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Research Paper

Functional habitat suitability and urban encroachment explain temporal and spatial variations in abundance of a declining farmland bird, the Little Bustard *Tetrax tetrax*

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ABSTRACT. Species response to land use can be examined under a functional perspective, where habitats are described according to species' resource dependencies. Distribution or abundance models based on resource availability rather than land use types can be more informative about the ultimate processes behind observed population or distribution trends. Habitat use may depend on resources available, as well as disturbances that affect accessibility to such resources. Increasing human presence and urban encroachment may thus alter the relationships between habitat suitability and species abundance. Using 10 years of field data, we investigated whether variability in Little Bustard (*Tetrax tetrax*) abundance was explained by functional habitat suitability (assessed through resource-based models) and urban encroachment. We found that spatial and temporal variations in Little Bustard abundance were explained by functional habitat suitability and avoidance of urban areas, but that the significance of each variable varied with spatial scale. Little Bustard abundance at each observation point significantly increased with local nesting but not foraging habitat suitability, and decreased with increasing proportion of urban areas. At larger spatial scales, temporal changes in Little Bustard abundance were highly significantly related to changes in foraging habitat suitability. Moreover, the positive relationship between foraging habitat suitability and Little Bustard abundance weakened as the proportion of urban areas increased, and almost disappeared when the proportion of urban areas was more than 5%. Our results underline the benefits of using resource-based models to better understand processes that relate animal abundance and habitat suitability, while simultaneously considering avoided elements of the landscape.

L'adéquation fonctionnelle de l'habitat et l'empiètement urbain expliquent les variations temporelles et spatiales de l'abondance d'un oiseau champêtre en déclin, l'Outarde canepetière, *Tetrax tetrax*

RÉSUMÉ. Le comportement des espèces en fonction de l'affectation des terres peut être examiné dans une perspective fonctionnelle, selon laquelle les habitats sont décrits suivant la dépendance des espèces envers les ressources. Les modèles de répartition ou d'abondance fondés sur la disponibilité des ressources, plutôt que sur le type d'affectation des sols, peuvent être plus informatifs sur les processus ultimes qui sous-tendent les tendances observées en matière de population ou de répartition. L'utilisation de l'habitat peut dépendre des ressources disponibles et des perturbations qui affectent l'accessibilité à ces ressources. La présence humaine croissante et l'empiètement urbain accru peuvent donc modifier les relations entre l'adéquation de l'habitat et l'abondance des espèces. En utilisant 10 ans de données prises sur le terrain, nous avons cherché à savoir si la variabilité de l'abondance de l'Outarde canepetière (*Tetrax tetrax*) s'expliquait par l'adéquation fonctionnelle de l'habitat (évaluée par des modèles basés sur les ressources) et l'empiètement urbain. Nous avons constaté que les variations spatiales et temporelles de l'abondance de l'Outarde canepetière s'expliquaient par l'adéquation fonctionnelle de l'habitat et l'évitement des zones urbaines, mais que l'importance de chaque variable variait selon l'échelle spatiale. L'abondance de l'outarde à chaque point d'observation a augmenté significativement avec l'adéquation de l'habitat local pour la nidification mais pas pour l'alimentation, et a diminué avec la proportion croissante de zones urbaines. À des échelles spatiales plus grandes, les changements temporels de l'abondance de l'outarde étaient fortement liés aux changements de l'adéquation de l'habitat pour l'alimentation. De plus, la relation positive entre l'adéquation de l'habitat pour l'alimentation et l'abondance de l'outarde a diminué à mesure que la proportion de zones urbaines augmentait, et l'espèce était presque totalement absente lorsque la proportion de zones urbaines était supérieure à 5%. Les présents résultats soulignent les avantages de l'utilisation de modèles fondés sur les ressources pour qu'on comprenne mieux les processus qui relient l'abondance des animaux et l'adéquation de l'habitat, tout en considérant simultanément les éléments du paysage qui sont évités.

Key Words: *foraging habitat suitability; human avoidance; nesting habitat suitability; population declines; population processes; resource-based models*

INTRODUCTION

Habitat change is one of the most important drivers of alterations in species distribution or abundance. The potential effects of changing landscapes on species' dynamics have been frequently addressed through correlative models whereby species–habitat associations are estimated by relating presence or abundance to the availability of particular land cover types (Dormann et al. 2012). While these models have provided valuable information for understanding species ecological requirements and conservation threats (e.g., Carone et al. 2014, Phifer et al. 2017, Tarjuelo et al. 2020), they commonly fail when extrapolated outside the area or habitat conditions for which the model has been calibrated (Graf et al. 2006). Furthermore, even when significant correlations between species abundance or trends and land use changes are found, those associations do not always allow for an understanding of the processes underlying them (Buckley et al. 2010, Dormann et al. 2012).

