ranged from 30% to 50%, whereas in the present study sites they approached nearly twice

TABLE 4

Results of the binomial logistical regression model of the incidence of hatching asynchrony in relation to laying date, clutch size and year.
[Resultados del análisis de regresión logística binomial de la presencia y ausencia de asincronía de eclosión en función de la fecha de puesta, el tamaño de puesta y el año para las cuatro especies de alondras.]

Species *[Especie]*	Parameter *[Parámetro]*	Laying date *[Fecha de puesta]*	Clutch size *[Tamaño de puesta]*	Year *[Año]*
Skylark *[Alondra Común]*	Maximum likelihood χ^2	5.579	5.687	6.565
	df [*gl*]	1	2	4
	P	0.018	0.058	0.161
Short-toed Lark *[Terrera Común]*	Maximum likelihood χ^2	1.266	5.305	11.358
	df	1	2	4
	P	0.261	0.070	0.023
Thekla Lark *[Cogujada Montesina]*	Maximum likelihood χ^2	4.901	21.231	3.681
	d.f.	1	3	5
	P	0.027	< 0.001	0.596
Lesser Short-toed Lark *[Terrera Marismeña]*	Maximum likelihood χ^2	12.957	10.366	11.066
	df	1	2	5
	P	< 0.001	0.006	0.050

these levels (Suárez *et al.*, 1993; Yanes & Suárez, 1996a). The high predation rates compel females to lay replacement clutches, construction of new nests beginning as soon as four days after nest loss (Cramp, 1988; *own data*). These replacement clutches make laying date distributions continuous throughout the season as in single-clutch species, at least in years of high nest predation rates (see also Yanes & Suárez, 1996b). The laying of multiple clutches cannot be detected in such continuous distributions except through individual marking.

When comparing the length of the breeding season in the two study areas, noticeable differences were found, it being 15-20 days longer at Cabo de Gata than at Layna. This is enough time to allow the latest females females to lay additional or replacement clutches and to have more breeding attempts per season, increasing the reproductive success at the more southern locality (see also Dhondt *et al.*, 2002). This finding contradicts the results obtained by Tieleman (2004), in a bibliographical review covering a wider range of habitats, in which at species level the number of clutches laid per breeding season declines with aridity, although this reproductive trait is difficult to establish due to individual variation (Delius, 1965).

It is also interesting to highlight the close association between the mean laying dates of the lower 25 percentile of clutches (early clutches) for the species at Cabo de Gata but not for those at Layna. In the first case, the two species are residents and hence subject to the same ambient conditions ahead of the laying period. In the second case, the Short-toed Lark is a trans-Saharan migrant constrained by migration dates, whereas the Skylark at Layna is a resident or partial migrant, which may explain the absence of a similar relationship between these two species even though they both start nesting at the same time. The trans-Saharan migrant could be restricted by date and other ecological constrains related to migration, and may be less able to adjust laying dates to local conditions (Sanz, 2002; Sanz *et al.*, 2003).

