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The role of natural habitats in agricultural systems for bird conservation: the case of the threatened Lesser Grey Shrike

David Giralt · Lluis Brotons · Francisco Valera · Anton Krištín

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Abstract Birds of agricultural systems are one of the most threatened groups of birds in Europe mainly due to their sharp population decline in recent decades. Habitat intensification resulting from more productive agricultural practices has been proposed as a major cause for these declines. However, especially in some regions such as Eastern European and Mediterranean countries, little is known about the ultimate factors linked to habitat intensification that drive population declines for different species. The Lesser Grey Shrike is a good study species for a better understanding of such processes since it is closely related to agricultural habitats in Europe and has suffered a strong decline in range and population size across the western half of the continent. In this study, we explored variations in breeding parameters of this shrike related to habitat composition and food supply at the territory level. We found that fledgling success of early breeders was related to the presence of natural (shrub lands) and semi-natural (fallows) habitats in the predominantly agricultural matrix that dominated breeding territories. Their influence on fledgling success appeared to be mediated by a higher arthropod availability on these habitats. Indeed, Lesser Grey Shrike showed a strong preference for these habitats as hunting locations. Our results highlight the importance of natural habitats in intensified agricultural land mosaics for the conservation of bird species. We suggest that management plans should pay special attention to the availability of habitats which serve as high quality food reservoirs and can potentially contribute to enhance the species population viability in an area. Finally, we

Centre Tecnològic Forestal de Catalunya, 25280 Solsona, Spain e-mail: david.giralt@ctfc.es

L. Brotons e-mail: lluis.brotons@ctfc.es

F. Valera Estación Experimental de Zonas Áridas (CSIC), 04001 Almeria, Spain e-mail: pvalera@eeza.csic.es

D. Giralt $(\boxtimes) \cdot L$. Brotons

discuss the possible link between agricultural intensification and Lesser Grey Shrike population declines in Western Europe.

Keywords Agro-ecosystems · Arthropod availability · Biodiversity conservation · Fallows · Habitat selection · *Lanius* · Natural habitats · Reproductive success · Shrub-land

Introduction

Birds of farmland and grassland habitats have the worst conservation status in Europe (BirdLife International 2004). Estimates of population change available since 1970 indicate alarming declines, with 58% of these species undergoing significant decreases during 1990–2000 (BirdLife International 2004). These declines have been attributed to widespread deterioration and fragmentation of agricultural habitats across the continent (BirdLife International 2004). Intensification of agricultural practices, such as crop specialization, pesticide use and elimination of natural and semi-natural habitats such as margins or fallows have been proposed causes underlying the reported decreases in the quality of agricultural habitats (Tucker and Evans 1997). Although it is clear that no single mechanism is responsible, changes in agricultural practices over the last decades have been successfully related to the onset and the continuous tendency of bird population declines or range contraction (Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2001; Benton et al. 2002).

The main mechanisms linked to agricultural habitat deterioration proposed to affect negatively bird dynamics through a combination of lower survival rate (Siriwardena et al. 1998) and reproductive output (Brickle et al. 2000; Siriwardena et al. 2000), have been: a reduction on food supply (Britschgi et al. 2006; Hart et al. 2006), the loss of key habitat features for nesting (Chamberlain et al. 1999; Browne et al. 2004) or foraging (Devereux et al. 2004; Butler et al. 2005) and direct mortality caused by specific farming practices (Crick et al. 1994; Corbacho et al. 1999). However, especially in some regions such as Eastern European and Mediterranean countries, we still ignore the ultimate demographic factors behind population changes for some conservation priority bird species (Donald et al. 2004; Newton 2004; Robinson et al. 2004).

Similar to other farmland birds, including shrikes, the populations of Lesser Grey Shrike have sharply declined and the species range contracted in Europe in the course of the last century, especially in the western half of the continent, from where it became extinct in many countries (Lefranc and Worfolk 1997). Threats for the species have been suggested to occur both in the breeding or winter quarters (Lefranc and Worfolk 1997; Herremans 1998), although there are more evidences supporting that causes acting during the breeding period have had a major role in population declines (see Lefranc and Worfolk 1997; Isenmann and Debout 2000; Giralt and Valera 2007). Agricultural intensification via the decrease in the abundance of large insect prey, as well as climatic processes, such as consecutive wet summers in central Europe leading to high rates of nest failure, have been suggested as important factors driving the population dynamics of this species (Krištín 1995; Lefranc 1995; Giralt and Valera 2007). As a result of the contraction and fragmentation of the western species range, small isolated populations remain now in areas of north eastern Spain and southern France, with less than 25 breeding pairs in each country (Giralt and Bota 2003; Rufray and Rousseau 2004; Giralt and Valera 2007).