As an alternative to using structural land cover types in modeling approaches, land use–species relationships might be better examined under a functional perspective, where habitats are described on the basis of resource dependencies of a species or a group of species (Fahrig et al. 2011, Butler and Norris 2013). Developing distribution or abundance models based on resource availability rather than land use types is likely to allow more robust predictions, even under changing environmental conditions, and can be more informative about the processes behind observed population or distribution trends (Butler and Norris 2013); e.g., the relative importance of modified nesting versus foraging resources.

Nonetheless, habitat use may not just depend on resources provided by different land covers but also on disturbance levels that might affect accessibility of individuals to such resources. In particular, increasing human presence and urban encroachment in many landscapes may alter the relationships between habitat suitability and species abundance. Exposure to human-related disturbances may increase stress in wildlife, alter behavior, and modify habitat use (Arlettaz et al. 2007, Carrete and Tella 2010, Tarjuelo et al. 2015, Casas et al. 2016, Arroyo et al. 2017, Rabdeau et al. 2021). The presence of human infrastructures may also lead to avoidance of certain areas, even if they are covered by land uses that provide valuable resources (e.g., Eldegard et al. 2012, Díaz-Ruiz et al. 2016, Filla et al. 2017). Avoidance of those areas may result in changes in distribution and, ultimately, population sizes (e.g., López-Jamar et al. 2011). In a time when the presence of humans and their infrastructures is increasing everywhere, this should be taken into account to better understand the relationships between habitat suitability and species abundance (Torres et al. 2016).

Farmland is a particularly dynamic social-ecological system that under certain conditions can support rich biodiversity (Pain and Pienkowski 1997). However, the process of agricultural intensification experienced from the second half of last century has led to much higher agricultural production (Tilman et al. 2011) but also to a decline in farmland biodiversity, including birds (Donald et al. 2001, Benton et al. 2002, Gregory et al. 2019, Reif and Vermouzek 2019), which it is ongoing. There is a crucial need to assess the effect of current and future potential changes in agricultural landscapes on farmland biodiversity to identify

contexts where both agronomic and ecological sustainability may be simultaneously attained (Firbank 2005). With this aim, it is important to have a better understanding of the processes responsible for declines in farmland bird populations that are associated with changes in land use or management in order to design solutions that are compatible with present-day agriculture (Henle et al. 2008). Following this perspective, Cardador et al. (2014) developed a resource-based model framework to estimate habitat suitability for target farmland bird species, according to information on two of their key resource requirements: diet and preferred vegetation height in foraging or nesting habitats. This approach provided habitat suitability estimates that correlated with local species distribution (Cardador et al. 2014) and allowed the impacts of several alternative farming systems on farmland bird habitat suitability to be anticipated (Cardador et al. 2015). Such a framework could also be used to explain variations in abundance of target species. Moreover, buildings and human infrastructures are increasingly abundant within farmland areas, as in many other habitat types, and this may alter the relationship between resource availability and species abundance patterns (Rabdeau et al. 2021). Exploring whether species abundance is related to patterns of habitat suitability assessed through resource-based models, and whether this relationship is modulated by human infrastructures in the farmland matrix, may help identify the most relevant processes behind abundance changes (e.g., loss of foraging resources versus loss of available places for nesting), which is a crucial step for developing more effective policies to protect declining species.

We explored the associations between habitat suitability inferred from resource-based models and abundance of a farmland bird of conservation concern, the Little Bustard (*Tetrax tetrax*). This species has suffered strong declines throughout its breeding range in western Europe (Morales and Bretagnolle 2021), which are associated with changes in agricultural land uses and practices that are thought to reduce availability of suitable nesting areas or food supply (e.g., Wolff et al. 2001, Martínez and Tapia 2002, Traba and Morales 2019), although the specific processes behind the declines or the relative contribution of different processes are still not clear in all areas. Additionally, this species is known to be sensitive to human disturbance (Casas et al. 2009, Tarjuelo et al. 2015, Estrada et al. 2016), and increasing pressure from infrastructures in farmland is considered a threat to the species (Silva et al. 2021). The proximity of houses and built-up areas, beyond the direct effects of disturbance, may enhance the negative effects of habitat degradation by reducing access to available resources.

