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SHORT-TERM DYNAMICS AND SPATIAL PATTERN OF NOCTURNAL BIRDS INHABITING A MEDITERRANEAN AGRICULTURAL MOSAIC

DINÁMICA A CORTO PLAZO Y PATRÓN ESPACIAL DE LAS AVES NOCTURNAS EN UN MOSAICO AGRÍCOLA MEDITERRÁNEO

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SUMMARY.—*Short-term dynamics and spatial pattern of nocturnal birds inhabiting a Mediterranean agricultural mosaic.*

Understanding the interaction between abundance fluctuation and spatial pattern of populations is crucial for designing conservation strategies, particularly in systems such as Mediterranean agricultural mosaics subjected to intensification and weather fluctuations. We investigated the effects of a severe drought on short-term population dynamics of nocturnal birds, a threatened and declining group of species that has been little studied. We addressed three levels (i.e. species, food guild and assemblage) for three consecutive years. The highest fluctuation in abundance occurred for species which feed on invertebrates, and the lowest abundance corresponded to the year after the severe drought. Species that feed on invertebrates occupied different sites in the different season sampling periods, whereas species that feed on vertebrates tended to occur at the same sites throughout the year. At the assemblage level, species composition did not change between years. Patterns of site occurrence and population abundance in different years were mostly spatially congruent; thus, habitat features that are strictly space-dependent are more critical for explaining these patterns than other factors that change over time such as weather. The spatial segregation of little owl *Athene noctua* and Eurasian scops owl *Otus scops* is partially attributed to the sedentary character of the former and the migratory character of the latter. The low population fluctuations observed for most species make their conservation more

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straightforward since harsh years in relation to weather were not associated with abrupt population declines except for stone curlew *Burhinus oedicnemus*, a vulnerable species that should be prioritised for conservation actions.

Key words: abundance, food guild, occurrence, population fluctuations, severe drought.

RESUMEN.—*Dinámica a corto plazo y patrón espacial de las aves nocturnas en un mosaico agrícola mediterráneo.*

Comprender la interacción entre la fluctuación de la abundancia y el patrón espacial de las poblaciones es crucial para el diseño de estrategias de conservación, particularmente en sistemas como los mosaicos agrícolas mediterráneos, sometidos a intensificación y fluctuaciones climáticas. Se investigaron los efectos a corto plazo de una sequía severa en la dinámica de poblaciones de aves nocturnas, un grupo de especies amenazado y en declive, que ha sido poco estudiado. Se abordaron tres niveles (especies, gremios tróficos y comunidad) durante tres años consecutivos. La mayor fluctuación de abundancia se detectó en las especies que se alimentan de invertebrados y la menor abundancia se observó un año después de una sequía severa. Las especies que se alimentan de invertebrados ocuparon lugares diferentes en las distintas estaciones del año muestreadas, mientras que las especies que se alimentan de vertebrados tendieron a ocupar los mismos lugares a lo largo de todo el año. En relación a la comunidad, la composición de especies no cambió entre años. Los patrones de ocupación espacial y de abundancia de las poblaciones en diferentes años fueron en su mayoría espacialmente congruentes. Por lo tanto, las características del hábitat que son estrictamente dependientes del espacio son más importantes para explicar estos patrones que otros factores que cambian con el tiempo, como el clima. La segregación espacial del mochuelo común *Athene noctua* y el autillo *Otus scops* se atribuye parcialmente al carácter sedentario de la primera y el carácter migrador de la segunda. Las pequeñas fluctuaciones poblacionales observadas para la mayoría de las especies hacen su conservación más simple, debido a que los años climáticamente severos no se asociaron con acusados descensos de sus poblaciones, excepto para el alcaraván *Burhinus oedicnemus*, una especie vulnerable que debe priorizarse en los planes de conservación.

Palabras clave: abundancia, aparición, gremio trófico, fluctuación de poblaciones, sequía severa.

INTRODUCTION

Explaining the spatial and temporal variation in the abundance of species is a central question in ecology. Incorporating information on such variation into conservation planning is often critical for both population persistence and biodiversity conservation.

Assemblage composition and population abundance are driven by a variety of factors including those that are strictly space-dependent (e.g. site characteristics that determine habitat quality; Rodenhouse *et al.*, 1997; Ives and Klopfer, 1997; García *et al.*, 2007) and those that vary at a time-scale that is relevant for a particular species or taxonomic group (e.g. inter-annual weather variation, Benton *et al.*, 2006; Newey *et al.*, 2007). This is particularly true for agricultural landscapes, which are subjected to rapid human-induced alterations, a major cause of species decline (Fox, 2004; Wretenberg *et al.*, 2007; Firbank *et al.*, 2008).

Agricultural systems are often dynamic and heterogeneous as a result of farming practices. A characteristic feature of these systems is that they consist of mosaics of distinct land uses or vegetation types, ranging from patches of natural or semi-natural vegetation to highly modified areas (Haslem and Bennet, 2008). Conservation managers need guidance on effective ways to reconcile retention or enhancement of biodiversity in farming systems with maintenance of economic productivity (Haslem and Bennet, 2008; Rey Benayas *et al.*, 2008). In addition, Mediterranean weather varies greatly within and between years. Further, global climate change is increasing the frequency of regional and local extreme events such as severe droughts and heat waves that may affect habitat suitability and patterns of population abundance (Saether *et al.*, 2004). As an end consequence, it is pressing to understand how the spatial and temporal components of agricultural landscapes interact to affect the dynamics of species assemblages of conservation value in Mediterranean regions.