The Lesser Grey Shrike occupies a variety of open habitat systems ranging form steppe, pseudo-steppe, grassland and farmland habitats, sparsely dotted with trees where it can build the nest. Territories include vineyards and fallows in France (Isenmann and Debout 2000),

short-grass steppes in Hungary (Lovászi et al. 2000), meadows, orchards and bare ground in Slovakia (Wirtitsch et al. 2001) cereal and pasture in Italy (Guerrieri et al. 1995) and cereal, sparse shrub land and fallows in Spain (Giralt and Bota 2003). The wide variety of occupied land-uses across the range of the species suggests that some agricultural practices are compatible with the presence of the species as far as some key vegetation features (coverage of bare ground/herbaceous/shrub) and/or certain insect prey are maintained (Krištín 1995; Lefranc and Worfolk 1997; Isenmann and Debout 2000; Wirtitsch et al. 2001).

Many authors have paid attention to the scarcity of large arthropods as a key aspect behind the decline of the species in intensified agro-ecosystems in Central and Western Europe (Krištín 1995; Lefranc and Worfolk 1997; Isenmann and Debout 2000). Krištín (1995) found that food-niche width was relatively small when compared to the one of a related, ecologically very similar species such as the Red-backed Shrike (*Lanius collurio*), since the Lesser Grey Shrike relied on a narrower range of insects in relation to their body size (large prey items of 23 mm on average) and taxonomic group (feeding almost exclusively on *Coleoptera* and *Orthoptera*) (see also Cramp and Perrins 1993; Giralt et al. 2004; Hoi et al. 2004). In spite of these disperse pieces of evidence on the importance of large insect prey availability and the presence of particular habitats or vegetation structures, there is a lack of detailed information about the mechanisms how these factors influence breeding the parameters of the Lesser Grey Shrike and may drive current population declines. In fact, the only study performed in this direction failed to find any relationship between habitat composition and breeding parameters (Wirtitsch et al. 2001).

In this paper, we aim to explore the potential relationship between food availability and habitat composition and use and their combined effects on the breeding performance of the Lesser Grey Shrike in a declining population at the south western border of its range. We hypothesise that food availability is a major criteria for shrikes' habitat selection and breeding performance and, thus, we predict: (i) habitat exploitation behaviour mediated by food abundance, and (ii) a direct relationship between habitat composition, food availability and breeding success. We focus on fledgling success (number of fledglings per successful nest) rather than on nest failure rate (failed nests in the population) given that the former was the only breeding parameter differing between the Spanish population and a healthy and stable population in Central Europe (own unpublished data, Krištín et al. 2000). The lower fledgling success in the Spanish population, caused by a high rate of partial losses of nestlings (23% of hatched eggs), is therefore probably liable for much of the decline in this region. Furthermore, we discuss to which degree the decline in western European populations may have been linked to the widespread loss of key habitats in the context of agriculture intensification. Because this shrike is always associated to partially or totally extensively managed agricultural habitats and appears to rely on the presence of large insects, it becomes a good study species to assess the effects of agricultural intensification process on farmland birds and biodiversity. In addition, given its unfavourable conservation status in Europe and its critical situation in isolated south western populations such as the Spanish one, our ultimate aim is to identify the key habitat features in order to develop adequate management aimed at stabilizing the remaining populations.

Study area and methods

Study species

The Lesser Grey Shrike is a long-distance migrant passerine that overwinters in the Kalahari basin, southern Africa, and breeds in warm, flat, open areas in Eurasia, extending from Kazakhstan in the east to northern Spain in the west and reaching to $54-55^{\circ}$ to the north in some areas of its distribution (Lefranc and Worfolk 1997). The breeding period typically extends from first days of May to mid July, laying taking place between the mid May and the first week of June. Incubation lasts 15–16 days and the nestling period normally between 16 and 18 days. Second clutches are not known, although replacement ones can be produced until the end of June. It is a monogamous and relatively gregarious species, breeding territories usually covering 6–8 hectares (Lefranc and Worflok 1997). Diet mainly consists of insects, particularly coleopterans and orthopterans, though sporadically can include vertebrates (Krištín 1995).