Using 10 years of field data on this species in a study area in central Spain (Casas et al. 2019), we evaluated whether spatial or temporal variability in Little Bustard abundance was explained by functional habitat suitability (i.e., variations in nesting or foraging habitat suitability), and whether urban encroachment modified the relationships between habitat suitability and the species' abundance.

METHODS

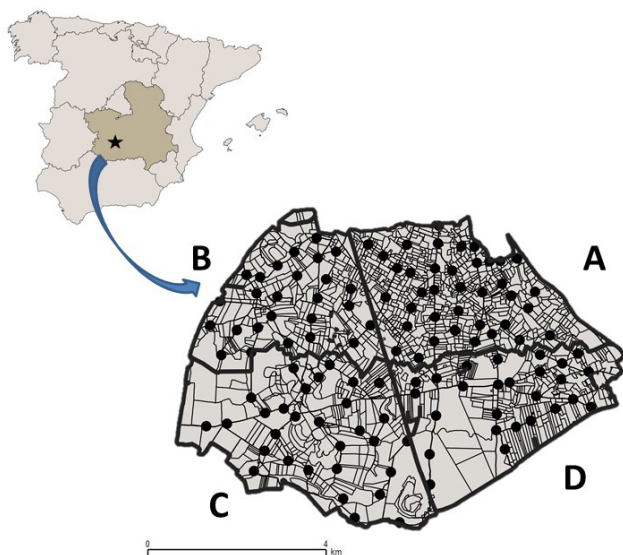
Study area and species

The Little Bustard is a charismatic species of European agroecosystems, and its most important Western European breeding

populations are in Spain (García de la Morena et al. 2018). The species suffered strong population declines throughout its range during the last century (Morales and Bretagnolle 2021) and has disappeared from many European countries (Schulz 1985). It is classified as “Near Threatened” worldwide and “Vulnerable” in Europe (BirdLife International 2015). At the end of the last century, major declines in the Little Bustard population occurred in the highly intensified farmland of western France (Jolivet and Bretagnolle 2002); at the beginning of the 21st century, a decline was also first noticed in the cereal and long-term fallow mosaic areas of southwestern Iberia (De Juana 2009, Delgado and Moreira 2010). A recent national survey indicated that populations in Spain had declined approximately 50% in 10 years (García de la Morena et al. 2018).

Our study was conducted in Campo de Calatrava (Ciudad Real, central Spain, approximately 38°54' N, 3°55' W) (Fig. 1) within a Special Protection Area. The area, which covers 54.66 km², is flat to slightly undulating (590–685 masl); it is used primarily for the cultivation of dry cereal (> 75%) and to a lesser extent includes olive groves (*Olea europaea*, 3–5% of the area), leguminous crops (1–5% of the area), and vineyards (*Vitis vinifera*, approximately 3% of the area). Cereal is grown in a traditional way, which creates a mosaic of sown, ploughed, stubble, and fallow fields of different ages. Grape vines are grown either in a traditional way—free standing without any attachment (goblet-shaped)—or as trellised vines with partial irrigation. The area has been highlighted as a hot spot for steppe birds (Traba et al. 2007) and supports a significant population of breeding Little Bustards, which has declined steeply in recent years (Casas et al. 2019).

Fig. 1. Location of the study area within the Castilla-La Mancha Region (black star), distribution of 120 observation points within the study area (black circles), and delimitations of the four subareas (thick lines and letters). Thin black lines delimit agricultural plots.



Little Bustard abundance and habitat data

Field surveys were conducted at the peak of Little Bustard breeding display activity (April) from 2002 to 2011. Each year, a survey of the whole study area was conducted over 2–7 consecutive days. Surveys were based on point count methods and were carried out in the first 3 hours after sunrise and the last 3 hours before sunset; the hottest central hours of the day when bird activity is lowest were avoided, as were adverse weather conditions (Bibby et al. 1992). Using binoculars, observers counted Little Bustards for a period of 10 minutes from points situated along tracks. Six highly experienced observers participated over the years, four of them in multiple years. Observation points (totaling 120) were regularly distributed throughout the study area (Fig. 1). Each year, 110 ± 8 (mean ± SD) of those points were surveyed (range 91–116). Little Bustards observed from each point were plotted on a map, and double counting among consecutive points was avoided (if a bird was spotted in the same place, it was considered to be the same individual as in the nearby point and was not counted again [see Casas et al. 2019 for more details]). We detected both males and females, but most observations were of males; females accounted for about 13% of the total 1489 Little Bustard observations over the years. Given their different detectability, we used only males for analyses. However, it is known that males of this species display at locations that include resources that are useful to females for breeding (Jiguet et al. 2002), and that female observations are more common in areas with higher numbers of males (Jiguet and Bretagnolle 2006), so our assumption was that observed male abundance at different scales is also a proxy of female abundance.

