

Fear in grasslands: the effect of Eurasian kestrels on skylark abundances

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Abstract Predation has received considerable theoretical and empirical support in population regulation. The effect of predators, however, could be achieved in direct (killing) or indirect effects (such as displacement). In this paper, we explored the relationship between Eurasian kestrels *Falco tinnunculus* and skylarks *Alauda arvensis* in Mediterranean grasslands. First, we analysed the presence of skylarks in the kestrel diet over 9 years. We also compared a grassland area of experimentally increased kestrel density and a second grassland as control area to evaluate the direct or indirect effect on skylark abundance. We also considered two different habitats, grazed and ungrazed plots. If skylark abundance decreased as the kestrel breeding season progressed in high-density kestrel area compared with the control area, it would suggest a direct effect (predator hypothesis). If skylark abundance remains constant in both areas of contrasting kestrel density, it would suggest that skylarks avoid kestrels (avoidance hypothesis). We found that skylark abundance decreased in the kestrel area from

the beginning of kestrel nest-box installation to recent years. The rate of skylark consumption decreased in a 9-year period as kestrel abundance increased, although the total amount skylark consumption did not show a decreasing trend. In addition, skylarks were more abundant in the kestrel-free area than in the kestrel area. Finally, we found that skylark abundance did not change through the kestrel breeding period in relation to grazing. We suggest that an increased breeding density of kestrels during their breeding period may force the skylarks to breed in other areas, which may explain the decline of their abundance.

Keywords Eurasian kestrels · *Falco tinnunculus* · Skylarks · *Alauda arvensis* · Grasslands · Mediterranean area · Predator–prey relationships

Introduction

Predation is an important demographic process in many vertebrate populations, and its role in population regulation has received considerable theoretical and empirical support (Krebs 2001). Thus, predators can influence the abundance and distribution of their prey species (Eng and Gullionj 1962; Geer 1968). The reduction of prey abundance due to predator presence could be achieved in two different ways (Meese and Fuller 1987; Suhonen 1993; Suhonen et al. 1994): a direct reduction due to predation or an indirect reduction by predator avoidance (Norrdahl and Korpimäki 1998). Therefore, it is expected that prey species may reduce the risk of predation by avoiding areas with high densities of predators (Kennedy et al. 1994; Hileman and Brodie 1994; Flowers and Graves 1997), avoiding areas close to nests of predatory birds (Suhonen et al. 1994; Norrdahl and Korpimäki 1998) or avoiding habitats where

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they are susceptible of being attacked (Brown et al. 1988; Ferguson et al. 1988; Suhonen et al. 1994).

Two general contexts have been suggested to characterise direct and indirect effects of predators on their preys. The predation hypothesis (direct effect) suggests that if the abundance of prey species is directly affected by predation, prey abundance should decline as the breeding season advances as predators deplete their populations. Alternatively, the avoidance hypothesis (indirect effects) suggests that if preys avoid predators, their abundance should remain constant from the beginning to the end of the breeding season. However, in the light of foraging theory, it is expected that raptors forage in patches, yielding the greatest net energy gain, (Stephens and Krebs 1986) and because prey species are not randomly distributed, the relationship between predators and particular preys could be mediated by the habitat type (Thirgood et al. 2002). Thus, the particular relationship between a predator and their prey might differ depending on the habitat selected by the prey species.

In this paper, we explored the relationship between Eurasian kestrels *Falco tinnunculus* and skylarks *Alauda arvensis*. Skylark abundance seems to decrease in kestrel nest proximity (Norrdahl and Korpimäki 1998). The effect of the vicinity of kestrel nests on bird community has been studied in northern Europe (Korpimäki and Norrdahl 1991; Suhonen et al. 1994; Norrdahl and Korpimäki 1998). However, the particular relationship between kestrels and skylarks remains to be tested in areas of contrasting kestrel density and different habitat structure. In addition, predator–prey systems are different from northern Europe and Mediterranean areas (Reif et al. 2001, 2004; Gaibani et al. 2005). This kind of study is particularly important when the prey is a threatened species, such as the skylark (Tucker and Heath 1994). If skylarks in Mediterranean areas follow the same predator-avoidance pattern reported in northern Europe (Suhonen et al. 1994; Norrdahl and Korpimäki 1998), we would expect similar abundances from the beginning to the end of the breeding season in two areas of contrasted abundance of predators.