Study area and population

The Spanish Lesser Grey Shrike population is located at the Ebro basin, NE Spain, a flat area with a Mediterranean continental climate and only 300–400 mm of annual rainfall. The current population size is 20–25 pairs, divided in three small nuclei, two of them located 5 km far from each other and the third and smallest one, located 40 km away from the other two nuclei (Giralt and Bota 2003). Here we study one of these three nuclei that has been declining during the study period (2001–2005), holding 50% (7 out of 14 pairs) of the Spanish population in 2001 and only 15% (3 out of 15 pairs) in 2005. The study area is located along a 6 km long channel section where large trees are available for nesting. The channel separates dry cereal crops and natural and semi-natural habitats to the south from irrigated fruit trees to the north.

Foraging habitat selection

Foraging habitat selection was analysed for a total of 9 out of 26 breeding pairs (35%) in 2002–2004: 5 out of 11 pairs in 2002, 3 out of 8 in 2003 and 1 out of 7 in 2004. Several reasons account for this reduced sample size: (i) breeding failure precluded monitoring the foraging activity of eight pairs during the study period, (ii) four nests were located at the end of the breeding period and foraging activity could not be recorded, (iii) interannual overlapping territories with the same habitat composition, were not considered so as to avoid pseudo replication (five territories). Indeed, we only considered one repeated territory (2003–2004) since habitat composition differed markedly between years and, thus, we assumed that they were independent samples. Territory overlapping in the same year was observed for four pairs in 2002 but always represented less than 50% of the area of each plot (mean plot overlapping was $20.9 \pm 8.3\%$ SE, range 0–48.1%, n = 9).

We assessed habitat selection by comparing land use availability around each nest with the observed hunting areas of the respective adults. Land uses were mapped on a 1:5.000 scale at the start of the breeding period (second half of May) and updated at the beginning of June, after mowing and ploughing. Main habitats in the breeding area were crops, specifically dry cereal (barley and oats) and irrigated fruit-trees (apple and pear), while irrigated cereal occupied an insignificant area (see Results). Natural and semi-natural habitats were present and included shrub land (*Thymus vulgaris, Thymelea hirsuta*, etc.) and annual herbaceous fallows (*Sonchus oleraceus, Lolium rigidum*, etc.). Cereal fields were larger (2.58 \pm 0.43 ha, *n* = 10 fields) than irrigated fruit-tree fields (0.26 \pm 0.05 ha, *n* = 10), probably as a consequence of the lower economic profitability of the former, while natural and semi-natural patches had intermediate values in terms of size (1.74 \pm 0.51 ha, *n* = 8). All habitats remained stable (no human management) during the whole shrike breeding period, except for the dry cereal which was mowed and often ploughed during the laying period,

always before hunting activity data were collected. When ploughing occurred at that time of the season it was superficial still keeping cereal remains on the field. Thus we considered all stubbles in the same habitat category. Due to prevailing aridity of the study area, stubbles remained with low or very low plant cover (less than 15%) during the breeding period.

Whereas natural shrub-land and semi-natural fallow differed in dominant vegetation type (bush like in the first versus more herbaceous in the second), these two habitats keep meaningful similarities: (i) both had a null or very low degree of human management during the year, (ii) vegetation structure was very similar, with abundant patches of bare ground and sparse vegetation cover (<75% and very often between 25 and 50%, unpubl. data), (iii) the scarcity of precipitations (<400 mm of annual rainfall) and the hot spring and summer, precluded major seasonal changes in biomass, vegetation structure and floristic composition. Therefore, both habitat types were pooled in a single habitat category. In contrast to the surrounding cultivated land, shrub land and fallows showed a much higher degree of complexity in floristic composition, what is known to favour insect population density and stability (Morris 2000; Woodcock et al. 2007).

Land use availability was expressed as the percentage of area occupied by each habitat type in a 150 m radius plot centred on each nest. We considered this distance, equal to 7.1 ha, because it included most of the observed hunting events ($69.5 \pm 6.5\%$ SE; n = 9 pairs) in our study area, as well as for other populations (Lefranc and Worfolk 1997; Wirtitsch et al. 2001; own unpublish. data). Moreover, in our study area habitat composition farther from the nests closely resembles the one within the plot here considered.

Foraging use of each pair was surveyed with binoculars and telescope along the breeding period and expressed as the percentage of ground hunting events in each habitat, which were recorded during adults' trips from nest to hunting areas. One hunting event was defined as every flight to the ground or to the air to catch a prey done by a perching bird. Observations for each pair were gathered in series of 1-2 h of intensive visual tracking distributed in 3–4 non-consecutive days. During each series of intensive tracking, hunting events were considered independent and thus included in the analysis, if they were recorded in different trips from the nest to the hunting area. A total of 290 ground chases and 47 aerial chases were recorded for nine pairs, which averaged 32.2 ± 3.8 (SE) and 5.2 ± 1.5 (SE) hunting events per pair respectively. Since aerial chases were frequently difficult to relate to a specific habitat type and since the frequency or such chases was low compared to ground ones (1:6), we focused foraging selection analysis on the latter. To assess habitat selection for each pair, we compared the percentage of area of each habitat type around nests (150 m nest-centred plots) with the observed percentage of ground hunting events in each habitat.