Previous research on bird distribution has mostly addressed how landscape and habitat structure affects assemblage composition and species abundance (Heikkinen *et al.*, 2004; De la Montaña *et al.*, 2006; Haslem and Bennet, 2008) and their temporal dynamics (Bengtsson *et al.*, 1997; Franklin *et al.*, 2000; Hakkarainen *et al.*, 2003; Aldridge and Boyce, 2007; Devictor and Jiguet, 2007). Less attention has been devoted to explain the spatial congruence (i.e. the coincidence or overlap at particular sites) of fluctuating animal populations and how it changes through time (Böhning-Gaese *et al.*, 1994, Steen *et al.*, 1996; Sundell *et al.*, 2004) as a basis to design conservation strategies.

Some nocturnal species have the value of being specialised rodent predators and thus useful to farmers (Mikkola, 1983). Sergio *et al.* (2005) studied nocturnal raptor species that differ widely in their diet and habitat associations to show that sites occupied by these predators were consistently associated with high biodiversity, and argued that conservation focusing on top predators can be ecologically justified because it delivers broader biodiversity benefits. In this study, we considered the short-term dynamics and spatial patterns of nocturnal bird assemblages at three different levels (i.e. species, food guild and community) in a Mediterranean agricultural mosaic over three consecutive years of contrasting weather conditions, including a severe drought.

Specifically, we address four questions: (i) do the abundance and site occurrence of species and assemblage composition differ among years? We expect that population abundance will be lowest during the severe dry event due to shortage of food availability in accordance with the hypothesis of food limitation as a key factor in determining population abundance (Morin and Lawler, 1995); (ii) does fluctuation of species that belong to distinct guilds differ? We hypothesise that the abundance of species that predate on insects will fluctuate more than the abundance of species that predate on birds and mammals because insect availability is more dependent on weather conditions (Valkama *et al.*, 2005); (iii) are patterns of site occurrence and population abundance between the studied years spatially congruent? We expect higher spatial congruence between years of similar climatic conditions; and (iv) do species occupy the same sites in different seasons? We expect that species that predate on invertebrates will be less faithful to particular sites in the different seasons than species that predate on vertebrates because invertebrate availability fluctuates more across seasons (Williams, 1961; Marone, 1992). As far as we know, this is the first study that addresses the dynamics of an entire nocturnal bird assemblage at the landscape level.

MATERIAL AND METHODS

Study Area

We studied five adjacent 10 x 10 km squares (500 km^2 in total) located in La Mancha, central Spain. Mid coordinates for the area are 38º 46’ 48” North and 3º 15’ 05” West. Altitude ranges between 678 and 1,013 m a.s.l.

The area is a mosaic of different crops including rain fed grain crops (39.7% of the total area), vineyards (34.9%), olive groves (11.6%), and evergreen shrubland and woodland (10.4%). As in many other Mediterranean landscapes, the agricultural land is subjected to intensification (e.g. irrigation of vineyards and olive groves) and land use change, including abandonment and afforestation. Approximately 14% of the studied land has changed the type of use between 2004 and 2008 (unpublished data).

The climate in the region is dry continental Mediterranean, with cold winters and warm, dry summers. For the years that our bird survey spanned (2005-2007), precipitation in the first six months (when surveys were carried out) was 174, 394 and 439 mm, respectively, and mean temperature was 15.1, 15.7 and 14.9 ºC, respectively (averaged data from the three climate stations of the Instituto Meteorológico Nacional located in the area). When compared with the average climate conditions in the region for a 30 year reference period, years can be considered as follow: (a) year 2005: "very warm" (T > 80% of the warmest year) and "very dry" (Pp. < 20% of the wettest year); (b) year 2006: "extraordinarily warm" (T above the T of the warmest year) and of "normal precipitation" (Pp. at the 40-60% interval –i.e. the median value- of the wettest year); and (c) year 2007: "warm" (T between 20-40% of the warmest year) and "wet" (Pp. between 20-40% interval of the wettest year; labels according to Instituto Meteorológico Nacional).

Study species

Nine nocturnal bird species may potentially occur in the study area according to published distribution maps of the Iberian avifauna (Spanish Breeding Bird Atlas available at http://www.vertebradosibericos.org/atlasaves.html): barn owl *Tyto alba*, little owl *Athene noctua*, short-eared owl *Asio flammeus*, long-eared owl *Asio otus*, eagle owl *Bubo bubo*, Eurasian scops owl *Otus scops*, tawny owl *Strix aluco*, stone curlew *Burhinus oedicnemus* and red-necked nightjar *Caprimulgus ruficollis*. All species are sedentary in the study area except the Eurasian scops owl and the red-necked nightjar, which migrate to Africa in winter, and stone curlew, which is a partial winter migrant.

Barn owls, short-eared owls, long-eared owls, eagle owls and tawny owls prey on mammals and, occasionally, on birds; little owls and stone curlews mostly prey on invertebrates and, occasionally, on small rodents, whereas Eurasian scops owls and red-necked nightjars predate on large insects (Mikkola, 1983; Barros and De Juana, 1997). The conservation status in the European Union-25 is "vulnerable" for stone curlews, "declining populations" for barn owls, little owls and short-eared owls and "depleted population" for Eurasian scops owls (Birdlife International, 2004). The Eurasian scops owl is also included in the Spanish Red List of bird species as an almost threatened species.