To explore this, we compared skylark abundances in two contrasting areas of kestrel densities including two areas of different vegetation coverage in a Mediterranean area. First, we described the importance of skylark in the diet of kestrels over a 9-year period. Also, we explore the relationship between kestrels and skylarks by comparing an area where the breeding density of kestrel was increased by providing nest boxes (Fargallo et al. 2001) with a paired area of similar habitat where breeding kestrels were rare and dispersed. In both contrasting kestrel density areas and during their breeding period, we also explored grazed and ungrazed areas, where kestrels forage differentially (Village 1990). This is a different approach than used by Norrdahl

and Korpimäki (1998) in northern Europe as this study was carried out in grasslands rather than in farmlands, and we explored two habitats in two areas differing in predator (kestrel) abundances instead of comparing the response of bird abundances to the proximity of kestrel nests. We specifically expected (1) lower skylark abundances in areas of higher kestrel density. Following the predator avoidance hypothesis, it should be expected that (2a) differences in abundances between areas of low and high density of kestrels remain constant from the beginning of the breeding period. On the opposite, if our results support predation hypothesis, higher differences in skylark abundances are expected at the end of the breeding period than at the beginning (2b) between the two kestrel density areas considered. Finally, because higher vegetation cover may decrease predation risk (Evans et al. 2006), we expected (3) a habitat-mediated relationship between kestrels and skylarks.

Materials and methods

Breeding density and breeding performance of kestrels

This study was carried out in Campo Azálvaro region (40° 40'N, 4°20'W, 1,300 m a.s.l.), a montane grassland in central Spain. The area is a treeless flat and wide valley where the only trees present are located close to farms or in isolated small patches (for more details, see Fargallo et al. 2001). Four nest boxes were erected in 1988. Fourteen new nest boxes were installed in winter 1993–1994, 11 more in 1994–1995, 16 more in 1996–1997 and 5 more in early spring 1998. A total of 50 nest boxes were finally in place in 2004 in an area of 22 km². As a result of the nest-box installation, breeding density of kestrels in the 10-km² core area is stabilized around 3.1 pairs/km² from 1998 onwards (Fargallo 1999; Fargallo et al. 2001). A part of kestrels in our study area are sedentary while another fraction of the population migrates to Africa (unpublished data). We considered the nest-box area as a high-density area of kestrels. In the same valley, a similar control area of low density of kestrels was selected 8.5 km apart, a longer distance for the home range described for breeding kestrels in general (Village 1990). In this second area, the density of kestrels remained constant from 1994 to the year of this study in about 0.25 pairs/km² (Fargallo 1999, and own unpublished data). Both areas are plain, very homogenous in vegetation structure (100% grassland) with similar altitude (1,300 m a.s.l.), and no between-area differences have been detected in terrestrial or avian predators with the exception of kestrels (Fargallo 1999). In both areas exists about 1ha fenced exclosures where grazing has been avoided before 1994, allowing taller grass (Fargallo 1999;

Torre et al. 2007). In total, four exclosures are in the low-kestrel-density area and four in the high-kestrel-density area, with similar total surface coverage (about 5% of the total surface in high- and low-kestrel-density area). Our study area provides an excellent scenario to explore the effect of predation risk and the potential mediated effect of vegetation coverage. We visited nests during laying and nestling periods, allowing us to estimate laying, hatching date and fledging date (30 days after hatching). In the study area, beginning of laying starts at mid-April, and nestlings usually fledge in mid-July (own data). The average of each period for the population defined three categories: laying–incubation, chick rearing and fledging of kestrels.

Inter-annual variation in skylark predation

To analyse the inter-annual variation in the consumption of skylarks by kestrels, we recorded prey remains at kestrel nests over 9 years from 1995 to 2004 (we were not able to collect data in 1999) during the breeding season of kestrels, from laying to fledging just in the high-kestrel-density area. The mean \pm SD number of visits carried out per nest during the nestling period was 2.1 ± 0.3 , varying from 1.6 ± 0.8 in 1997 to 2.7 ± 1.5 in 1998. During all visits, excluding incubation, all prey remains found out in or around nests were recorded. When the presence of a skylark was noted, we removed the remains from the nest once it was completely eaten by kestrels to avoid double counts of the same individual. When possible, we aged the skylark remains as fledgling (with growing feathers) or full-feather-developed birds. The index of skylark prey remains each year was defined as the number of skylarks found divided by the number of sampled nests. We also obtained an index of skylark predation to evaluate the relative impact of skylark predation considering the number of kestrel breeding pairs each year. This was obtained by multiplying skylark-prey remains by the number of kestrel breeding pairs for each year.