Arthropod availability

Arthropod availability was estimated in 2003 and 2004 using pitfall traps (Cooper and Whitmore 1990). Pitfall traps are commonly used to sample ground-dwelling insects such as *Coleoptera* but they are less frequently used for sampling *Orthoptera* because they can underestimate their abundance (Gardiner et al. 2005). However, as *Orthoptera* caches have been shown to be unaffected by habitat type and being mostly related to insect density and activity (Topping and Sunderland 1992), we assumed that any possible bias could occur at similar levels in all habitats, allowing us to compare relative biomass between them.

The traps were distributed throughout the four most common habitat types within the breeding territories: cereal stubbles, irrigated fruit trees, fallows and sparse shrub-land. We selected three fields of each habitat type, all of them inside the shrikes' territories. In each

field we set four traps (10 cm of diameter) in a row 1.5 m apart from each other. All insects collected in each group of four traps per field were afterwards pooled and considered as our sampling unit. Thus, we obtained three sampling units (one per field) per habitat.

We sampled arthropod availability in two different periods (24 h each one): the first one between 1st and 3rd June, corresponding to the onset of Lesser Grey Shrike incubation period, and the second one between 30th June and 2nd July, corresponding to the second half of the nestling period. Thus, a total of three samples per four habitats, two periods and 2 years (=48 sampling units) had to be obtained, though pitfalls in two sampling points in 2004 were lost due to occasional sheep trampling, thus resulting in a final number of 46 sampling units.

Collected arthropods were preserved in 70% ethanol, identified in the laboratory at the family or genus level and assigned to a body length according to the most common size of each taxa. Only *Orthoptera* and *Coleoptera* larger than 10 mm were considered because they make up most of the diet of adult nestling shrikes (85–90% of prey items) (Krištín 1995; Giralt et al. 2004; Lepley et al. 2004). A total of 75 (year 2003) and 55 (year 2004) items were finally considered to calculate dry biomass (mg), on the basis of regression equations specifically performed for different families of insects (see Hódar 1996). Because we pooled different shaped and sized arthropods in the same analysis, biomass estimation should provide a more accurate picture of the occurring functional process than abundance (Saint-Germain et al. 2007). Therefore, arthropod availability is given as the dry biomass per sampling unit (four traps) and time (24 h.). Finally, given that Lesser Grey Shrike relies on the availability of large-bodied arthropods (Cramp and Perrins 1993; Krištín 1995) we separately estimated biomass for medium (11–20 mm) and large (>20 mm) sized items.

Effect of habitat types on fledgling success

We studied the relationship between habitat composition 150 m around the nest (area occupied by each habitat) and the number of fledglings produced by each pair (fledgling success). This analysis was performed for 22 breeding pairs, thus 61% of the studied population (2001–2005), from which the required information was available. We controlled for possible seasonal effects on clutch size or fledgling success by including hatching date in the analysis (Verhulst et al. 1995). Nests were checked during the breeding period (1–3 visits per nest) so as to provide accurate estimates of laying or hatching date. Fledgling success was obtained by counting the chicks with binoculars and telescope at the calculated fledgling date in order to minimise nest disturbance when fledglings were ready to fly.

We classified pairs in early and late breeders, considering their mean hatching date (17 June, n = 22). Mean hatching date of early and late breeders was 13 June (± 0.7 SE, range: 9–16 June, n = 11) and 22 June (± 1.3 SE, range: 17–30 June, n = 11) respectively. Then, we analysed the relationship between fledgling success and habitat composition and food availability for two different periods of the breeding season separately. In this way, any possible relationship between fledgling success and habitat composition could be better interpreted with data from our arthropod sampling periods, since the prevailing conditions for early breeders are best represented by our first sampling (all chicks of these pairs fledged before the second arthropod sampling) while the conditions experienced by late breeder are better represented by the second sampling.