Study design and bird surveys

The nocturnal bird assemblage in each 100 km^2 square was surveyed by means of 13 regularly distributed sites (65 sites in total) that were placed *a priori* on the map, thus maximizing the distance among sites (the modal distance between two proximate stations was 2.8 km, ranging between 2.0 and 3.2 km). This survey site density is high even for the smallest species surveyed (two and a half higher than recommended by the survey protocol of the SEO/BirdLife *Noctua* Program for long-term monitoring of nocturnal birds, http://www.seo.org/programa_seccion_ficha.cfm?idPrograma=3&idArticulo=224). When it was difficult to reach the exact location of a site, we surveyed at the closest site to that location that could be reached, always < 0.5 km and usually < 300 m away from it.

Every site has been surveyed three times per year during the whole study period (2005-2007), i.e. winter (1-15 February), mid spring (15-30 April) and late spring (20 May-8 June). For a survey day, the first survey started right after sunset and the entire survey lasted for a maximum of three hours to avoid later lower detectability. Each site was always surveyed for 15 minutes. Our survey time was 2,925 minutes per year, 146.25 hours in total. We recorded visual and aural contacts of every detected nocturnal bird and thereby determined the relative abundance of all species at each site.

We assessed the relative abundance of owl species in all sites by using taped playback of conspecific vocalizations that followed the courtship phenology of the different species: tawny owls and eagle owls in winter; little owls, long-eared owls, barn owls and short-eared owls in mid spring; Eurasian scops owls, little owls, barn owls and short-eared owls in late spring. The vocalisation sequence followed an increasing species size to minimise the effects on detection of inter-specific competition and even predation (Crozier *et al.*, 2006). The taped vocalisation of every species was played once at each site, it lasted for 2 minutes and the vocalisations of the different species were regularly distributed during the 15-minute survey. We did not use taped playback vocalisations of stone curlews and red-necked nightjars because they are easier to detect spontaneously and in order to avoid saturating the 15 minute listening with playback vocalisations.

We used the maximum relative abundance at each site of the three counts in a year for each species in all statistical analyses but in one specific analysis addressed to visualise the spatial association of species abundance in different seasons (see below). Tawny owl is characteristic of forest habitats under rainier climate conditions and was recorded only once, so it was not included in the analyses.

Statistical analyses

To address the question of whether abundance and site occurrence of species and assemblage composition differ among years, we performed a Repeated Measures ANOVA and an analysis of Multivariate Homogeneity of Groups Dispersions (Anderson, 2006) for testing differences of overall species abundance and assemblage composition, respectively, among years. We also used non-parametric Friedman's ANOVAs for dependent samples and contingency tables to test differences in abundance and site occurrence, respectively, of individual species among years. The sample units in the analyses were the survey sites.

The Repeated Measures ANOVA used species as a categorical factor and year as a within-effects factor (see appendix for details). Abundance is expected to vary among species because they are very different in body size (Webb *et al.*, 2007). The analysis of Multivariate Homogeneity of Groups Dispersions is based on a Principal Coordinates Analysis (PCO) performed on a matrix of Bray-Curtis dissimilarity of species abundance for each pair of year-site combinations (Anderson, 2006; see appendix for details).

To answer the question of whether fluctuation of species that belong to distinct guilds differ, we performed another Repeated Measures ANOVA with guild as a categorical factor. The species were grouped in two food guilds: predators of vertebrates and predators of invertebrates (barn owls, short-eared owls, long-eared owls and eagle owls were grouped as predators of vertebrates, and little owls, Eurasian scops owls, stone curlews and red-necked nightjars as predators of invertebrates). Food guilds were determined from the literature (e.g. Mikkola, 1983), not on the analysis of the diet of the study population. As for the ANOVA at the species level, we assured the spherecity assumption for this analysis and spatial independence of the ANOVA residuals.

To answer the question of whether patterns of site occurrence and population abundance between the studied years were spatially congruent, we used the Syrjala's (1996) test of spatial congruence between two distribution patterns (see appendix for details). For each species, we compared the spatial pattern of site occurrence between every pair of years (i.e. 2005 vs. 2006, 2005 vs. 2007 and 2006 vs. 2007). Because Syrjala's test is insensitive to abundance difference, we completed this test with non-parametric Spearman correlations. We did not carry out these analyses for barn owls and short-eared owls because they were species that did not occur in all years. The short-eared owl is actually a very rare species in the region; barn owls have experienced a rapid population decrease during the last few years and sometimes does not respond to playback vocalisation (personal observations; Alonso, *pers. obs.*). To answer the question of whether species occupy the same sites in different seasons, we used a Non-metric Multidimensional Scaling (NMDS) test performed on species abundance averaged at each site, year and season to visualise the spatial association of species across seasons.

We corrected Friedman ANOVAs, contingency tables, Syrjala's tests and correlation analyses for multiple test comparisons using

TABLE 1

Abundance (mean ± SD, in number of individuals per site) and occurrence (mean ± SD, in percentage of the 65 sites where species occurred) along the three-year survey of nocturnal bird species. Statistical tests are non-parametric Friedman ANOVAs for abundance and contingency table χ^2 for occurrence. Bolded P-values are significant at P = 0.05 after correcting for multiple tests.

[Abundancia (media ± DE, en número de individuos por sitio) y aparición (media ± DE, en porcentaje de los 65 sitios donde apareció la especie) a lo largo del muestreo de tres años de aves nocturnas. Los tests estadísticos son ANOVAs de Friedman no paramétricos para la abundancia y tablas de contingencia χ^2 para la aparición. Los valores P en negrita son significativos para una P = 0,05 después de corregir el efecto de tests múltiples.]