Skylark abundance

Skylarks are sedentary in our study area and start laying in mid-May (own data). We estimated skylark abundance using observation points along the road that crosses the valley in 1998, 2002, 2003 and 2004 in areas of high density of breeding kestrel. At regular distances of 800 m, six points were selected. All points were visited for 5 min on which we recorded the number of visual contacts of skylarks at both sides of the road early in the morning during mid-April and mid-May. Mean values of April and May were considered to estimate breeding-skylark abundance. Strong windy and rainy days were avoided. We considered this method just for grazed areas because visual

contacts of the species in ungrazed areas were not possible from the road. Road censuses in 2002 showed higher skylark densities in the kestrel-free area (see “Results”), for which we decided to carry out a more detailed estimation in 2003.

In 2003, we carried out foot transects in grazed and ungrazed habitats. In both areas of low and high density of kestrels, we selected two grazed and two ungrazed plots. A minimum of three transects were carried out in each plot during the three breeding periods of kestrels described above, from mid of April until mid of July. Relative skylark abundance was measured by means of lineal transects in early morning in two consecutive days, always avoiding maximum sun exposure in summer. Probably, conspicuousness of skylarks change through the kestrel breeding period, and our method may be biased to detect these birds, but we assumed the same sampling error for both areas of breeding kestrel density. We measured the length of each transect with a Global Positioning System. In each transect, we recorded visual contacts on both sides of the transect line. Due to the high density of skylarks in some areas, we reduced the width of the band suggested in precedent works (25 m in Suárez et al. 2003) to 10 m to avoid replication of contacts. Relative abundance was standardized to number of skylarks per 100 m². Similar distances were surveyed between grazed and ungrazed and between kestrel areas. In both kinds of surveys, strong windy and rainy days were avoided.

Vegetation measurements

We measured the structure of the vegetation by means of a scored stick that was stood up five times around each point. We noted whether each stick touched herbaceous plants at 0, 0–5, 5–25, 25–50 and >100 cm height intervals. We also noted the height (to the nearest 10 cm) of the tallest contact of the vegetation with the stick. Therefore, we considered six variables for characterization of vegetation coverage. Average vegetation profiles for each area were derived from the proportion of contacts of each category out of the 40 sticks per area.

Statistical procedures

We used general linear mixed models (GLMM) with identity link and normal distribution of errors in SAS 9.1 software. When the dependent variable was number of skylarks, we considered Poisson error and log link function. Because we monitored skylark abundance in different plots within each area, the plot in which transects were carried out were included as a random factor to avoid pseudoreplication. Density of breeding kestrel (low and high), grazing (grazed or ungrazed) and breeding period (laying–

incubation, chick rearing and fledging), were considered as fixed factors. The variables representing vegetation cover were reduced by using a principal components analysis (PCA), extracting orthogonal components that can be interpreted as gradients of vegetation structure. To analyse differences in vegetation structure between grazing areas or kestrel density, we used the GLMM models with components extracted from PCA analyses as dependent variables. To explore temporal variations of skylark abundances (normally distributed, Kolmogorov–Smirnov test, $p > 0.10$) between habitats and areas, we performed analyses of variance of repeated measures in which averages of skylark abundances were considered as dependent variable. To control by potential effect of the time of the day at which the survey was carried out, we included this variable as covariate.

Results

Skylark consumption

From 541 vertebrate prey remains, 5.5% ($n = 32$) were skylarks, and 78.1% of them were fledglings, and from them, 21.9% were adults or with undetermined age. Within the same period, we found that skylark predation rate decreased significantly (GLMM, estimate = -0.05 ± 0.07 , $R^2 = 0.60$, $F_{1,8} = 10.67$, $p = 0.014$; Fig. 1a) from 0.67 to 0.19 skylarks per nest as the number of kestrel breeding pairs increased in the area (linear regression, estimate = 1.96, $R^2 = 0.82$, $F_{1,8} = 11.54$, $p = 0.007$. Fig. 1a). The index of skylark prey remains found each year was not affected by the mean number of visits to the kestrel nests ($F_{1,7} = 0.18$, $p = 0.683$). The index of skylark predation shows that peaks in 1997 decrease in 2001, and then increase again from 2002 to 2004 (Fig. 1b) and was not correlated with kestrel abundance (GLM, $F_{1,7} = 0.87$, $p = 0.217$).