Because our purpose was to study food-mediated habitat effect on fledgling success, we previously excluded from the analysis the failed pairs and one pair with only one fledgling, as we assumed that complete failure and heavy partial losses are probably more related to weather and predation than to food-mediated processes (Zanette et al. 2006). In addition, to

avoid pseudo replication on habitat composition, one pair in 2002 was excluded as its plot overlapped more than 50% with a neighbouring one. The mean overlap between adjacent territories was $10.6 \pm 4.1\%$ (SE) (range 0–48.1%, n = 22). Thus, our study was finally performed with 65% (11 out of 17) and 58% (11 out of 19) of the early and late breeding pairs of the population during the study period (2001–2005). As no inter annual variation was detected in fledgling success for early (Kruskall–Wallis test, H = 1.792, d.f. = 3; P = 0.617) or late breeders (Kruskall-Wallis test, H = 0.049, d.f. = 2; P = 0.976) we pooled data from all the study period in the respective regression analyses. Given that hatching dates were not evenly distributed among years, it was necessary to ensure that the relationship between habitat and fledgling success was not an artifact due to a year effect. Preliminary analyses of the data showed that removing any possible year effect made no difference to the aforementioned relationship.

Statistical analyses

To assess habitat selection for each pair, Chi-square analyses were applied by comparing observed and expected percentages of hunting events in the different habitats. Expected percentages were obtained by multiplying the total hunting events by the relative area occupied by each habitat in the 150 m plots. Yates' correction for continuity was applied for the cases when only two habitats had been used to hunt (Zar 1999).

Arthropod biomass was log-transformed and analysed by means of general linear models (GLM, Type III Sum of Squares), considering habitat, year and period as fixed factors.

Finally, the potential relationship between fledging success and the available types of habitat was analysed by means of multiple regression analysis using a forward selection procedure. Previously, to ensure independence of the area covered by the three main habitats in the plots, we performed a Factor Analysis (Varimax rotation), extracting two factors that explained 95% of the variance of the original variables. The two resulting factors and hatching date were then used as predictors in the multiple regression analysis.

Means and standard errors are given in all analyses unless otherwise stated.

Results

Foraging habitat selection

The mean number of habitats in nest-centred plots was 3.4 ± 1.7 (range: 3–4) (n = 9) as plot composition was clearly dominated by cereal stubbles ($38.2 \pm 4.9\%$, n = 9), irrigated fruit trees ($32.7 \pm 3.9\%$, n = 9) and natural habitats ($23.3 \pm 4.8\%$, n = 9) (Fig. 1). Irrigated cereal was almost residual ($4.0 \pm 2.6\%$, n = 9) and the remnant 1.8% of the area corresponded to "others" category (buildings, woody areas, etc.).

The main habitat types for hunting was the natural ones (Fig. 1), where $71.0 \pm 7.7\%$ of the hunting events were recorded (n = 9). The other two available habitats were avoided but for different reasons. First, irrigated fruit trees, in spite of being extensively available for all pairs, were clearly ignored, as only 3 out of 290 chases from 2 out of 9 pairs were recorded in this habitat (and thus excluded from most chi-square analyses). Second, all pairs often used cereal stubbles as a hunting habitat ($26.7 \pm 8.3\%$, n = 9) but always below the expectations according to their availability in the landscape (Fig. 2).

Foraging habitat selection of early and late breeders followed the same pattern, both groups showing a clear preference for natural habitats and a negative selection for cereal stubbles and irrigated fruit-trees (Fig. 2). However, intensity of selection appeared to be



Fig. 1 Percentage of area occupied by the main habitat types on 150 m circular nest-centred plots (filled squares) and percentage of ground hunting events in each habitat (empty squares) (n = 9 territories). Mean percentages and standard errors are represented



Fig. 2 Mean residuals of Chi square analyses for each foraging habitat type by early (n = 6) (stripped bars) and late (n = 3) (filled bars) breeders. Sample size in irrigated fruit-trees is one territory both for early and late breeders as this habitat had to be excluded from most of the analyses. Means and standard errors are represented

higher in early than in late breeders, as it is reflected by the higher absolute values of residuals in the former (Fig. 2). Finally, aerial chases (n = 47 observed in the nine pairs) showed a similar pattern than ground chases: 40% were performed within natural habitats, 19% in cereal stubbles and 0% in irrigated fruit-trees (the remnant 41% of aerial chases could not be attributed to a single habitat type).