Land use (the cover of each agricultural plot within the study area) was determined in the field each year (except in 2007, the year for which land use data were not available) when conducting the surveys, and was then entered to geographical information system software (QGIS 2.8.0). We considered the following land uses: cereal (rain fed), ploughed fallow field (a field left as annual fallow, which was ploughed to avoid the growing of weeds), unmanaged fallow (a field left as annual or pluriannual fallow, which was not ploughed and thus had vegetation), traditional vineyard, trellised vines, olive groves, pastures, alfalfa, other leguminous crops (*Vicia* spp. and *Pisum sativum*), cereal mixed with leguminous crops, beetroot, maize, riverine vegetation, buildings (isolated constructions, mainly secondary houses with a garden, all of them surrounded by a fence), and roads and tracks.

Resource-based modeling

We followed the framework described and validated in Cardador et al. (2014) to estimate functional habitat suitability in the study area for different periods. This approach first identifies the pool of potential land uses based on their agronomic characteristics in a particular study area (in our study case, those mentioned in the previous paragraph). The framework consists of four steps: (1) construction of a matrix to describe the species' resource requirements (*r*) for each vital activity (i.e., nesting and foraging) and for each categorized time period, (2) quantification of resource availability in each land use and for each time period, (3) calculation of habitat suitability indices for each vital activity in each land use and for each time period, and (4) temporal and/or spatial integration of habitat suitability indices to encompass temporal and spatial variation at the scales at which the vital

activities occur. We adapted the model developed by Cardador et al. (2014), which considered vegetation height and diet as variables for estimating resources, by integrating an additional variable, vegetation cover, which is known to be important in determining habitat use by the Little Bustard (Delgado et al. 2010, Lapiedra et al. 2011, Morales et al. 2013, 2014). The following provides details of each step:

Step 1. We categorized resource requirements (r) for Little Bustards on the basis of preferred vegetation height and cover for foraging or nesting, or presence of a given food resource in the diet, based on published literature (Jiguet 2002, Silva et al. 2007, Morales et al. 2008, Morales and Traba 2009, Martinez 2011, Ponjoan et al. 2012, Bravo et al. 2017, Cabodevilla et al. 2021). Four vegetation height categories (0–25 cm, 25–50 cm, 50–100 cm, >100 cm) and five vegetation cover categories (0–5%, 5–25%, 25–50%, 50–75%, 75–100%) were defined to describe foraging and nesting resources related to habitat characteristics. For each vegetation height or cover category, the r_i value assigned reflected an assessment of the capability of Little Bustards to use vegetation height or cover i (0 – not preferred; i.e., vegetation heights/cover never used or avoided; 0.5 – vegetation heights/cover used occasionally; 1 – preferred; i.e., vegetation heights/cover where a high proportion of the individuals forage or nest) (see Table A1 for values used). We considered nesting resources to analyze male abundance because males display at locations that include resources that are useful to females for breeding (Jiguet et al. 2002). For dietary resources, we considered four food types (plants, seeds, invertebrates, and vertebrates), with values that reflected an ordinal measure of the degree of preference for each food type by Little Bustards (0 – not used or very rarely consumed; 0.5 – consumed secondarily, when usual food is not widely available; 1 – a primary and frequent food resource). Values were derived for two periods, spring (April–June) and summer (July–September), to reflect temporal changes in resource requirements through the breeding season; e.g., invertebrates are more important in summer because they are essential in chicks' diet (see Table A2 for values used).

Step 2. Resource availability data for both habitat and dietary resources are described in a habitat type \times resource table ($A = [a_{kj}]$) for each time period. Each a_{kj} value is a measure of the availability of resource j in habitat unit k . We used available information on agricultural practices applied to different cover types in our study area (i.e., sowing and harvesting dates, fertilizers used, irrigation, and ploughing), in combination with our expert knowledge based on 10 years of field surveys, to qualitatively describe the probability of a given land use k having a given vegetation height or cover j in each time period (0 – not possible; i.e., vegetation height/cover category never or very rarely present; 0.5 – rare; i.e., infrequent or marginal vegetation height/cover category; 1 – usual; i.e., dominant vegetation height/cover category) (see Table A3 for values used). We then transformed these values to relative frequencies by dividing the score of each category by the sum of scores of all categories in a given time period and land cover type so that the sum of all categories was 1. Values were derived monthly according to vegetation growth patterns and land management.

