Coarse landscape features predict occurrence, but habitat selection is driven by specific habitat traits: implications for the conservation of the threatened Woodchat Shrike *Lanius senator*

Running head: Habitat selection in Woodchat Shrike

Author Head: M. Brambilla *et al.*

Mattia Brambilla[1,2,3]*, Marco Gustin[1], Egidio Fulco[4], Alberto Sorace[1,5], Claudio Celada[1]

[1] Lega Italiana Protezione Uccelli (LIPU/BirdLife Italia), Via Trento 49, I-43100 Parma, Italy

[2] Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976 1, I-20822 Seveso, MB, Italy

[3] Museo delle Scienze, Sezione di Zoologia dei Vertebrati, Via Calepina 14, I-38122 Trento, Italy

[4] Studio Naturalistico Milvus, C/da Pantano 134, I-85010 Pignola PZ, Italy

[5] SROPU, Via R. Crippa 60, I-00125, Roma

*Author for correspondence;

e-mail: brambilla.mattia@gmail.com

Summary

Habitat selection has fundamental implications for species conservation, and in birds is often regarded as a multi-scale process. We investigated (under an information-theoretic approach) habitat selection in Woodchat Shrikes (one of the most severely declining species in central and western Europe) in Italy, considering five main types of potential determinants of shrike occurrence at the territory scale (1 ha): general structure (coarse landscape), woody vegetation, grassland habitats/bare ground, herbaceous crops, management variables. The most supported models for species occurrence were those including general structure and woody vegetation traits. Variation partitioning suggested that overall landscape general structure and woody vegetation explained the highest variation in shrike occurrence, and management the lowest; however, considering the exclusive variation explained by single level, all levels performed nearly equal, but general structure did not explain any exclusive proportion of variation. A multi-level analysis suggested that shrike occurrence was eventually associated with specific habitat traits: isolated trees, shrubland and (secondarily) olive grooves (all with positive effects), and dirty roads (negative effect). The most parsimonious multi-level models included only variables from woody vegetation and management traits, suggesting that the likely true determinants of species occurrence are highly specific and fine-scaled habitat traits, consistently with variation partitioning. Woodchat Shrikes inhabit semi-open landscapes, within which they are attracted to shrubland and isolated trees (secondarily to olive grooves), and avoid dirty roads. Suitable habitat conditions for the species depend on a trade-off between abandonment and intensive farming, and Rural Development Programmes may be crucial for the conservation (or loss) of such conditions.

Keywords

agricultural intensification; conservation; habitat preferences; land abandonment; Passeriformes

Introduction

Habitat selection is a key process with fundamental implications for species conservation (Cody 1985, Jones 2001). It is defined as the process an organism uses to choose its habitat, which results in habitat preferences consisting in differential use of specific resources relative to their availability (Hall *et al.* 1997).

The choice of a habitat by a species has often been regarded as the outcome of a process interesting multiple spatial scales (e.g. Johnson 1980, Orians and Wittenberger 1991, Jones 2001, Brambilla *et al.* 2010a). In several bird species, habitat selection seems to occur firstly at coarser scales, and then at finer scales, according to a hierarchical process (Johnson 1980, Jones 2001, Battin and Lawler 2006, Brambilla *et al.* 2006). Therefore, multiple scales representing 'coarse' and 'fine' habitat variables are often considered in habitat selection studies, especially for avian species.

Several birds species are threatened by unfavourable changes to their breeding habitat at different levels (Tucker and Evans 1997), and a particularly alarming case is represented by farmland birds (Fuller *et al.* 1995, Siriwardena *et al.* 1998, Krebs *et al.* 1999), which are dramatically and widely declining largely because of agricultural intensification (Tucker and Evans 1997, Chamberlain *et al.* 2000, Donald *et al.* 2001, 2006), especially through loss of ecological heterogeneity (Benton *et al.* 2003, Vickery and Arlettaz 2012), and land abandonment (e.g. Brambilla *et al.* 2010b). Both intensification and abandonment may affect the habitat of a species at different levels, from landscape structure (Suarez-Seoane *et al.* 2002, Benton *et al.* 2003, Brambilla *et al.* 2010b) to fine-scaled vegetation traits (e.g. Vickery and Arlettaz 2012).