Arthropod availability in the habitats

A total dry biomass of 16,003 mg of medium sized (11–20 mm) and large sized (>20 mm) orthopterans and coleopterans was collected during 2003 and 2004, corresponding



Fig. 3 Dry biomass (mg) of large arthropods (>20 mm) by habitat and period (filed and empty squares correspond to the first and second sampling period respectively). Means and standard errors are represented

basically to three families: *Tenebrionidae* (*Coleoptera*) 32%, *Gryllidae* (*Orthoptera*) 28%, and *Carabidae* (*Coleoptera*) 20%. A mean dry biomass of 397.5 \pm 104.3 mg (n = 24 sampling units) and 293.8 \pm 68.4 mg (n = 22) was collected in 2003 and 2004 respectively. Per habitats, mean biomass per sampling point was 463.1 \pm 102.5 mg (n = 24) in natural habitats, 340.7 \pm 87.8 mg (n = 10) in cereal and 123.5 \pm 81.2 mg (n = 12) in irrigated fruit-trees. Mean dry biomass at the start and at the end of the breeding season was 401.9 \pm 103.5 mg (n = 23) and 293.9 \pm 73.5 mg (n = 23) respectively.

Large arthropod (>20 mm) biomass variability was partially explained by the habitat factor (Table 1) (GLM, Habitat: F = 3.33, P = 0.04, d.f. = 2), natural habitats supporting two to three times higher biomass than irrigated fruit-trees and cereal stubbles (Fig. 3). These differences tended to be more pronounced at the start than at the end of the breeding season, although the large variability observed probably hindered significance of the interaction effect (GLM, habitat*period: F = 2.5, P = 0.09, d.f. = 2). Dry biomass variability of medium sized insects (11–20 mm) was not explained by any of the considered variables (Table 1), although cereal stubbles tended to have higher medium-sized insect availability in 2004 (GLM, habitat*year interaction F = 2.81, P = 0.07, d.f. = 2).

Effect of habitat on fledgling success

Mean fledgling success was 4.3 ± 0.2 (range 2–7) fledglings/pair (n = 22), being higher for early (4.8 ± 0.2 , range 4–6, n = 11) than for late breeders (3.8 ± 0.4 , range 2–5, n = 11) (Welch test, t = 6.37; d.f. = 1,14.9; P = 0.023).

The three main habitats present around the nests were summarized in two factors explaining 95% of the total variance in the original variables (Table 2): the first factor ("human management") explained 62% of the variance and included natural habitats and cereal stubbles, and thus was related to a gradient from cropped (negative values) to abandoned

Dependent variable	Effect	Sum of squares	df	F	Р
Log arthropod	Habitat	9.79	2	3.33	0.047*
>20 mm	Year	0.05	1	0.04	0.850
	Period	0.05	1	0.03	0.856
	Habitat*Year	1.59	2	0.54	0.587
	Habitat*Period	7.34	2	2.51	0.095
	Habitat*Period*Year	0.58	2	0.20	0.823
	Error	51.42	35		
Log arthropod 11–20 mm	Habitat	7.07	2	2.62	0.087
	Year	0.64	1	0.47	0.497
	Period	0.00	1	0.00	0.983
	Habitat*Year	7.59	2	2.81	0.074
	Habitat*Period	3.19	2	1.18	0.319
	Habitat*Period*Year	0.59	2	0.22	0.804
	Error	47.26	35		

Table 1 Effects of habitat type, year and period on log10 of arthropod biomass (mg) (GLM type III)

Table 2 Factor analysis of thethree main available habitat types	Original variables	Factor 1	Factor 2	
(Varimax rotation)	Cereal stubbles Irrigated fruit-trees Natural habitats Explained variance <i>R</i> ²	-0.869 0.071 0.967 62%	-0.412 0.988 -0.100 33%	

Table 3 Effect of parameters related to habitat composition (factor 1 = human management, factor 2 = irrigated cultures) and hatching date on fledgling success (no. of fledglings/successful pairs) of early Lesser Grey Shrike breeders (n = 11)

Variables	Beta coefficient	Р	Model
Constant	4.879	0.000	$F = 16.83, P = 0.003, R^2 = 0.61$
Factor 1	0.608	0.003	
Factor 2	-0.071	n.s	
Hatching date	0.016	n.s	

or less managed areas (positive values). The second factor (33% of the variance) included the extension of irrigated fruit-trees and thus provided information about the presence of irrigated land around shrike nests.

A forward multiple regression analysis provided a significant model (F = 16.8, d.f. = 10; P = 0.003) with the "human management" factor explaining 61% of fledgling success variability of early breeders (t = 4.1, P = 0.003) (Table 3). Indeed, the area occupied by natural habitats around nests was positively correlated with fledgling success of early breeders (Pearson correlation, r = 0.79, P = 0.004, n = 11) (Fig. 4). Although the mean area occupied by natural habitats around nests was similar for early (1.4 ± 0.2 ha, n = 11) and late (1.7 ± 0.3 ha, n = 11) breeders (Welch test, t = 0.63; d.f. = 1,16.5; P = 0.44), this positive effect did not arise for late breeders (no significant model was found), whose clutches hatched on average 9 days later (13 June vs. 22 June). Furthermore, the "irrigated cultures" factor had no effect on fledgling success of early or late breeders.