(a) χ^2 could not be performed because at least one cell in the contingency table contained < 5% of the observations.

(a) *No se pudo realizar el test χ^2 porque al menos una celda de la tabla de contingencia contenía < 5% de las observaciones.*

	Abundance/site			**ANOVA**		**Occurrence (% of sites)**			**Cont. table**	
	2005	2006	2007	F_2	P	2005	2006	2007	χ^2_2	P
Tyto alba	0.05 ± 0.21	0.06 ± 0.24	0.00 ± 0.00	4.33	0.11	4.6	6.2	0.0	(a)	(a)
Asio flammeus	0.03 ± 0.17	0.00 ± 0.00	0.02 ± 0.12	2.00	0.37	3.1	0.0	1.5	(a)	(a)
Athene noctua	1.06 ± 0.90	0.91 ± 0.93	1.08 ± 1.02	1.88	0.39	72.0	58.5	69.2	1.03	0.59
Asio otus	0.06 ± 0.30	0.05 ± 0.21	0.08 ± 0.27	0.73	0.69	4.6	4.6	7.7	0.72	0.69
Bubo bubo	0.06 ± 0.24	0.11 ± 0.40	0.15 ± 0.41	2.17	0.34	6.2	7.7	9.7	0.4	0.82
Otus scops	0.57 ± 0.81	0.51 ± 0.75	0.77 ± 1.04	5.54	0.063	38.5	36.9	66.1	0.79	0.67
Burhinus oedicnemus	0.12 ± 0.41	0.31 ± 0.58	0.48 ± 0.79	13.05	**0.0015**	9.2	24.6	33.2	8.89	0.012
Caprimulgus ruficollis	0.34 ± 0.62	0.20 ± 0.44	0.31 ± 0.58	2.63	0.27	27.7	18.5	26.2	1.32	0.52

Bonferroni corrections. We used Statistica for ANOVAs, contingency tables and correlation analyses, SPSS for NMDS, the R package "vegan" (Oksanen *et al.*, 2007) for the analysis of Multivariate Homogenity of Group Dispersions, and the R package "ecespa" (De la Cruz, 2008) for Syrjala tests.

RESULTS

Dynamics of abundance and occurrence

We recorded 666 contacts of 475 individuals of all species together during the three-year survey (overall, 7 barn owls, 198 little owls, 3 short-eared owls, 12 long-eared owls, 21 eagle owls, 120 Eurasian scops owls, 59 stone curlews, and 55 red-necked nightjars). As expected, population abundance was different among species ($F_{6,\,448}$ = 39.66, P < 0.0001; table 1). The Repeated Measures ANOVA indicated that overall population abundance fluctuated among years and that this fluctuation was species-dependent ($F_{14,\,1024}$ = 2.35, P = 0.0033 for the species * year interaction; table 1). If the two least frequent species in our survey (barn owls and short-eared owls) were excluded from the Repeated Measures ANOVA, still year and species * year interaction results were significant (P = 0.0018 and 0.031, respectively).

Mantel tests revealed spatial independence of the ANOVA residuals at P = 0.05 for all 22 combinations of eight species and three years (two species did not occur in one year each) except for Eurasian scops owls in years 2006 and 2007; the correlation coefficients for this species and years were very low (r = 0.175 and 0.189, respectively).

Non-parametric Friedman's ANOVAs after correcting for multiple tests indicated population fluctuations only for stone curlews (table 1); it was least abundant during the severe dry event and most abundant during the wet year. Consistently, contingency tables to test site occurrence among years resulted in marginal significant differences only for this species (table 1). Population abundance of Eurasian scops owls exhibited as well a trend to fluctuate among years but not in parallel with stone curlews.

The analysis of Multivariate Homogeneity of Groups Dispersions resulted in non-significant differences of assemblage composition among years ($F_{2,\,164}$ = 2.191, P = 0.125; fig. 1).

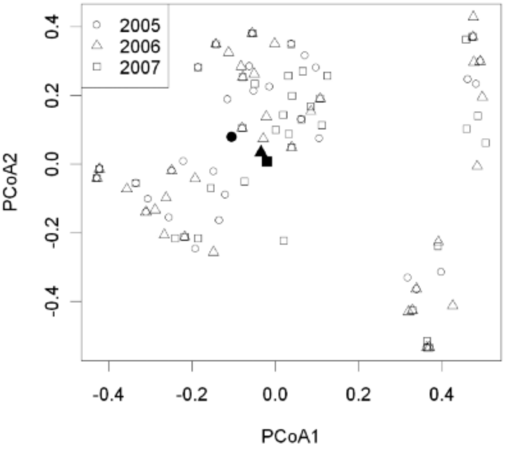

FIG. 1.—Site location according to their species composition on axes 1 and 2 of the Principal Coordinate Analysis performed on the nocturnal bird assemblages in the three studied years. Symbols for centroids of each year are solid and of larger size. The ANOVA of the distances to year centroids provided non significant figures among year assemblage composition.

[Posición del sitio de muestreo según su composición de especies en los ejes 1 y 2 de los análisis de coordenadas principales realizado en la comunidad de aves nocturnas en los tres años estudiados. Los símbolos de los centroides de cada año aparecen rellenos y son de mayor tamaño. El ANOVA de las distancias a los centroides de cada año no proporcionó resultados significativos entre la composición de la comunidad de cada año.]