Understanding the factors affecting habitat selection and the scale at which they act is thus necessary to promote species conservation and particularly urgent for threatened farmland birds. Among them, Woodchat Shrike *Lanius senator* is probably one of the most severely declining species in a large part of Europe, showing a continuous decrease since some decades in central and western Europe, whereas recent trends for southeastern Europe are less negative (BirdLife

International 2015). This species was formerly distributed in all the Mediterranean region and in central Europe, but has underwent large population decline and range contraction and now occurs mostly in southern Europe, where it is anyway still declining in the western countries (BirdLife International 2015). The decline of the species in Italy is particularly alarming: the species' population underwent a 70-80% reduction in the period 2000-2012 (Nardelli *et al.* 2015) and is currently classified as ‘Endangered’ (Peronace *et al.* 2012), with a ‘bad’ conservation status (cf. Brambilla *et al.* 2013a). Similar declines have been reported in the recent past for other countries, such as Spain, France, Switzerland, Germany, Poland, Croatia and Greece (BirdLife International 2015).

The Woodchat Shrike has been reported to be associated with different natural and anthropic landscape traits (Table 1). On the basis of the previous knowledge, we identified some main types of potential determinants of species occurrence: i) general habitat structure, i.e. coarse landscape characteristics, ii) woody vegetation (e.g. trees, shrubs), iii) grassland habitats and bare ground, iiii) cultivated (herbaceous) crops, and iiiii) human-related variables (grazing management, roads, fences). The general habitat structure included environmental variables allowing for a coarse description of land cover and topography in the cells: this kind of variables are comparable to the ones which can be extracted by commonly available GIS layers. The other levels included more detailed descriptors of the species, which should be generally recorded in the field (as it was in our study case), or obtained by means of more sophisticated approaches.

[Table 1 approximately here]

With this work, we aim at identifying the habitat factors affecting species occurrence at the territory level and at evaluating the relative importance of different categories of habitat factors, corresponding to the five groups outlined above, which have been already reported as potentially important for the species (Cramp and Perrins 1993, Shochat *et al.* 2002, Filippi-Codaccioni *et al.*

2010). Those individual levels represent different kinds of environmental factors which can potentially affect the occurrence of Woodchat Shrike at the territory level. Evaluating their relative importance has important implications for conservation, as the maintenance or restoration of suitable conditions for the species should be pursued by means of different strategies (e.g. landscape planning vs. agri-environmental schemes), according to what types of factors drive shrike occurrence.

Methods

Study areas and fieldwork

Woodchat Shrikes were censused in two different study areas (Fig. 1): Tolfa (Central Italy, Rome province, Lazio region) and hilly areas of Matera province (Southern Italy; Basilicata region). The two areas were selected as representative of extensive farming landscapes of the Mediterranean region, i.e. the most important macro-habitat of the species in Europe. Within the two areas, we defined seven and 12 sample plots, respectively, each one covering some tens of hectares. These plots include open and semi-open landscapes in areas with climate suitable for Woodchat Shrike. To each area, four visits were made by the same observers (A.S. in Tolfa, E.F. in Basilicata), in April–June 2011. The observers annotated all shrike contacts on maps (1:2000), recording all territorial and breeding behaviours, such as carrying food for chicks, member of a pair seen together, singing males, aggressive behaviours, calling of juveniles, nest alarm, occupied nests. Pair territories were defined on the basis of all contacts with the species and were distinguished among each other mostly on the basis of simultaneous observations of different pairs or singing males, as usually done with passerine birds (e.g. Birrer *et al.* 2007, Ceresa *et al.* 2012, Brambilla *et al.* 2013b).

[Figure 1 approximately here]

A grid of 100 m × 100 m cells (1 ha-cells) was then superimposed to each study plot. The specific cell size was established on the basis of the territory size of the species reported in literature (Harris and Franklin 2000, Lefranc and Worfolk 1997), often being fairly small (no more than 1 ha) (Cramp and Perrins 1993). A cell was defined as occupied by the species when it included one territory of the species (in one single case, two territories were comprised within the same cell). When needed, the exact location of the cells including territories was manually adjusted to better match the territory extent. Grid cells were then used as sample units for territories and control plots, and all habitat variables recorded referred to the 1-ha cells. Within each one of the 19 sample plots (see above), unoccupied 'control' cells were randomly selected in the same number of occupied ones. This led to an average number of 1.7 occupied and 1.7 control cells within each sample plot; this balanced design prevented clustering of territories within the two areas and the associated potential spatial biases.