Fig. 4 Correlation between fledgling success of early Lesser Grey Shrike breeders and availability of natural habitats (hectare) at the 150 m nest-centred plots

Discussion

Habitat selection mediated by arthropod availability

Adult Lesser Grey Shrikes did not hunt at random within their breeding territories; rather they showed a clear habitat selection pattern both for early and late breeders. First, permanent natural areas proved to be the key habitat during foraging since they received 70% of total hunting events, much more than expected by the availability of this habitat (Figs. 1, 2). Second, even though cereal stubbles were visited by shrikes (about 25% of hunting events) they were used less than expected from their availability. Finally, irrigated fruit-trees were clearly avoided as less than 1% of the hunting events were recorded in this habitat. Percentage of aerial chases showed the same pattern of habitat usage than ground chases, thus confirming that habitat selection was independent of the displayed hunting technique.

This pattern of selection was congruent with among-habitat differences in large arthropod (>20 mm) abundance measured by means of dry biomass (Fig. 3). Natural habitats had two to three times more biomass of large insects than the other habitats. Therefore, a higher probability to find large orthopterans and coleopterans in every hunting trip would be determinant in the foraging habitat selection pattern shown by adult shrikes in the breeding territories. A trend for a reduced difference between habitats in arthropod availability at the end of the nestling period existed, although a larger sample size would be needed to confirm this seasonal effect (Fig. 3). On the other hand, abundance variability of medium sized insects (11–20 mm) could neither be attributed to the habitat type nor to the sampling period and year (Table 1).

Apart from insect abundance, other factors such as vegetation cover or perch availability and thus, prey access, can play a complementary role on foraging habitat selection as it has been demonstrated for shrikes and other "sit & wait" predators (Stephens and Krebs 1986; Yosef and Grubb 1994). In this sense, Wirtitsch et al. (2001) found in a stable and dense, slovak Lesser Grey Shrike population located in a traditionally managed agrosystem with high arthropod abundance, that mowed meadows and bare ground were the key habitats for hunting, as their lower plant cover offered higher prey access to shrikes. In southern France, the Lesser Grey Shrike population seemed to profit from ecotones of rich-food habitats (fallows) and low vegetation cover areas (vineyards), although foraging selection and arthropod availability was not directly analysed (Isenmann and Debout 2000). Although we did not assess prey access, plant cover did not seem to be a limiting factor in our arid study area (less than 400 mm of annual rainfall), since all habitats offered patches of bare ground (pers. obs.). Thus, in contrast to the Slovak population, for Spanish birds, the presence of natural habitats with large insect abundance appeared to be a key aspect in foraging selection, probably as a result of a higher degree of agriculture intensification in cropland habitats: for example, 37% of the area around shrikes' nests was occupied by fruit-trees, which were continuously sprayed with pesticides during the whole Lesser Grey Shrike breeding period because of the high risk to develop fungal and insect pathologies (spraying was very rare in the study area of the Slovak population, pers. obs.). Effectively, considering total biomass of medium and big arthropods, irrigated fruit trees was the poorest habitat in terms of food resources. With reference to cereal crops, the second most abundant habitat in our study area, mowing and very often ploughing occurred just at the start of the breeding season. This agricultural practice is known to negatively affect insect availability, especially of larger insects (Beintema et al. 1991).

Effect of natural habitats on reproductive output

Concerning early breeders, our results support the prediction that fledgling success is favoured by the availability of rich-food hunting habitats. We found that the number of fledglings produced early in the season by a successful pair was positively related to the extension of natural habitats in the 150 m nest-centred plots (Table 3, Fig. 4). Furthermore, cereal stubbles as well as irrigated-fruit trees had no significant effect on reproductive output, which was in accordance with the fact that they were negatively selected during hunting trips and that they held lower availability of large insects. In the context of central place foraging theory (Orians and Pearson 1979) and considering that the Lesser Grey Shrike is a single-prey loader (Krištín 1995), we thus suggest that higher availability of large arthropods in natural habitats allows shrikes to improve their energy trade off during hunting activity, bringing more food per trip to chicks and thus minimizing nestling mortality (Sejberg et al. 2000; Redpath et al. 2006).