Skylark abundances

In the high-density kestrel area, from the data obtained from road transects in 1998, 2002, 2003 and 2004, we found that skylark abundance decreased since 1998 (GLMM, estimate = 0.40 ± 0.11 , $F_{3,62} = 4.48$, $p = 0.06$, Fig. 2) which was driven by difference between 1998 and any other year (GLM, 1998 and 2002; 1998 and 2003; 1998 and 2004; all $p < 0.004$). No effect of sampling date was found (GLMM, $F_{3,62} = 1.25$, $p = 0.087$).

Road censuses from 2002 showed that the abundance of skylarks was lower in the area of high density of breeding kestrels (5.26 ± 0.66 and 1.72 ± 0.70 skylarks in low- and high-kestrel-density areas, respectively; GLMM, $F_{1,55} = 15.71$, $p < 0.001$, observation point as random variable, $Z = 1.49$, $p = 0.068$). There was no effect of seasonality on this

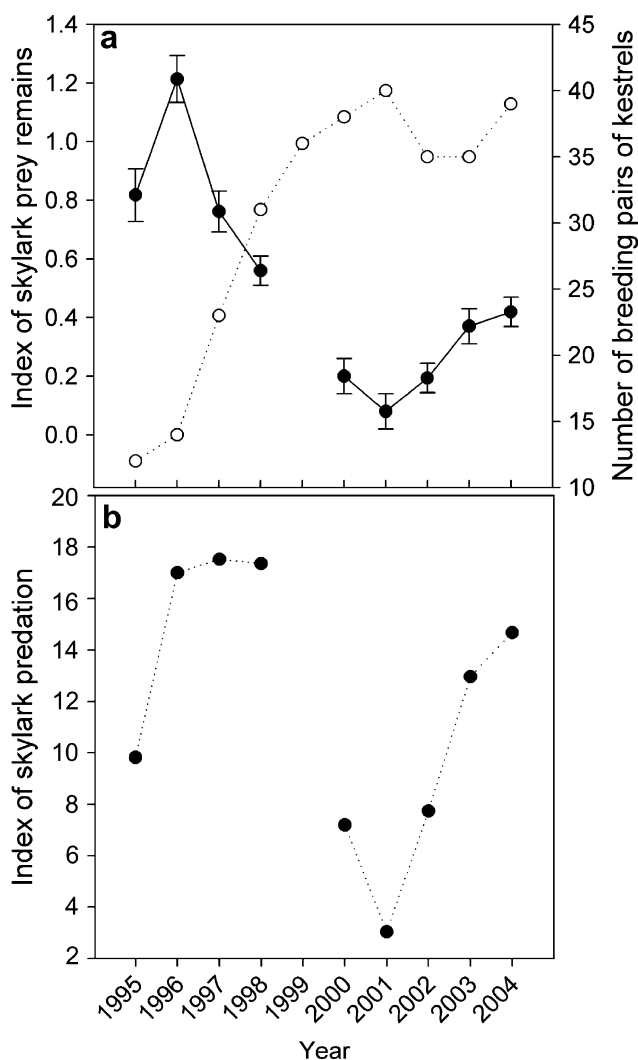


Fig. 1 Relationship between skylark predation and Eurasian kestrels. **a** The mean \pm SD of the index of skylark prey remains collected in kestrel nests (error bars) in relation to breeding density of kestrels (empty dots) during 10 years. Note that we did not record information for 1999. **b** The index of skylark predation obtained by multiplying the total number of breeding pairs of kestrels by the index of skylark prey remains (see “Materials and methods” for more details)

variation (GLM repeated measures, interaction reproductive period \times kestrel density, $F_{2,12} = 1.26$, $p = 0.268$).