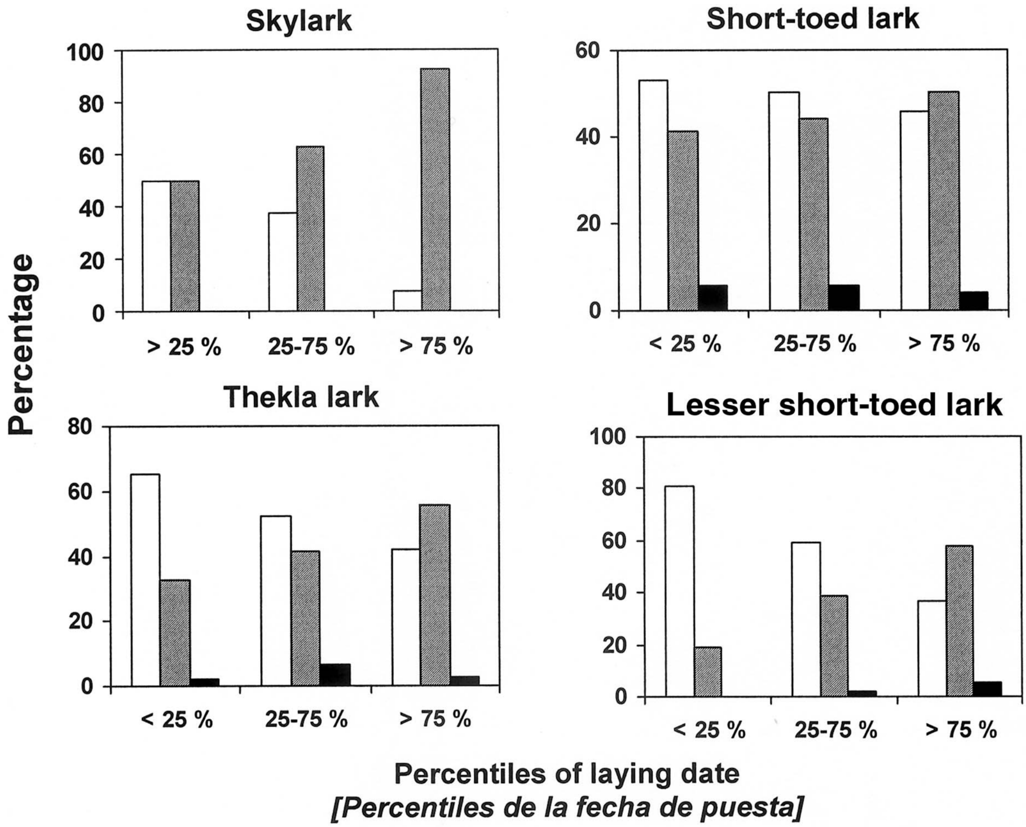

FIG. 5.—Percentage occurrence of different degrees of hatching asynchrony in relation to laying date. Unfilled = no asynchrony; Hatched, 1-day asynchrony; Solid, > 1-day asynchrony.
[Frecuencia de aparición de nidos de eclosión asincrónica en relación a la fecha de puesta. Barras blancas = nidos no asincrónicos; Barras rayadas = asincronía de 1 día; Barras negras = asincronía mayor de 1 día.]

Clutch size and egg volume

Clutch size in larks has been associated with aridity, being smaller in the species inhabiting the most xeric environments (Tieleman, 2004). The results given here agree partially with this finding. On the one hand, clutches of species at Layna (higher latitude, less xeric environment) were larger than at Cabo de Gata (lower latitude, more xeric environment). On the other hand, the two *Calandrella* larks, which are similar-sized species and congeneric, do not differ significantly in clutch size between Cabo de Gata (rainfall, 220 mm/year) and Layna (500 mm/year). The difference from the results of Tieleman (2004) may be due to her study having covered a much broader aridity range, from deserts with an annual rainfall of less than 100 mm to eurosiberian pastures receiving over 800 mm.

Regarding the between-year variation in clutch size, all the species except the Thekla Lark show a high degree of constancy in this parameter between years, which suggests that fecundity is relatively independent of climatic factors (precipitation and temperature) for these species. This absence of relation with the climatic conditions can be explained by the nest predation rates, which varies in an unpredictable way between years (Slagsvold, 1984).

On the other hand, the temporal distribution of clutch size was similar in all of the four species studied. Females lay maximum clutch sizes on intermediate dates within the breeding season, earlier or later clutches being smaller, a pattern which has been considered characteristic of multibrooded species (Crick *et al.*, 1993; Soler *et al.*, 1995; Gil-Delgado *et al.*, 2005). Prey availability increases in the course of the breeding season in the localities studied (J. Herranz, *unpubl. data*), which allows a reduction in the foraging costs of females and an expected increase in clutch size at the end of the breeding period. But there are two main factors that could play an important role in explaining this result: first, physiological condition of females declines during the course of the season, at least in the two larks at Cabo de Gata (Suárez *et al.*, 2005), which agree with the observed smaller clutch size at the end of the season. Second, smaller clutches imply reduced costs to females in laying and raising the brood (Hussell, 1972; Ricklefs, 1974) and a reduction in predation related to the shortening of the nesting period (Slagsvold, 1984). However, this pattern can be also explained by the fact that the females which lay first, with a lower clutch size, have a higher probability to re-lay during the same breeding season. The females that lay in intermediate laying dates, can not re-lay, and use the strategy of laying a larger clutch. The decline observed at the end of the season will be due to second or third clutches laid by low quality females (Soler *et al.*, 1995).

As in most passerines (Christians, 2002), mean clutch volume seem relatively constant in relation to annual variation in three of the larks studied. Nevertheless, in the Thekla Lark a significant inter-annual variation in mean clutch volume was observed. It is difficult to explain why this species differs from the others, but results from this study on clutch size and mean clutch volume suggest that this species seems to be more stressed by environmental conditions than the other species studied. More focussed studies are needed to answer this question.

The within-clutch differences in egg volumes have been interpreted as a mechanism to reduce the effect of asynchronous hatching on nestling size, the last egg being normally larger than the others («brood survival strategy», Moreno, 1989; Hillström, 1999). Our results for the Thekla Lark agree with this scenario but not for the other three species, where the last egg is similar to the others. In the same species, differences were found in the first egg which is the smallest. The reduction in volumes of first eggs could serve also to reduce the effect of asynchronous hatching, since in this species the first nestling weighs less than the others at hatching (Suarez *et al.*, *unpubl. data*).