For dietary resources, a_{kj} values indicate the relative abundance of resource j in cover type k in a given time period. We assumed

that the abundance of dietary resource j in cover type k was inversely related to both the number of agricultural practices that negatively affect that resource (n) and the intensity of the production system (f). Specifically, we calculated relative food abundance for each resource as $a_{kj} = 1/(n \cdot f + 1)$, where $n \cdot f + 1$ was used to avoid infinite a_{kj} values. For these calculations, we considered the effect of the main practices known to be directly related to food abundance: agro-chemical use, irrigation, ploughing, and harvest (Table A4). These practices can lead to a reduction in food supply for Little Bustards directly (e.g., reduction in weed availability through the use of herbicides) or indirectly (e.g., elimination through competition of many broad-leaved plant species and invertebrates associated with them by stimulation of crop growth due to crop irrigation or fertilizer use). We used a scaling factor for production system intensity (f), based on expert criteria, considering yield (tonnes/ha) and the intensity of implementation of management practices. This scaling factor was set to 1 for fallow lands and pastures (this, however, did not take into account whether fallow land plots were subject to intensive management when cultivated in previous years, so this may be an overestimation). Expected food abundance was calculated for spring (April–June) and summer (July–September) (Table A4).

Step 3. For each ecological requirement considered (i.e., dietary resources, foraging vegetation, or nesting vegetation) and time period, suitability s_i of habitat type i was defined as the scalar product of the corresponding vectors of matrices A (availability) and R (requirements). In the case of foraging suitability, we calculated the product of the suitability derived from habitat characteristics and that from food abundance. Suitability values derived from vegetation characteristics were, by definition, bounded between 0 and 1. Similarly, suitability values associated with food abundance (which represent the cumulative suitability of all types of food resources, and thus can sum to more than 1) were bounded between 0 and 1 (namely, values above 1 were set to 1); given that a species can use complementarily different food resources within the species' trophic niche, the maximum value would indicate that food requirements are fully provided in a given land use and month (regardless of by which food type/s).

We calculated suitability values monthly according to the temporal resolution of vegetation height and cover data. However, we assumed that (1) food preferences remained constant across months within both spring (April–June) and summer (July–September), and (2) expected food abundance was also constant within each period. Nesting habitat suitability was calculated only for those months when nesting activity occurs (April–June), whereas foraging habitat suitability was calculated for all breeding months (April–August). Table A5 presents the final suitability values for each land use/period.

We attributed the foraging and nesting habitat suitability estimates for each plot in the study area in relation to the land use. Areas covered by non-farmland land uses (i.e., buildings, tracks or roads, riverine vegetation) were considered to have suitability 0.

Step 4. We calculated the suitability for each observation point and year as the average suitability in a radius of 400 m around each point (83% of Little Bustards were observed within that distance from the observation point). For this, information about

suitability was rasterized (to pixels of 10 m). We generated two raster layers for each year: one for nesting habitat suitability, and the other for foraging habitat suitability. We then performed zonal statistics on each raster layer for each observation point buffer. Similarly, we calculated foraging and nesting suitability for the whole study area as the average value for all pixels within. Additionally, we divided the study area into four subareas of roughly the same size (Fig. 1), and we calculated foraging and nesting suitability for each subsector of the study area each year as the average value for all pixels within.

All indices were implemented in R 3.4.3 software (R Development Core Team 2018), and GIS manipulations were done with QGIS 2.8 (QGIS Association 2015).

Analyses of factors affecting variation in Little Bustard

Habitat suitability was calculated in relation to resources provided by each land use, and areas covered by land uses other than crops (buildings, tracks and roads, riverine vegetation) were considered to have suitability 0 for the Little Bustard. However, built-up areas, in addition to not providing resources for Little Bustards, may disrupt key behavioral processes for the species, thereby preventing the effective use of resources provided by nearby plots. We explored this by considering the variable “proportion of surface covered by buildings” (hereafter urban land) as an explanatory variable in models, in addition to nesting or foraging suitability. Tracks or roads may also locally influence Little Bustard occurrence and thus spatial distribution (Martínez-Marivela et al. 2018). Therefore, we also included the proportion of surface covered by roads and tracks (hereafter “tracks-roads”) in the initial models for analyzing spatial variations in Little Bustard abundance.