Food guilds

Abundance and abundance fluctuation were statistically different in the two food guilds. Species that prey on vertebrates were less abundant than species that mainly feed on invertebrates ($F_{1,518}$ = 162.83, P < 0.0001). Predators of vertebrates did not fluctuate in abundance among years, whereas predators of invertebrates did so (fig. 2). This guild exhibited the lowest abundance in the year after the extraordinary dry event. Again, Mantel tests revealed spatial independence of the Repeated Measures ANOVA residuals with a nominal P-value = 0.05 (results not shown).

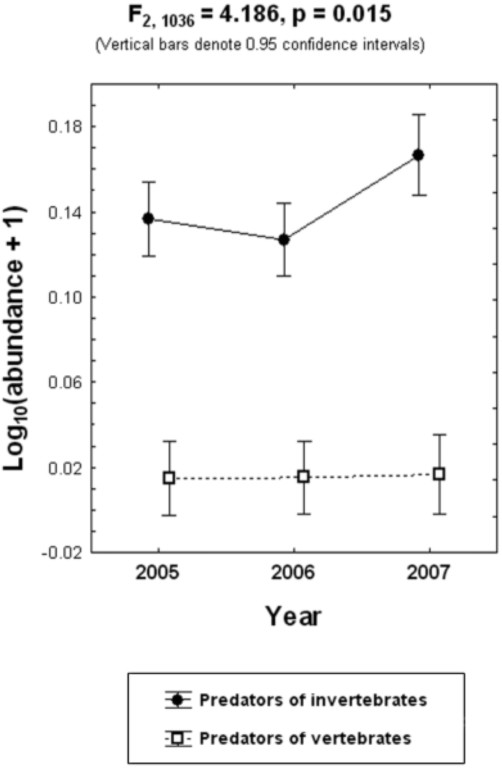

FIG. 2.—Variation in abundance of the two food guilds of nocturnal birds along the surveyed period. The ANOVA reported refers to the interaction of food guild and year.

[Variación en la abundancia de los dos gremios tróficos de aves nocturnas a lo largo del período de estudio. La información del ANOVA se refiere a la interacción del gremio trófico con el año.]

Spatial pattern of populations

Species occurrence was highly spatially congruent for all species in years 2005 and 2006 (p-values ranged between 0.13 and 0.41) and for all species but the stone curlew in years 2005 and 2007 (P-values ranged between 0.26 and 0.43, stone curlews excluded) according to Syrjala's test (table 2). Occurrence of all species but stone curlews and Eurasian scops owls tended to be non-congruent in years 2006 and 2007 (P < 0.09 except for these two species, table 2 and fig. 3).

Non-parametric correlations of species abundance across sites for two different years were mostly positive and significant, particularly for little owls, eagle owls and Eurasian scops owls (table 2).

Spatial association of species abundance in different seasons

The NMDS ordination depicted a clear spatial segregation between little owls and Eurasian scops owls in the breeding period (early spring and late spring), as the long relative distances between the positions occupied by these species mean that they have been detected at different survey sites (fig. 4). The ordination also highlighted that both stone curlews and red-necked nightjars were surveyed at the same locations in early spring and late spring, but these locations differed in these two sampling periods. Conversely, long-eared owls and eagle owls were located in similar locations in all seasons, which were relatively close to locations where barn owls occurred.

TABLE 2

Results of Syrjala's (1996) test of spatial congruence of species occurrence (ψ) and non-parametric correlations (r_s) between species abundance in two different years across 65 sites. Bolded numbers are significant at $P = 0.05$ after correcting for three comparisons within species; bolded underlined numbers are significant after correcting for overall comparisons.

[Resultados del test de Syrjala (1996) de congruencia espacial de la aparición de cada especie (ψ) y correlaciones no paramétricas (r_s) entre la abundancia de cada especie en dos años diferentes en los 65 sitios de muestreo. Los números en negrita son significativos para una P = 0,05 después de corregir para tres comparaciones dentro de la especie; los números en negrita y subrayados son significativos después de corregir para todas las comparaciones.]

B. oedicnemus	2005	2006	*O. scops*	2005	2006
2006	$\psi = 1.499$, $P = 0.41$ $r_s = 0.08$, $P > 0.1$			$\psi = 0.185$, $P = 0.37$ $r_s = \underline{\mathbf{0.64}}$, $P = 0.0001$	
2007	$\psi = 1.640$, $P = 0.06$ $r_s = \mathbf{0.30}$, $P = 0.014$	$\psi = 0.479$, $P = 0.30$ $r_s = 0.27$, $P = 0.031$		$\psi = 0.154$, $P = 0.27$ $r_s = \underline{\mathbf{0.67}}$, $P = 0.0001$	$\psi = 0.305$, $P = 0.40$ $r_s = \underline{\mathbf{0.50}}$, $P = 0.0001$
A. otus			*A. noctua*		
2006	$\psi = 9.388$, $P = 0.37$ $r_s = -0.05$, $P > 0.1$			$\psi = 0.289$, $P = 0.13$ $r_s = \mathbf{0.30}$, $P = 0.014$	
2007	$\psi = 3.301$, $P = 0.26$ $r_s = -0.06$, $P > 0.1$	$\psi = 8.639$, $P = 0.09$ $r_s = -0.06$, $P > 0.1$		$\psi = 1.084$, $P = 0.35$ $r_s = \mathbf{0.36}$, $P = 0.004$	$\psi = 0.471$, $P = 0.07$ $r_s = \underline{\mathbf{0.47}}$, $P = 0.0001$
C. ruficollis			*B. bubo*		
2006	$\psi = 0.712$, $P = 0.32$ $r_s = 0.15$, $P > 0.1$			$\psi = 2.064$, $P = 0.25$ $r_s = \underline{\mathbf{0.39}}$, $P = 0.002$	
2007	$\psi = 1.084$, $P = 0.35$ $r_s = 0.06$, $P > 0.1$	$\psi = 0.471$, $P = 0.07$ $r_s = 0.08$, $P > 0.1$		$\psi = 2.338$, $P = 0.43$ $r_s = \underline{\mathbf{0.58}}$, $P = 0.0001$	$\psi = 0.932$, $P = 0.05$ $r_s = \underline{\mathbf{0.70}}$, $P = 0.0001$