In 2003, we carried out 58.7 km of linear transects, 30.88 km (52.61%) in the area of high density of kestrels and 27.81 km (47.39%) in the lower one and in grazed and ungrazed areas. PCA summarized the six variables considered for vegetation characterization of these two habitats in two components that explained 76.76% of the overall variance (Eigenvalues, PC1 = 2.51, PC2 = 1.84 explaining 45.53 and 31.23% of the variance, respectively). The first component was a direct gradient of herbaceous vegetation volume and height. The second component was associated with coverage of short herbs. We found significant differences between grazed and ungrazed areas in both compo-

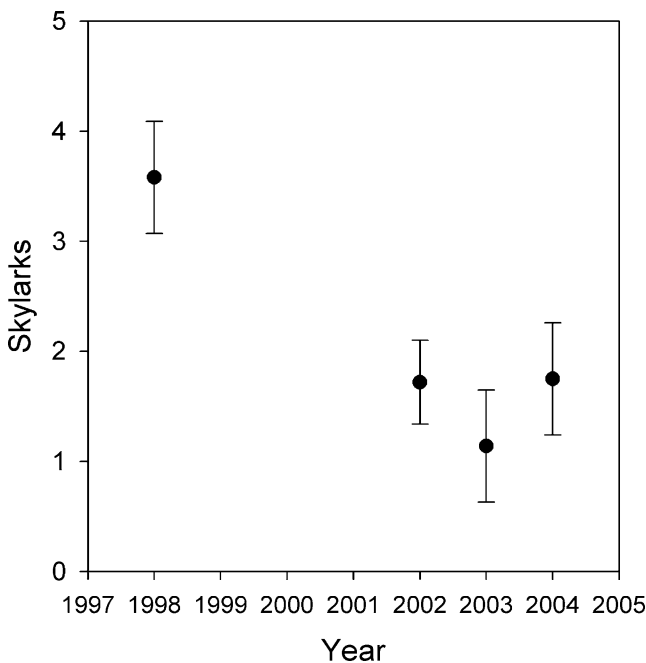


Fig. 2 Mean±SD of skylark counts in relation to year of monitoring within the high-density kestrel area

ment scores (GLMM, PC1, $F_{1,79} = 138.49, p < 0.001$; PC2, $F_{1,79} = 6.00, p = 0.015$), but not within areas in the different kestrel breeding density (grazed: component 1, $F_{1,79} = 0.05, p = 0.818$, component 2, $F_{1,79} = 1.78, p = 0.186$; ungrazed: component 1, $F_{1,79} = 1.59, p = 0.212$, component 2, $F_{1,79} = 1.20, p = 0.277$). Specifically, we found that ungrazed areas reached higher values for the first component and lower for the second component.

Skylark abundances were higher in the low density kestrel area ($F_{1,30} = 23.15, p = 0.006$). In addition, the interaction between habitat and kestrel density was significant (Table 1). Specifically, skylark abundances were always higher in grazed areas, but the difference in skylark abundances between grazed and ungrazed areas was greater in the low density of breeding kestrel area (interaction kestrel density × area, Table 1, Fig. 3a). GLM repeated measures suggested that there were no significant differences in skylark abundances among periods and between areas (interaction reproductive period×kestrel density, $F_{2,12}=0.27, p=0.620$, Fig. 3b). We did not find that this

interaction was affected by habitat type (GLM repeated measures, interaction reproductive period×kestrel density×habitat, $F_{4,12}=1.03, p=0.435$).

Discussion

Skylarks represent a small fraction of the vertebrates consumed by kestrels, and if taken, they were mainly fledglings. Their presence as prey remains decreased as the breeding kestrel density increased over the 9-year study period. Also, a decrease in skylark abundances was detected in an area of high density of breeding kestrels during a 4-year study period. Comparing high- and low-kestrel-density areas, we found that kestrels influenced skylark abundance. This relationship was mediated by habitat structure and remained constant during the kestrel breeding period.