Hatching asynchrony

The incidence and/or the extent of asynchrony are similar in all the species studied. Hatching asynchrony increases with clutch size and laying date (Figs. 5 and 6), this variation being significant in three of the four species studied, and also varies with year in the two *Calandrella* larks. This pattern of variation is relatively common in passerines (Stoleson & Beissinger, 1995) and may apply to larks generally on the basis of our data. The higher degree of asynchrony in the two larger species (Skylark and Thekla Lark) may be explained by their having larger clutches than the two *Calandrella* larks. The degree of asynchrony notably increases with laying date, except in Short-toed Lark.

Conclusions

To summarise, this study shows that the four species studied have different reproductive strategies which cannot be explained solely in terms of their body mass or biogeographical affinities. The Thekla Lark is at one extreme, showing inter-annual variation in clutch size and mean clutch volume, seasonal changes in clutch size, within-clutch variation in egg volume and a high degree of hatching asynchrony, although without between-year variation in the incidence or extent of asynchrony. It seems, therefore, that this species is more influenced in its reproductive parameters by environmental conditions, both by large-scale variations (year to year variations in environmental conditions) and short-scale variations (seasonal variation). The Skylark is at the other extreme, showing little inter-annual or seasonal variation in clutch size and egg volume, both within and between clutches, although it shows seasonal variation in the incidence/degree of hatching asynchrony, as in the other species. The two *Calandrella* larks share similar patterns, resembling those of the Skylark, although there is variation between years in the incidence/degree of asynchrony in both species. In general, and except for the Thekla Lark, the extent of seasonal and inter-annual variation in the reproductive parameters considered is scarce, which is unexpected considering that the Mediterranean climate is very variable, especially in semi-arid areas. Larks are birds of open landscapes and well adapted to conditions of maximum aridity (De Juana *et al.*, 2004), and it may be that some species have evolved to more conservative reproductive strategies in the Mediterranean region which are distinct from those observed in more xeric environments (MacLean, 1970; Willoughby, 1971; Tieleman, 2002). Two main factors are likely to play an important role in determining the stability of breeding parameters in these species: habitat seasonality and migratory status of the species involved. More studies are needed to evaluate how these factors affects breeding success in larks in Mediterranean habitats as well as the implications of those effects in terms of demography and population dynamics.

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BIBLIOGRAPHY

BARBIER, L. 2001. Elements for a skylark (*Alauda arvensis*) management plan. *Game and Wildlife Science*, 18: 45-83

CHRISTIANS, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, 77: 1-26.

CRAMP, S. 1988. *The Birds of the Western Palearctic. Vol. V.* Oxford University Press, Oxford.

CRICK, H. Q. P., WINGFIELD GIBBONS, D. & MAGRATH, R. D. 1993. Seasonal changes in clutch size in British birds. *Journal of Animal Ecology*, 62: 263-273.

DE JUANA, E. 2004. Changes in the conservation status of birds in Spain, years 1954 to 2004. *Ardeola*, 51: 19-50.

DE JUANA, E., SUÁREZ, F. & RYAN, P. 2004. Larks Alaudidae. In, J. del Hoyo, A. Elliott & D. Christie (Eds.): *Handbook of the Birds of the World, Vol. 9*, pp. 496-541. Lynx Edicions, Barcelona.

DELIUS, J. D. 1965. A population study of skylarks *Alauda arvensis*. *Ibis*, 107**:** 466-492.

DHONDT, A. A., KAST, T. L., & ALLEN, P. E. 2002. Geographical differences in seasonal clutch size variation in multi-brooded bird species. *Ibis*, 144: 646-651.

DONALD, P. F. 2004. *The Skylark*. T & AD Poyser, London.

DONALD, P. F., GREEN, R. E., & HEATH, M. F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London, Series B*, 268: 25-29.

GIL-DELGADO, J. A., MARCO, E., PAREDES, M & VIVES-FERRÁNDIZ, C. 2005. Seasonal clutch size variation of multi-brooded species: comparisons between breeding season and latitudes. *Ibis*, 147: 206-212.

GUERRIERI, G., SANTUCCI, B., CASTALDI, A. & DE-VITA, S. 1997. Reproductive biology of the calandra lark, *Melanocorypha calandra*, in central Italy. *Rivista Italiana di Ornitologia*, 67: 133-150.

HERRANZ, J., MANRIQUE, J., YANES, M. & SUÁREZ, F. 1994. The breeding biology of Dupont's lark, *Chersophilus duponti*, in Europe. *Avocetta*, 18: 141-146.