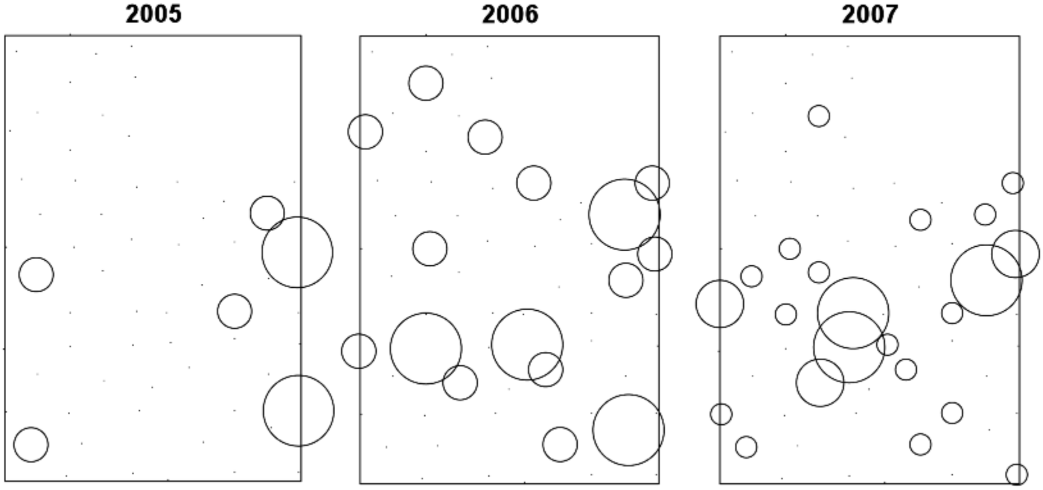

FIG. 3.—Spatial distribution of *Burhinus oedicnemus* surveyed in the three different years. The shaded north-east corner was not surveyed in this study. The circle size is proportional to the number of individuals detected at a site. Dots indicate surveyed sites where this species did not occur. According to Syrjala's test (table 2), years 2005-2006 and 2006-2007 are spatially congruent, and years 2005-2007 are marginally incongruent.

[Distribución espacial de Burhinus oedicnemus *en los tres años de estudio. La esquina sombreada en el noreste no fue muestreada en este estudio. El tamaño del círculo es proporcional al número de individuos detectados en cada sitio. Los puntos indican sitios muestreados donde la especie no apareció. Según el test de Syrjala (tabla 2), los años 2005-2006 y 2006-2007 son espacialmente congruentes, y los años 2005-2007 son marginalmente incongruentes.]*

DISCUSSION

Fluctuation in species abundance, occurrence and assemblage composition

We found overall population fluctuations but different responses of particular species. Inter-annual fluctuation and geography of bird abundance following weather variation is a well-documented phenomenon (Forsman and Monkkonen, 2003; De Juana and García, 2005). For homeothermic species, this pattern mostly leans on the hypothesis of food limitation in years that are less favourable for productivity (Gawlik, 2002). The effects of extraordinary weather events, for instance droughts, have also been reported (Jaksic, 2001; Mazia *et al.*, 2004).

We hypothesised population abundance to be lowest during the severe dry event due to shortage of food availability (Morin and Lawler, 1995). At the species level, only populations of stone curlews fluctuated in abundance and occurrence among the three years considered. In accordance with this result, Dean and Milton (2001) and De Juana and García (2005) did not find a direct correlation between precipitation and bird abundance in a Mediterranean landscape. However, the stone curlew seems to be sensitive to the severe drought. This result may be attributed to the fact that the reproductive success of the stone curlew greatly depends on the availability of insects (Barros and De Juana, 1997; Giannangelli *et al.*, 2004), whose abundance often depends strongly on weather conditions

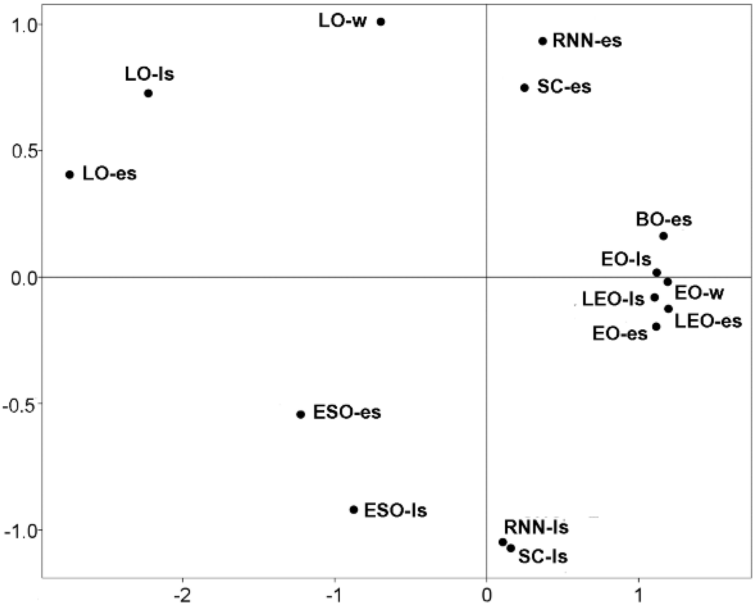

FIG. 4.—NMDS ordination diagram of the maximum abundance of every nocturnal bird species in each weather season. Stress = 0.13 and $R^2 = 0.94$. The position of each species and season in the diagram is represented by the species initials in capital letters followed by the season label (w = winter, es = early spring, ls = late spring).