Although the number of skylark prey remains found in each nest decreased as kestrel population increased, the total number of skylark consumed by the kestrel population represented by the index of skylark consumption was not correlated with kestrel abundance. The Eurasian kestrel is a generalist predator (Korpimäki 1986; Village 1990; Aparicio 2000) whose density in our study area is explained by vole and lizard abundances (forthcoming paper), and it is expected to change to alternative prey species (such as probably skylarks) when these prey species become scarce. This could explain the variation of the observed index of skylark consumption (Fig. 1b). This index decreased from the beginning of nest-box installation to 2001 and then increases again from 2002 to 2004 to approach the 1997/1998 level. However, in 1995, the consumption rate was lower compared with values observed in 1996, 1997 and 1998. This was probably due to a demographic explosion of *Microtus* voles observed during the winter–autumn in 1994 in the northern Iberian plateau (González-Esteban et al. 1995), in whose southern boundary is located our study site. The drastic increase in vole abundance was probably the cause of an unusual breeding onset in our kestrel population (1 month earlier) and also the occurrence of second clutches in the population (Fargallo et al. 1996),

Table 1 GLMM of the effect of kestrel abundance and habitat on skylark abundances

Dependent variable	Independent variables	Rejected terms	Estimate	F	Gl	P
Skylark abundances	Kestrel density Habitat Kestrel density×habitat			41.75	1.43	<0.001
				16.97	2.43	<0.001
				17.01	2.43	<0.001
		Kestrel breeding period	−0.0205	2.59	2.41	0.2734
		Day of sampling	0.0000	0.00	1.40	0.9919
		Daytime of sampling	0.0004	0.04	1.34	0.8326

Other potential interactions were not significant ($p>0.731$).

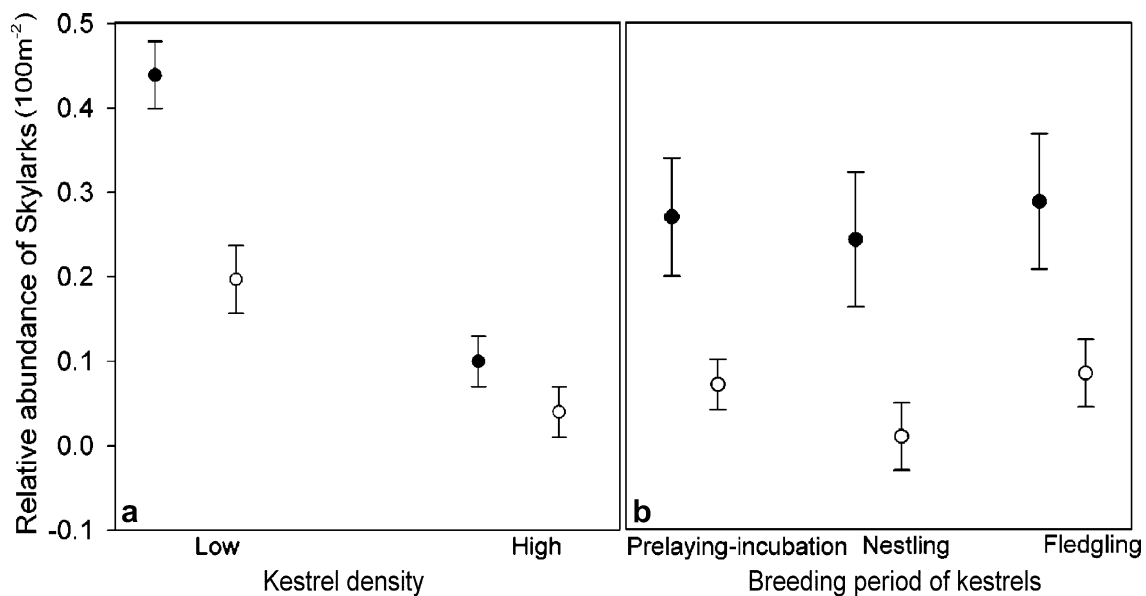


Fig. 3 Mean±SD of skylark relative abundance in relation to kestrel density and habitats (a). Open circles show grazed plots and filled circles show ungrazed plots. Mean±SD of skylark relative abundance

in relation to kestrel reproductive period (b) is also shown. Open circles suggest high density of kestrel area, while filled circles show low density of kestrel area

never observed again. In addition, the pattern found in skylark abundances during the period 2002–2004 was different from that found in the index of skylark consumption during the same period. This indicates that skylark predation rates by kestrels is not a good index to estimate skylark abundance, which is expected from a generalist predator able to change prey species. Therefore, the decline in skylark prey remains itself probably does not explain if kestrels depleted the skylark population or if skylarks avoided higher kestrel densities to minimise predation risk.