To analyze factors that affected spatial variations in Little Bustard abundance (i.e., variations in abundance among observation points), we first used a generalized linear mixed model in R 3.4.3 (*glmer* in package *lme4*) (Bates et al. 2015), with the number of Little Bustard males counted at each observation point during yearly bird censuses as the dependent variable with a Poisson error distribution (log link function). The model included two random factors: “observation point identity”, to account for repeated measures at the same point in different years, and “year”, to account for variations among years in variables not measured in this study. Nesting and foraging suitability, and the proportion of built-up areas and tracks-roads were included as fixed explanatory variables. We assessed collinearity among explanatory variables with the variance inflation factor. All variance inflation factor values were lower than 1.5, indicating lack of collinearity between them (Zuur et al. 2009). Spatial distribution of Little Bustards may be aggregated due to conspecific attraction (Morales et al. 2001, Martínez-Marivela et al. 2018); therefore, there may be a potential lack of independence among sampling points. We conducted a Moran’s test of the generalized linear mixed model residuals (with the DHARMA package), and it confirmed a significant ($P < 0.00001$) spatial correlation of abundance observations up to 2.5 km (Fig. A1). Therefore, we fitted a spatial regression model (*fitme* function in *spaMM* package), where a spatial component was included as a random term including the X and Y coordinates in a Matern

correlation function (Rousset and Ferdy 2014). The model also included the two random factors and the four fixed explanatory variables previously described. We checked that the model fit was correct by inspecting plots of residuals.

Spatial distribution of Little Bustards may change interannually in relation to changes in land use associated with crop rotation (Morales et al. 2005). To evaluate temporal trends in abundance, it is advisable to analyze numbers at a larger spatial scale than the observation point to avoid the noise created by distribution changes among years (Morales et al. 2005). We therefore assessed abundance each year as the total number of Little Bustards observed in the study area. This rendered a data set of 10 data points (one per year) for analyzing trends, which did not allow us to adequately explore additive effects of several explanatory variables and their interactions. In order to further explore results obtained with this limited data set, we divided the study area into four subareas of roughly the same size (Fig. 1), each of which included a sizeable number of observation points and differed in land use characteristics, and assessed abundance each year in each subarea as the total number of Little Bustards observed there. To analyze trends in abundance, we used generalized linear models (GLMs), and fit the response variable (number of males observed) with a Poisson distribution, and used the number of observation points (log transformed) as an offset (to account for sampling effort variations because not all observation points could be monitored each year, and to have a response variable that was comparable across subareas and years). The abundance model at the study area level included year as a continuous explanatory variable. The abundance model at the subarea level included year, subarea identity, and their interaction as explanatory effects. Temporal trends in habitat suitability or urban land area were also analyzed with GLMs at the two spatial scales by fitting response variables to a normal error distribution and using the same explanatory variables as those specified in the models for temporal trends in abundance. Interactions were removed from the models when they were not significant in order to correctly assess the significance of direct effects (Zuur et al. 2009).

Finally, we tested whether abundance at the study area and subarea levels was related to habitat suitability. For this, we constructed GLMs with abundance as the response variable (Poisson distribution) and (log-transformed) number of observation points as an offset. When analyzing abundance at the study area level, we included foraging suitability, nesting suitability, and proportion of built-up areas as explanatory variables. When analyzing abundance at the subarea level, we included foraging suitability, nesting suitability, proportion of urban land, subarea identity, and the two-way interactions as explanatory variables. The latter model was over-dispersed (dispersion parameter > 2). We therefore fitted the response variable in this model with a negative binomial distribution (with function *glm.nb*). When interactions were not significant, they were removed from the models.

R^2 values of models were calculated with function *rsq* (Zhang 2020). The only exception was the spatial regression model, for which this function did not work and for which we could not estimate R^2 values.

RESULTS

Habitat suitability, urban land, and spatial variations in abundance

The abundance of Little Bustard males varied between 0 and 8 individuals per point (mean \pm SD: 1.31 \pm 1.54).

Little Bustard abundance at each observation point significantly increased with nesting habitat suitability, and significantly decreased with increasing proportion of urban land around each point, even when controlling for spatial autocorrelation (Table 1). No significant relationships were found with either foraging habitat suitability or the surface covered by tracks-roads (Table 1).

Table 1. Results of the spatial regression model explaining variation in numbers of male Little Bustards observed at each observation point. The model included “year”, “point identity”, and the spatial component as random terms.