Habitat variables

We recorded directly in the field some habitat variables describing the following habitat characteristics: i) the general structure of the habitat, ii) the specific features of the woody vegetation, i.e. trees, shrubs and permanent (woody) crops, iii) the type of the herbaceous layer and the occurrence of rocky or bare surfaces, iiii) the features of cultivated (herbaceous) crops, and iiiii) variables describing human management and impact, such as road and fence length and occurrence of grazing domestic animals (Table 2). Habitat variables were recorded in all the selected cells (occupied and unoccupied; see above).

[Table 2 approximately here]

Statistical analyses

Land-cover variables were arcsin square-root transformed before analyses. In each subset, VIF (Variance Inflation Factor) values were lower than 2.2 in all cases; in the multi-scale final model (see below), VIF values were lower than 1.6.

To qualitatively describe the habitats occupied by the species, we performed a comparison of habitat features between occupied (N = 33) and unoccupied cells (N = 33), evaluating differences by means of a t-test or a χ^2-test (the latter adopted for grazing occurrence; Table 3).

Then, we built GLM models with territory occurrence as the dependent variables, by relating it to the different habitat variables. We adopted an information-theoretic approach (Burnham and Anderson, 2002), performing a two-steps analysis. As a first step, to evaluate the relative importance of each group of variables and of individual factors within each group, all possible models for each group were ranked using the Akaike Information Criterion corrected for small sample sizes (AIC_c). We checked the potential occurrence of quadratical relationships by entering the squared term of each variable, and then retained in the set of variables entered in the model the quadratic terms that showed a negative effect coupled with a positive effect of the linear term. As a second step, from each of the five different types of habitat traits, we selected the variables included in the most parsimonious models (models with $\Delta AIC_c < 2$) for each group, with the exception of the 'uninformative parameters' (cf. Arnold 2010). The latter are variables included only in models that comprised more parsimonious and simpler models as nested ones (Ficetola *et al.* 2011); AIC_c used as the unique criterion for model selection may indeed over-select complex models (Richards 2005). With the resulting set of variables, we worked out a single, multi-scale model. Then, all possible models were ranked according to AIC_c, and an average model was obtained by averaging the most supported models (models with $\Delta AIC_c < 2$).

Model ranking according to AIC_c and model averaging were done using the package

'MuMIn' (Bartoń 2014) in R (R Development Core Team 2013).

We finally performed a variation partitioning analysis to compare the contribution of variables measured at different scales in affecting habitat selection by Woodchat Shrike. This analysis makes a partition of the variation in habitat selection into components associated with different levels. To reduce the number of levels (maximum number allowed for the analysis is four), we summarised our levels into the following ones: i) general structure, ii) woody vegetation, iii) grassland, bare areas and cereals, iiii) management and anthropic traits. The fractions of variation were calculated from the adjusted R^2, which allows an unbiased estimation of the portions of the variation explained by single levels and by their combination (Peres-Neto *et al.* 2006). This analysis was carried out by means of the “vegan” package (Oksanen *et al.* 2013) in R.

Results

Woodchat Shrikes (34 territories occurring within 33 cells) occupied cells characterized by a prevalent cover of grassland, which on average occurred over around half of the cell, and with a significantly higher availability of isolated trees and shrubland than unoccupied cells (Table 3).

[Table 3 approximately here]

Among the different sets of candidate models reflecting different potential determinants of habitat selection in shrikes, the ones including the most supported models were general structure and woody vegetation (Table 4).

[Table 4 approximately here]

At the general landscape level, Woodchat Shrikes were associated with intermediate grassland cover and (small) patches of bare ground. Regarding woody vegetation, shrikes preferred areas with higher availability of isolated trees, olive grooves and shrubs (especially the ones below 1 m). The analyses based on descriptors of grassland and bare soil habitats revealed a quadratical effect of grazed grassland, and a minor negative effect of bare ground. Considering herbaceous crops, a quadratical relationship with cereal crops different from wheat and barley was found. Among human and management traits, the most important factor was the length of dirty roads within the cell, which exerted a negative effect on species occurrence.