We found that skylark abundances were higher in areas where the breeding density of kestrel was lower. However, skylark abundance was similar at the beginning of the kestrel breeding season compared to its end. Energy requirements of breeding kestrels increase as the season progresses because of the higher energy intake of kestrel nestlings (Village 1990). Thus, if kestrels were reducing skylark density directly (predation hypothesis), it would be expected that skylark abundance would decline as the season progressed in the area of high kestrel density but not when kestrels are absent. With two different methodologies, we found that skylark abundances remained constant as the breeding season progressed in high- and low-kestrel-density areas. Higher predation on adult skylarks in late winter or early spring could make decrease skylark abundances before our first survey, masking a support for the predation hypothesis. However, prey analyses from pellets in our study area before kestrel breeding season suggest that only invertebrates (beetles and mole crickets—*Grillotalpa grillotalpa*) together with common voles (*Microtus arvalis*) are the main preys taken. Thus, our results support the predator

avoidance hypothesis for the particular case of skylark and kestrel system (Norrdahl and Korpimäki 1998). It suggests that skylarks avoid the vicinity of breeding kestrels such that kestrels have an intimidator effect on skylarks. By considering our results, we suggest that an increased breeding density of kestrels during the last years may force the skylarks to breed in other areas, which may explain the decline in their abundance rather than because of a direct intake.

The index of skylark prey remains obtained in 2002 and 2003 showed intermediate values in the study period (Fig. 1a). Despite that our study was carried out in a year with lower consumption rate than in 1996–1998 or 2004 (suggesting a lower predation pressure on skylarks), our results showed significant effects on skylark abundances.

Results from road and foot transects did not show increasing skylark abundances at the end of the kestrel breeding period. Thus, if kestrel predation had a significant effect on skylark densities, we should detect a significant interaction in the abundance of skylarks between dates and contrasting kestrel density areas, either due to an increase in the low-kestrel-density area in the last census or by a decreasing in the high-kestrel-density area due to predation. We show that the pattern is similar in both zones, so kestrel predation had not a significant effect on skylark abundance with respect to the onset of the breeding season. Our results also may support the idea that our surveys were prone to detect more conspicuous birds as conspicuousness decreases at the end of the skylark breeding season. However, the aim of the road transects was to detect inter-annual variation of skylarks in our study area and not

to evaluate absolute abundances. Conspicuousness of skylarks change through the season, but the pattern found is similar in both contrasting kestrel breeding density areas. Thus, we are confident that our results reliably show inter-annual and between-habitats changes in skylark abundances.

Our results also show that despite skylark abundances being lower in the high-density-kestrel area, the effect of kestrel density differed between grazed and ungrazed areas. We found that the decline of skylark abundance was higher in ungrazed areas compared to grazed ones. In the light of foraging theory, it is expected that raptors forage in patches yielding the greatest net energy gain (Stephens and Krebs 1986), and where prey species are not randomly distributed, the relationship between predators and a particular prey could be mediated by habitat (Thirgood et al. 2002). For kestrels in our system, we would expect foraging effort to be maximised in ungrazed plots where microtus voles, a main prey of kestrels, are more abundant (Torre et al. 2007). Additionally, skylarks may be showing a stronger selection for ungrazed habitats in high-density areas of kestrels to minimise predation risk. Low-grazing areas are key for many ground nesting birds (Evans et al. 2005). Thus, our results also suggest that skylarks might select ungrazed areas for breeding to diminish kestrel predation risk. Grazing pressure did not affect skylark abundance as the kestrel breeding season progresses. This supports the idea that the avoidance hypothesis was consistent between habitats.

Our study has also conservation implications. This is the first study to explore skylark abundances in grasslands (see Wilson et al. 1997 for agriculture-related habitats; Pearce-Higgins and Grant 2006 for moors) in southern Europe and in relation to a generalist predator that emphasizes the role of grasslands for conservation in southern latitudes. Grazing management may improve the habitat for skylarks in Mediterranean grasslands if small exclosures are provided in extensive systems. This would similarly favour other species, such as small mammals (voles, shrews and mice—Torre et al. 2007) and lizards (authors, submitted manuscript).

In conclusion, we suggest that the contrasting densities of skylarks found in high- and low-kestrel-density areas indicates that a generalist predator can exert a measurable effect on prey species abundance, even when these species represent a small fraction of the predator's diet. Finally, our study supports the predator avoidance hypothesis (Norrdahl and Korpimäki 1998) and suggests that kestrels have an indirect effect on skylarks.

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