	DF	Parameter estimate (\pm SE)	Z value	P value
Intercept		-0.877 \pm 0.689	-1.273	0.20
Nesting habitat suitability	1	0.986 \pm 0.496	1.985	0.047
Foraging habitat suitability	1	0.364 \pm 0.549	0.664	0.51
Roads and tracks	1	-5.924 \pm 6.016	-0.985	0.32
Urban areas	1	-5.515 \pm 1.590	-3.469	< 0.001

Temporal trends in abundance, habitat suitability, and urban land

Little Bustard abundance in the study area declined significantly over the study period ($\text{Chi}^2_1 = 49.17$, $P = 0.0001$), with numbers in 2011 approximately 50% lower than those in 2002 (Fig. 2a). During the same period, suitability of foraging habitats in the study area also declined significantly ($\text{Chi}^2_1 = 24.6$, $P < 0.0001$) (Fig. 2b), whereas no such decline was observed for nesting habitat suitability ($\text{Chi}^2_1 = 0.65$, $P = 0.41$). Values for nesting habitat suitability were, overall, lower than those for foraging habitat suitability (Fig. 2b). The proportion of urban land in the whole study area increased approximately 1% over the study period (from 2.28% to 3.34%; $\text{Chi}^2_1 = 59.6$, $P < 0.0001$) (Fig. 2c). The area and distribution of tracks and roads did not change with time during the study period (Table A5).

Generalized linear models showed significant differences in Little Bustard abundance and foraging and nesting habitat suitability among subareas. Abundance and foraging habitat suitability temporally declined in all subareas (although the rate of decline differed among subareas), whereas nesting habitat suitability did not (Table 2). Both average values and temporal trends in urban land differed significantly among subareas (Table 2).

Temporal changes in Little Bustard abundance in the whole study area were positively correlated with changes in foraging and nesting habitat suitability at that scale but not with changes in urban land (Table 3). At the subarea level, GLM results showed a significant positive relationship between Little Bustard abundance and foraging habitat suitability, even when taking into account the strong subarea differences in Little Bustard

abundance, the slope of which (but not the intercept) was modulated by the proportion of urban land (Table 3); the positive relationship between foraging habitat suitability and Little Bustard abundance was marked when the proportion of urban land was small, but this relationship became much weaker as the proportion of urban land increased (Fig. 3). The additive effect of nesting habitat suitability was only marginally significant (Table 3).

Fig. 2. Temporal trends in Little Bustard abundance (a), habitat suitability (b), and proportion of urban land in the study area (c) (average \pm SE per point). The gap in graphs (b) and (c) in 2007 is due to a lack of land use data that year.

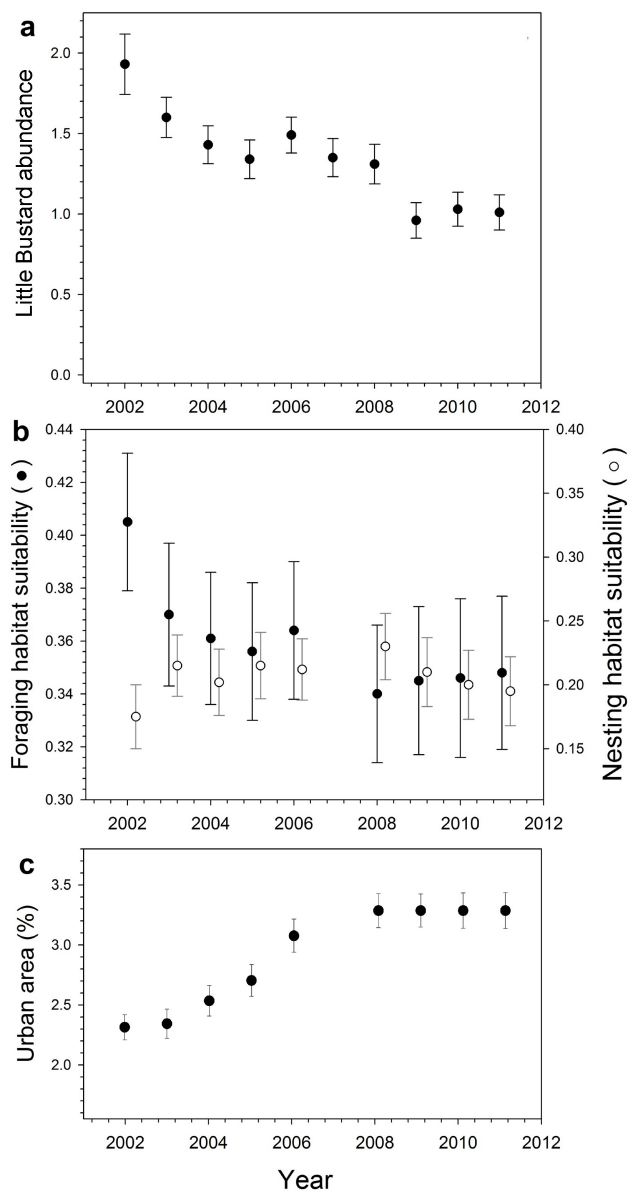
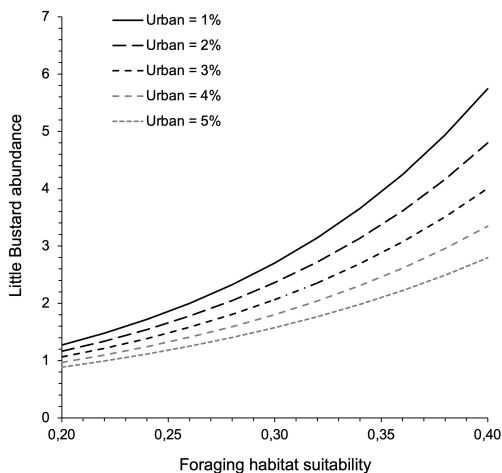