In the multi-level analysis, the most supported models (ΔAIC_c <2) were averaged and led to the model described in Table 5. Residuals of the two most parsimonious models approached a normal distribution, and the R^2 of both models was equal to c. 0.27. According to the averaged model, obtained from a set of possible models considering the most important factors from the different levels considered, shrike occurrence was favoured by isolated trees, shrubland and (secondarily) olive grooves, and negatively affected by dirty roads (Table 5).

[Table 5 approximately here]

Variation partitioning suggested that the landscape general structure and woody vegetation explained the highest variation in shrike occurrence, and management the lowest; however, when considering the variation exclusively explained by each single level, all levels are nearly equal, except for general structure, which did not explain any exclusive portion of variation (see Fig. 2).

[Figure 2 approximately here]

Discussion

In birds as well as in other animals species, the choice of the breeding habitats is a key process, and can be affected by environmental factors acting at different spatial scales (e.g. Ficetola *et al.* 2011), or of very different nature, e.g. from land-cover type to topographical and management attributes (e.g. Chiatante *et al.* 2014) and highly specific resources (e.g. Jedlikowski *et al.* 2014). Conservationists should thus identify the scale(s) and the factors likely most important for species habitat selection and focus on these key resources.

Several farmland bird species have been declining over decades in Europe and elsewhere, largely because of habitat changes induced by intensification and other modifications in the farming regime (Donald *et al.* 2001, Benton *et al.* 2002), but also because of land abandonment, which has negative impacts especially on Mediterranean birds (Preiss *et al.* 1997, Suárez-Seoane *et al.* 2002); both those pressures may alter habitat at different levels. Woodchat Shrike has been declining since some decades in most of its European range, which constitutes the major portion of its global distribution (BirdLife International 2015), this creating concerns on its future perspectives. Although conditions experienced in wintering areas and during migration are also potentially important for the species (Cramp and Perrins 1993), breeding habitat availability and quality are likely to be crucial for its conservation, as they are for other shrike species (e.g. Red-backed Shrike, *Lanius collurio*; Brambilla *et al.* 2009, 2010b), thus it is essential to identify factors driving species occurrence.

Here, we analysed some different kinds of potential determinants of shrike occurrence, considering different categories of habitat descriptors and evaluating their relative importance. Finally, from the output of this analysis, we selected the factors most likely involved in the habitat preferences of the species, and evaluated what are the most important habitat variables eventually associated with habitat selection by Woodchat Shrikes. Such habitat factors are likely also the most relevant for conservation through habitat preservation or restoration in breeding quarters, including Italy, where the species underwent a dramatic population decline coupled with a 15% range contraction in the last decade (Nardelli *et al.* 2015), and in the rest of the Mediterranean region, where the species usually inhabits similar semi-open landscapes.

Among the different subsets of candidate models, the one describing the general landscape structure and that characterizing woody vegetation included the most parsimonious models. The final models better describing habitat selection by Woodchat Shrikes included only variables from the woody vegetation and from human related traits. This could suggest that, although landscape 'coarse' variables are able to capture most of the variation when different sets of variables are considered in isolation, the true determinants of species occurrence are likely to be represented by highly specific and fine-scaled habitat traits. This is further confirmed by the variation partitioning analysis, which highlighted how the variables belonging to the landscape structure did not explain exclusive parts of variation, despite explaining a large amount of it in conjunction with other variables. In short, this means that landscape variables may be successfully used to predict species occurrence, but are likely less important when planning habitat management for conservation. This seems to be a rather common pattern for shrike species, which are associated to well-defined landscapes but show a strong selection (or avoidance) for very specific habitat traits within such landscapes (Brambilla *et al.* 2009, Chiatante *et al.* 2014).

The association with intermediate grassland cover detected at the landscape level clearly reflects the general link with semi-open habitats, characterized by a mosaic of grassland or grassland-like cover and shrubs and trees (Cramp and Perrins 1993, Nisoria 1994, Guerrieri and Castaldi 2000), whereas the positive selection for small extent of bare ground is likely due to the need for areas where the collection of invertebrate preys is enhanced by their high detectability and accessibility (cf. Nisoria 1994, Schaub 1996, Cramp and Perrins 1993). The positive effect of isolated trees, shrubs and olive grooves mirrors the need for nesting and perching sites well known for that species (Cramp and Perrins 1993 and references therein). Considering the other types of habitat traits, a quadratical relationship with cereal crop had been already reported from another area in southern Italy (Chiatante *et al.* 2014), and is consistent also with anecdotal evidence reported from central Italy (Guerrieri and Castaldi 2000). The analyses based on descriptors of grassland and bare soil habitats revealed a quadratical effect of grazed grassland, and a negative effect of bare ground in grazed grassland. The former is fully consistent with the association with semi-open landscapes (see above), whereas the latter is a bit contrasting with the selection for small patches of bare ground found at the landscape level, but it should be noted that such a negative effect of this specific type of bare ground is likely minor (the retention of the variable into the model resulted in a negligible improvement of model fit, see Table 4). The negative effect of dirty roads found in the human-related model had never been reported before, and suggests a negative effect of anthropic disturbance on the species.