[Diagrama de ordenación NMDS de la abundancia máxima de cada especie de ave nocturna en cada estación del año. Stress = 0,13 y R^2*= 0,94. La posición de cada especie y la estación del año en el diagrama están representadas por las iniciales de la especie en mayúsculas en inglés (BO* = Tyto alba*, LO* = Athene noctua*, LEO* = Asio otus*, EO* = Bubo bubo*, ESO* = Otus scops*, SC* = Burhinus oedicnemus *y RNN* = Caprimulgus ruficollis*), seguidas de las iniciales de la estación del año en inglés (w = invierno, es = principios de la primavera, ls = finales de la primavera)].*

(Williams, 1961). A possible explanation for lack of response of other species is their capability of feeding on alternative prey, the impact of epizooties and others (Martínez and Zuberogoitia, 2001; Martínez *et al*., 2008a).

Food guilds

Food guilds differed in abundance fluctuation and, as we hypothesised, species that prey on invertebrates fluctuated more than species that predate on vertebrates. Other studies have reported lower abundance fluctuation at upper trophic levels (Marone, 1992; Floyd, 1996). The lowest abundance of species that predate on insects, considered as part of the same guild, was mostly detected in the year that followed the severe drought and not during the severe drought, which could indicate low productivity during the scarcity period caused by low food abundance (Morin and Lawler, 1995). The different responses of insect-feeders and invertebrate-feeding birds may be due in part to specific differences in prey type and hunting strategy. The stone curlew feeds almost entirely on the ground, thus preying on invertebrates that inhabit the shallow layers of soil. Consequently, their abundance and accessibility would be strongly linked to rainfall. Little owls, Eurasian scops owls and red-necked nightjars mostly feed on active singing and mobile insects such as Orthoptera. Orthoptera can be relatively abundant in dry years, and their abundance may even increase and they also become more active with increasing temperature (Mikkola, 1983); as a result, predators of orthoptera can maintain their populations in warm dry years. We note that three of the four predators of invertebrates in our study are at least partially migratory, and therefore part of the predators of invertebrates vs. of vertebrates comparison overlaps with a resident vs. migratory comparison.

Spatial pattern

Patterns of site occurrence and population abundance among the studied years were mostly spatially congruent. This indicates that different abundances are associated with particular places on the landscape (Brown *et al.*, 1995). Consequently, habitat features and effects that are strictly space-dependent (e.g. nesting sites and shelter) appear to be critical for explaining these patterns at the studied temporal scale (Bengtsson *et al.*, 1997, Tworek, 2004; De Juana and García, 2005).

Beyond this general pattern, the substantial variation among the different species and years that was detected is interesting. We expected higher spatial congruence between years of similar climatic conditions. All species but the stone curlew were highly spatially congruent in years with most similar temperature, which coincided with those of most contrasting precipitation, and all species but the stone curlew and the Eurasian scops owl (the species that fluctuated most) were moderate to low spatially congruent in years with most contrasting temperature, which coincided with those of most similar precipitation. We did not find patterns of spatial congruence in relation to food guild. These findings point to the relative importance of temperature vs. precipitation, possibly mediated by microclimate conditions associated to habitat features, in driving the occupancy of habitat patches in landscapes with high inter-annual weather variation (Virkkala, 1991; Moegenburg and Levey, 2003).

Spatial association of species in different seasons

According to our hypothesis that species that predate on insects will be less faithful to particular sites in the different seasons than species that predate on vertebrates, we found that eagle owls and long-eared owls, which predate on vertebrates, are likely to share the same sites throughout the year, whereas species that predate on invertebrates (little owls, Eurasian scops owls, red-necked nightjars and stone curlews) occupied different sites in the different sampling periods. The eagle owl and the long-eared owl do not usually predate upon the same animals or nest on similar structures, and their prey fluctuates less than those of predators of invertebrates do, which allows for territorial overlap between these two species (Serrano, 2000; Martínez *et al.*, 2003; Navarro *et al.*, 2003; Rodríguez *et al.*, 2006). Spatial segregation between little owls and Eurasian scops owls can be attributed to competition for similar prey and shared hunting techniques, the sedentary character of little owls and the migratory character of Eurasian scops owls, and species-specific habitat selection (Mikkola, 1983). It has been suggested that sedentary species have competitive advantage over migratory species because the former would occupy the highest quality habitats first (Cox, 1968; Bell, 2000). Martínez and Zuberogoitia (2004) and Martínez *et al.* (2007) found a differential habitat selection by these two species (proximity to villages and forest patches, respectively). Red-necked nightjars and stone curlews were associated with the same locations throughout the year, even when both species moved their locations from early to late spring. These species do not share hunting techniques, as they are a ground-hunter and a flying-hunter, respectively. Apparently, that niche separation allows them to overlap their territories, enabling them to move in the landscape according to food abundance in each period of the year with little competence between them.