However, the reproductive output of late-breeders was not seemingly affected by habitat composition at the territory level. This is remarkable because late breeders still preferred to hunt on natural habitats (Fig. 2) and these pairs showed a non significant trend to occupy territories with higher availability of natural habitats (1.7 ha vs. 1.4 ha). In addition, we detected a marginal seasonal trend for large insects to decrease in abundance in natural habitats (Fig. 3), which could account for the lack of relationship and could be give sense to the observed lower fledgling success of late breeders. This temporal food decrease should be confirmed in further studies, since foraging behaviour indicated that no other habitat could replace natural habitats as a food source for chicks. Although natural habitats continued to

be the main food-reservoir of large insects at the end of the season, such decrease could lead insect availability below a certain threshold, insufficient to avoid nestling starvation or to allow us to detect a positive effect of this habitat on fledgling success. Finally, considering that we just detected a non significant prey biomass decrease of 25% across the season in natural habitats (Fig. 3), we cannot reject the existence of other major factors that could hinder the importance of territory habitat composition and prey availability for late-breeders. Although beyond the aim of this study, we suggest that predator processes (Zanette et al. 2006; Rastogy et al. 2006) or reproductive constraints imposed by the short breeding season and long-distance migratory behaviour (Siikamaki 1998; Hemborg et al. 2001) of this species, could be more essential for the reproductive output of late-breeders than habitat composition.

Conservation implications

Fragmentation and loss of uncultivated or non-crop habitats, such as open shrub land and fallows, has been a common process in the increasingly intensified agricultural ecosystems across Europe in the last century, parallel to the decrease of many agricultural birds (Bird-Life International 2004). As it has been described for the whole Iberian peninsula (De Juana et al. 1988), in our study area sparse shrub land has been progressively replaced during the last century by crops with the help of more powerful tractors and with the aim to increase crop production, while fallows have become much less essential due to a greater availability of fertilizers coming from pig livestock (Suárez et al. 1996). Here we find that these habitats, which are rapidly disappearing in current European agricultural landscapes, have a positive effect on fledgling success of at least a fraction of the Lesser Grey Shrike population (early breeders), because they provide higher resource availability, specifically through a higher abundance of large orthopterans and coleopterans. According to our results, at least 1.5 hectares of natural habitats at a maximum distance of 150 m from the nest (thus at least 20% of the surrounding area) should be necessary for a pair to produce five fledglings (Fig. 4), which is supposed to be the actual threshold for the viability of Spanish population (unpublished data). As natural habitats should represent more than 20% of the area in the surroundings of the Lesser Grey Shrike breeding territory to ensure the aforementioned productivity and population viability, we suggest to apply the same percentage at a landscape level in breeding sites where intensive nest search is not viable. Therefore, these habitats, which function as food reservoirs in intensified agricultural ecosystems improving Lesser Grey Shrike reproductive output and population viability, should be maintained and specially favoured at the territory and landscape level when developing and applying management plans. In fact, the presence of these habitats is often pointed out as an important requirement for the conservation of many other farmland birds in Europe (Tucker and Evans 1997; Brickle et al. 2000; Soderstrom et al. 2001). Nevertheless, we have found evidences that a seasonal reduction of large prey could be limiting the reproductive output of late breeders in our study population. Thus, further research is needed to identify and neutralize through management actions the factors that are limiting their breeding performance, as a way to increase their contribution to the overall reproductive success of the population.

To our knowledge, this is the first time for the endangered Lesser Grey Shrike that some habitat feature has been successfully linked to such an important demographic parameter (fledgling success). Thus, though very likely not the only one, we have identified an important mechanism linking habitat deterioration, resource availability and reproductive output. Despite the small population size from where these conclusions are extracted, it seems therefore feasible, as other authors have suggested (Krištín 1995; Lefranc and Worfolk 1997), that the species decline across Europe during the second half of the last century could be partly related to the process of substitution of natural and semi-natural habitats (margins, shrub land, fallows, pastures, etc.) by intensified crop monocultures. In the countries of EU 15, this process has been more pronounced in continental Europe than in Mediterranean areas (Donald et al. 2001), paralleling the extinction and fragmentation pattern of west European Lesser Grey Shrike populations: extinction in the north (e.g. northern France, Germany, Belgium) but small populations still existing in the south (Spain, south France and Italy). Due to the unfavourable conservation status of the Lesser Grey Shrike, it would be a priority for these remnant Mediterranean populations to detect and favour the key habitats that function as arthropod prey reservoirs. Finally, the same should be considered in eastern European countries that have recently joined the EU, such as Romania and Bulgaria, where the Lesser Grey Shrike has its last European strongholds.

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