Conservation implications

Woodchat Shrikes inhabit semi-open landscapes (on average, territories are made up by c. 52% of grassland, and c. 16% of arable land), within which they are attracted to shrubland and isolated trees (and secondarily to patches of olive grooves), whereas they tend to avoid dirty roads. As already reported for the Red-backed Shrike (Brambilla *et al.* 2007, 2009a, 2010, Ceresa *et al.* 2012) and for other farmland bird species in Italy (e.g. Brambilla *et al.* 2008, 2009b, 2013a, Rippa *et al.* 2011), the maintenance of suitable conditions for the species depends on a trade-off between abandonment and intensive farming, which are both highly detrimental to species preferring semi-open landscapes. The general model built upon the results of the single-level models confirmed the importance of isolated trees, shrubland, olive grooves and dirty roads, suggesting that the availability of nesting and perching sites and the lack of direct human disturbance could be key features for the species in semi-open Mediterranean landscapes.

Those results may be used for the definition of conservation measures and in particular for an updating or revision of agri-environmental measures, such as those included in the Rural Development Programme (RDP). The main implications of our findings are: i) the importance to conserve low-intensity farmland systems, which harbour a compact mosaic of open habitats, different crops and shrub/tree patches, positively selected by several species of conservation concern, including Woodlarks (Brambilla and Rubolini 2009, Brambilla *et al.* 2012), pipits (Morales *et al.* 2012), shrikes (Brambilla *et al.* 2010, Chiatante *et al.* 2014), buntings (Brambilla *et al.* 2012, Brambilla 2015); ii) the need to preserve some woody vegetation, and in particular shrubs and isolated trees, which have been reported to be favoured also by another threatened shrike species, the Lesser Grey Shrike *Lanius minor* (Chiatante *et al.* 2014). Some national or regional RDPs include among the measures adopted for grassland conservation the removal of trees and shrubs; controlling shrub encroachment is often needed to conserve open habitats, especially when they are facing abandonment, but should be done with care (Vassilev *et al.* 2011) to avoid the removal of breeding and perching sites for shrikes and other bird species (Nikolov 2010).

Furthermore, frequently RDPs include measures promoting the realization of new roads in cultivated areas to improve access to crops and fields. Considering the negative effect of dirty roads on the species occurrence, it would be important to prevent the realization of new roads in farms hosting Woodchat Shrikes or other sensitive species, and caution should be used about road promotion in RDPs.

In conclusion, our suggestions confirm and integrate previous recommendations for Woodchat Shrikes in Mediterranean landscapes, which focused on management primarily targeted at increasing perching and nesting sites, such as isolated trees and shrubs, in open landscapes with low levels of urbanization (Chiatante *et al.* 2014).

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Table 1. Factors affecting woodchat shrike occurrence and habitat selection according to the available literature.