HERRANZ, J., TRABA, J., MORALES, M. B. & SUÁREZ, F. 2005. Nest size and structure variation in two ground nesting passerines, the Skylark *Alauda arvensis* and the Short-toed Lark *Calandrella brachydactyla*. *Ardea*, 92: 209-218.

HILLSTROM, L. 1999. Variation in egg mass in the Pied Flycatcher, *Ficedula hypoleuca*: An experimental test of the brood survival and brood reduction hypotheses. *Evolutionary Ecology Research*, 1: 753-768.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk*, 96: 73-77.

HUSSELL, D. T. J. 1972. Factors affecting clutch size in artic passerines. *Ecological Monographs*, 42: 317-364.

MACLEAN, G. L. 1970. The biology of the larks (Alaudidae) of the Kalahari sandveld. *Zoologica Africana*, 5: 7-39.

MARTIN, T. E. & LI, P. 1992. Life history traits of open versus cavity-nesting birds. *Ecology*, 73: 579-592.

MOONEY, H. A. 1981. Primary production in Mediterranean-climate regions. In, F. D. Castri, D. W. Goodall & R. L. Specht (Eds.): *Ecosystems of the world II. Mediterranean type shrublands*, pp. 249-255. Elsevier, Amsterdam.

MØLLER, A. P. & JENNIONS, M. D. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia*, 132: 492-500.

MORENO, J. 1989. The breeding biology of the Wheatear *Oenanthe oenanthe* in South Sweden during 3 contrasting years. *Journal für Ornithologie*, 130: 321-334.

PEINADO, M. & RIVAS-MARTÍNEZ, S. 1987. *La vegetación de España y Portugal*. Universidad de Alcalá de Henares, Alcalá de Henares, Madrid.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. In, *Avian energetics*, pp. 152-297. Nuttall Ornithological Club, Cambridge, Massachusetts.

Sibley, C. G. & Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution.* Yale University Press, New Haven.

Sanz, J. J. 2002. Climate change and breeding parameters of great and blue tits throughout the western Palaearctic. *Climate Change Biology*, 8: 409-422.

Sanz, J. J., Potti, J., Moreno, J., Merino, S. & Frias, O. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region *Global Change Biology*, 9: 461-472.

Shkedy, Y. & Safriel, U. N. 1992. Nest predation and nestling growth rate of two lark species in the Negev Desert, Israel. *Ibis*, 134: 268-272.

Slagsvold, T. 1984. Clutch size variation in birds in relation to nest predation: on the cost of reproduction. *Journal of Animal Ecology*, 53: 945-953.

Soler, M., Moreno, J., Møller, A. P., Lindén, M. & Soler, J. J. 1995. Determinants of reproductive success in a Mediterranean multi-brooded passerine: the Black Wheatear *Oenanthe leucura*. *Journal für Ornithologie*, 136: 17-27.

Stoleson, S. H. & Beissinger, S. R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? *Current Ornithology*, 12: 191-270.

SPSS Inc. 2001. *SPSS for Windows (vers. 11.0).* SPSS Inc., Chicago.

Suárez, F., Yanes, M., Herranz, J. & Manrique, J. 1993. Nature reserves and the conservation of Iberian shrubsteppe passerines: The paradox of nest predation. *Biological Conservation*, 63: 77-81.

Suárez, F., Sánchez, A., Herranz, J., Traba, J. & Yanes, M. 2005. Parental body mass changes during the nesting stage in semi-arid lark species. *Journal of Arid Environments*, 62: 45-54.

Tellería, J. L., Suárez, F. & Santos, T. 1988. Bird communities of Iberian shrubsteppes: Seasonality and structure along a climatic gradient. *Holartic Ecology*, 11: 171-177.

Tieleman, B. I. 2002. *Avian adaptation along an aridity gradient: physiology, behavior and life history*. PhD thesis, University of Groningen.

Tieleman, B. I. 2004. Energy and water budgets of larks in a life history perspective: Parental effort varies with aridity. *Ecology*, 85: 1399-1410.

Willoughby, E. J. 1971. Biology of larks (Aves: Alaudidae) in the central Namib desert. *Zoologica Africana*, 6: 133-176.

Yanes, M. 2000. *La depredación en nido de aláudidos almerienses. Una aproximación desde la Biología de Conservación y la Ecología Evolutiva.* Instituto de Estudios Almerienses, Almería.

Yanes, M. & Suárez, F. 1996a. Incidental nest predation and lark conservation in an Iberian semiarid shrubsteppe. *Conservation Biology*, 10: 861-867.

Yanes, M. & Suárez, F**.** 1996b. Mortalidad en nido y viabilidad poblacional en aláudidos. *Ardeola*, 43: 57-68.

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