Conservation and management implications

A major goal of conservation biology is to provide a sound scientific basis for achieving population persistence of target species. Low population fluctuation among years of contrasting weather conditions makes conservation goals more straightforward because harsh years are not associated with abrupt population declines. In our study, different bird species responded to weather variations in their environment in quite different ways, but most species exhibited low population fluctuations. The overall high spatial congruence of populations between years also provides a good background for managers because it is possible to identify a range of sites where species occur or are abundant in different years (Ortego, 2007). The results of studies such as the one presented here have the potential to provide detailed maps of species occurrence and abundance of breeding individuals to conservation practitioners, which, in combination with detailed information on the characteristics of specific territories, help concentrate management efforts on the identified sites. This is important because the sole persistence of traditional territories can be a misleading indication of territory quality. For instance, for the Bonelli's eagle, Martínez *et al.* (2008b) reported significant variations in productivity attributable to differences in the quality of individuals (i.e. adult breeding pairs vs. pairs with one subadult), but not to variability among territories *per se*.

Two species exhibited moderate to high population fluctuations. Eurasian scops owls fluctuated moderately but it had a high spatial congruence. However, the stone curlew, a vulnerable species that is threatened by land use change and agricultural intensification, exhibited fluctuating populations and a moderate spatial congruence, and should be prioritized for conservation actions (Green and Griffiths, 1995). Avoiding land use change and agricultural intensification at the highly occupied sites is recommended for the species studied (Donald *et al.*, 2001).

One fundamental problem arising from animal surveys is that it is generally not feasible to completely census all individuals present in each sample unit (Royle *et al.*, 2007). Our studied species are of low and uncertain detectability, and possible census bias may include spatial coverage bias (not all individuals in the population are exposed to sampling) and detection bias (exposed individuals may go undetected). In fact, presumably only breeding individuals were surveyed in this study.

The extrapolation of population trends gained from local studies to a larger spatial scale should be interpreted cautiously (Virkkala, 1991; Sonerud, 1997; Webb *et al.*, 2007). Similarly, we must be cautious when extrapolating from the findings of short-term studies to longer temporal scales (Maron *et al.*, 2005). For instance, one year of severe drought apparently had little impact on the abundance of most studied species, but we do not know the impact of two or more consecutive dry events or any other event not covered by this study. Böhning-Gaese *et al.* (1994) found that species that had similar local year-to-year population fluctuations did not have similar long-term population trends, and species that had similar population dynamics in one region rarely exhibited similar dynamics in different regions where they occurred together. In spite of these considerations, we believe that studies simultaneously looking at assemblage dynamics and spatial patterns, as the one presented here, are useful for implementing management strategies for species of conservation value.

Another limitation of our study is that the sampling period was short and it did not include periods of scarcity of vertebrate prey, which form the bulk of the more spatially congruent predators found here. Such periods are relatively frequent in Mediterranean areas and elsewhere, and induce strong numerical and functional responses in owls (Taylor, 1994; Martínez and Zuberogoitia, 2001). Thus, in order to validate our results, further studies are needed, spanning over a number of years large enough to include possible population crashes of vertebrate prey, and its numerical effect on vertebrate-eating owls, which would influence intra- and inter-specific spatial congruence. A longer-term perspective would overcome the difficulties involved in carrying out complete annual censuses of large populations in large areas, and the distributional irregularities caused by the establishment of occasional breeding territories, or by short-term changes or gaps in territory locations (Solonen, 1993; Jenkins and van Zyl, 2005; Martínez *et al.*, 2008a). Similarly, further research on productivity, age structure, density and mortality on the map basis addressed here would increase the value of this study.

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APPENDIX 1 *[APÉNDICE 1]*

Details on statistical analyses

For the Repeated Measures ANOVA, we first assured that the spherecity criterion, a necessary and sufficient assumption for this analysis, was met for our data with a Mauchly's (1940) test. For raw abundance data (individual counts) at the species level, this criterion was violated ($W_2 = 0.973$, $P = 0.001$). Thus, abundance data were transformed as log10(x + 1), providing correct assumption for Repeated Measures ANOVA ($W_2 = 0.997$, $P = 0.49$). At the guild level, the spherecity assumption was also met ($W = 0.99$, $P = 0.57$ for log-transformed data). Next, we used a Mantel test with 1,000 permutations to check spatial independence of the ANOVA residuals.

The analysis of Multivariate Homogeneity of Groups Dispersions is a multivariate equivalent of Levene's test for homogeneity of variances, but the distance computed between group members and group centroids is Bray-Curtis instead of the Euclidean distance (members are survey sites and groups are years in our study). To test if one or more groups were more variable than the others, an ANOVA of the distances to group centroids was performed; the F-ratio was tested using permutation of the least-squares residuals. Bray-Curtis dissimilarity can be readily used with raw species abundances (Legendre and Legendre, 1998). Eighteen year-sites out of the 195 year-sites had no birds and these cases were excluded from the analysis. The first two PCO axes of every year-site survey were used to visualise the dispersion among years.

Syrjala's (1996) test of spatial congruence between two distribution patterns is designed to be sensitive to differences in the way that populations are distributed across the study area but insensitive to a difference in abundance between the two populations. It compares the observed ψ for two distributions with the ψ obtained for randomized distributions after 1,000 permutations. The observed ψ is defined as the sum, over all survey units, of the square of the difference between the cumulative distribution functions of the populations being compared. Syrjala's test is very conservative and rejection of the null hypothesis (spatial congruence between populations) is difficult (Fuller *et al.*, 2006).