Factor	**Type**	**Effect**	**Source**
landscape openness	landscape	semi-open landscapes occupied	Cramp and Perrins 1993
slope	landscape	flat or gently sloping areas preferred	Cramp and Perrins 1993, Chiatante *et al.* 2014
trees	woody vegetation	tall and sparse trees needed, wood pastures occupied	Cramp and Perrins 1993, Salvo 2004, Radišić *et al.* 2008
shrubs	woody vegetation	shrubs or scrubland required	Cramp and Perrins 1993, Guerrieri Castaldi 2000, Radišić *et al.* 2008
garigue	grassland and bare ground	garigues occupied	Cramp and Perrins 1993
shrubs	woody vegetation	shrubs of average height 3.4 m preferred	Guerrieri and Castaldi 2000
woody crops	woody vegetation	associated with old orchards	Cramp and Perrins 1993, Salvo 2004, Radišić *et al.* 2008
grazing	human management	areas grazed by domestic animals preferred	Tucker and Evans 1997, Guerrieri and Castaldi 2000
grassland	grassland and bare ground	preys chased in sparse grass	Nisoria 1994
bare ground	grassland and bare ground	preys chased in bare patches	Nisoria 1994
cereal crops	cultivated crops	included in territories when contiguous to grazed grassland	Guerrieri and Castaldi 2000
cereal crops	cultivated crops	associated with intermediate cover	Chiatante *et al.* 2014
pseudosteppe	cultivated crops	associated with steppe-like habitats	Chiatante *et al.* 2014
cables	human features	favoured by length of cables	Chiatante *et al.* 2014
urbanized areas	human features	negatively affected by suburban areas	Chiatante *et al.* 2014

Table 2. Habitat variables considered in this study to evaluate habitat selection according to five different levels of habitat traits.

Variable	**description**
general structure	
slope	slope in degrees within the cell
herb_layer	percentage cover of all grassland and grassland-like habitats (excluding arable land)
shrub_tot	percentage cover of all shrub habitats
bare_tot	percentage cover of all types of bare ground
urban	percentage cover of urbanized areas
arable	percentage cover of arable land
fine-level habitat: woody vegetation	
shrub_1	percentage cover of shrubland lower than 1 m
shrub_1_3	percentage cover of shrubland of height comprised between 1 and 3 m
shrub_3	percentage cover of shrubland taller than 1 m
woodland	percentage cover of woodland
isolated_shrubs	percentage cover of isolated shrubs
isolated_trees	percentage cover of isolated trees
shrubland	percentage cover of compact shrubland
olive_groove	percentage cover of olive grooves
fine-level habitat: grassland and bare areas	
grazed_grass	percentage cover of grazed grassland
unmown_grass	percentage cover of unmanaged grassland
rock	percentage cover of rocky areas
bare_ground	percentage cover of grazed bare soil
gariga	percentage cover of gariga (herbs and sparse shrubs of arid areas, height<50 cm)
fine-level: herbaceous crops	
pseudosteppe	percentage cover of pseudosteppe
wheat_barley	percentage cover of wheat or barley
other_cereals	percentage cover of cereals different from wheat or barley
mixed_fodder	percentage cover of mixed fodder crops
management and anthropic traits	
fences	length (m within the cell) of fences

paved_road	length (m within the cell) of paved roads
dirty_road	length (m within the cell) of unpaved roads
goats_sheeps	occurrence of grazing goats or sheeps (0/1)
cows	occurrence of grazing cows (0/1)
horses	occurrence of grazing horses (0/1)

Table 3. Average features of shrike territories and control plots; * indicates significant ($P < 0.05$) differences (assessed by means of a t-test on arc-sin square-root transformed variables for land cover and road length, and by χ^2-test for grazing occurrence).

Variable	**territory**	**control**
	mean ± SE	**mean ± SE**
general structure		
slope	13.94 ± 1.89	12.70 ± 1.85
herb_layer	51.55 ± 5.51	54.36 ± 6.43
shrub_tot*	25.06 ± 3.20	15.39 ± 2.68
bare_tot	1.76 ± 0.51	6.00 ± 2.22
arable	16.03 ± 5.47	23.33 ± 6.54
fine-level habitat: woody vegetation		
shrub_1	11.79 ± 3.15	7.12 ± 1.97
shrub_1_3	7.39 ± 1.45	4.48 ± 1.06
shrub_3	5.88 ± 1.58	3.79 ± 1.63
woodland	2.12 ± 1.19	1.82 ± 1.54
isolated_shrubs	5.24 ± 1.17	4.33 ± 1.15
isolated_trees*	4.06 ± 0.86	1.36 ± 0.36
shrubland*	12.73 ± 3.34	5.00 ± 2.01
olive_groove	0.91 ± 1.96	4.55 ± 8.08
fine-level habitat: grassland and bare areas		
grazed_grass	21.76 ± 5.32	27.88 ± 6.79
unmown_grass	4.09 ± 3.01	0.30 ± 0.30
rock	1.09 ± 0.42	0.76 ± 0.37
bare_ground	0.61 ± 0.36	4.09 ± 2.25
gariga	6.21 ± 3.84	8.18 ± 3.81
fine-level: herbaceous crops		
pseudosteppe	19.48 ± 5.73	18.00 ± 5.80
wheat_barley	4.76 ± 3.33	3.94 ± 2.75
other_cereals	8.79 ± 4.17	18.18 ± 6.36
mixed_fodder	2.48 ± 2.48	1.21 ± 0.95
management and anthropic traits		
fences	3.94 ± 2.38	11.82 ± 7.12
paved_road	1.52 ± 1.52	3.03 ± 3.03
dirty_road	0.61 ± 0.61	9.39 ± 4.81

goats_sheeps (frequency)	0.27	0.15
cows (frequency)	0.67	0.55
horses (frequency)	0.27	0.24

Table 4. Candidate models reflecting different potential determinants of habitat selection in Woodchat Shrikes. The most supported models (ΔAICc ≤ 2) are shown per each subset of variables. For categorical variables, the symbol + indicates inclusion in the model; for continuous variables, the β value is reported to illustrate the effect on species occurrence.

models							**AICc**	**Δ**	***ω***
general structure									
intercept	bare_tot	bare_tot^2	herb_layer	herb_layer^2	slope				
-0.46	15.80	-66.89	7.44	-6.22			86.0	0.00	0.080
-0.81	15.85	-69.70	7.79	-6.64	0.04		86.7	0.71	0.056
fine-level habitat: woody vegetation									
intercept	isolated_trees	olive_grooves	shrubs_1	shrubs_1_3					
-1.50	7.11	3.34	2.43				86.7	0.00	0.150
-1.24	5.99		2.47				87.8	1.11	0.086
-1.85	5.63	3.86	2.84	2.11			87.9	1.20	0.083
-0.79	6.03	3.12					88.3	1.63	0.066
fine-level habitat: grassland and bare areas									
intercept	bare_ground	grazed_grass	grazed_grass^2	rocky_areas	unman_grass				
0.11	-2.86	5.76	-5.65				91.1	0.00	0.106
-0.04		5.62	-5.44				91.4	0.25	0.094
-0.12		5.66	-5.41		1.92		92.4	1.24	0.057
0.04	-2.72	5.79	-5.61		1.74		92.5	1.32	0.055
-0.15		5.83	-5.62	2.19			93.1	1.93	0.040
fine-level: herbaceous crops									
intercept	other_cereals	other_cereals^2							
	4.32	-3.95					93.2	0.00	0.091
	-0.66						94.3	1.04	0.054
management and anthropic traits									
intercept	dirty road	cows	goats_sheeps	horses	fences	paved_roads			
0.12	-0.04						91.5	0.00	0.103

-0.21	-0.04	+					92.6	1.02	0.062
-0.01	-0.04		+				92.8	1.27	0.055
0.04	-0.04			+			93.4	1.84	0.041
0.15	-0.04					-0.01	93.4	1.90	0.040
0.15	-0.04				-0.01		93.5	1.95	0.039

Table 5. Average model obtained by averaging the most supported models ($\Delta AIC_c < 2$; uninformative parameters excluded) among the ones built combining the most important habitat variables from each single level (see text for details). For each variable, the coefficient in the model (± SE for the averaged model) and the relative variable importance are shown. The latter is calculated considering the sum of weights of the models in which each variable appears (Burnham and Anderson 2002).

model	**intercept**	**dirty_road**	**isolated_trees**	**olive_groove**	**shrubland**	**logLik**	**AICc**	**delta**	**weight**
1	-1.49	-0.07	9.76	3.53	3.11	-33.5	78.0	0.00	0.19
2	-1.21	-0.07	8.52		3.13	-35.09	78.8	0.84	0.12
averaged	-1.38 ± 0.51	-0.07 ± 0.05	9.27 ± 2.95	3.53 ± 2.44	3.11 ± 1.21				
variable importance		1.0	1.0	0.6	1.0				

Figure 1. Location of study areas in Italy. Each study areas included 7-12 plots within which fieldwork was carried out.

Figure 2. Results of variation partitioning for the occurrence of woodchat shrike in terms of fractions of variation explained by the different levels. Variation in occurrence is explained by four groups of explanatory variables (the two fine-level habitat types "grassland and bare areas" and "herbaceous crops" were considered together in this analysis; see text for details).