Table 2. Results of generalized linear mixed models explaining temporal trends in Little Bustard abundance and nesting and foraging habitat suitability at the subarea level. Results of type III Anova tests for each variable and model are presented. The nesting suitability model initially included the interaction between Year and Subarea, but it was removed as not significant for assessment of the direct effects.

Response variable	Explanatory variables	Chi ²	DF	P	Parameter estimates (± SE)	R ²
Model 1: Little Bustard abundance						78.6
					Intercept	87.22 ± 32.82
	Year	7.05	1	0.008	-0.04 ± 0.02	
	Subarea	14.70	3	0.002	A 148.35 ± 49.02	
					B 55.47 ± 58.19	
					C -40.82 ± 51.75	
	Year*Subarea	14.65	3	0.002	Year*A -0.07 ± 0.02	
					Year*B -0.03 ± 0.03	
					Year*C 0.02 ± 0.03	
Model 2: Foraging habitat suitability						86.8
					Intercept	10.56 ± 3.08
	Year	10.99	1	< 0.001	-0.005 ± 0.001	
	Subarea	12.64	3	0.005	A 6.99 ± 4.36	
					B -8.40 ± 4.36	
					C 0.76 ± 4.36	
	Year*Subarea	12.71	3	0.005	Year*A -0.0034 ± 0.0021	
					Year*B 0.0042 ± 0.0021	
					Year*C -0.0003 ± 0.0021	
Model 3: Nesting habitat suitability						55.8
					Intercept	-2.13 ± 2.29
	Year	1.03	1	0.31	0.001 ± 0.001	
	Subarea	38.22	3	< 0.001	A -0.0013 ± 0.0097	
					B 0.0318 ± 0.0097	
					C 0.0487 ± 0.0097	
Model 4: Urban areas						98.0
					Intercept	-3.51 ± 0.62
	Year	33.23	1	< 0.001	0.0018 ± 0.0003	
	Subarea	49.21	3	< 0.001	A -2.48 ± 0.87	
					B 2.08 ± 0.87	
					C 3.24 ± 0.88	
	Year*Subarea	49.48	3	< 0.001	Year*A 0.0012 ± 0.0004	
					Year*B -0.0011 ± 0.0004	
					Year*C -0.0001 ± 0.0004	

Fig. 3. Modeled relationship between Little Bustard abundance and the interaction between foraging habitat suitability and percentage of urban areas (from Model 2 in Table 3), for a nesting habitat suitability of 0.21 (mean value observed across all years).



DISCUSSION

Spatial and temporal variations in Little Bustard abundance were explained by functional habitat suitability and avoidance of urban land, but the relative importance of each variable changed as a function of spatial scale.

We observed significant spatial autocorrelation in the abundance of males at each observation point. This may be related to the reproductive system of the species, exploded leks (Morales et al. 2001), where social or behavioral aspects such as conspecific attraction may also be important in explaining the distribution of males. Nonetheless, even when taking this spatial autocorrelation into account, spatial variations in Little Bustard abundance were significantly related to variations in nesting habitat suitability and the occurrence of buildings in the farmland matrix. Male Little Bustards set up territories in areas containing resources that are potentially used by females to enhance the probability of encounter between the sexes (Jiguet et al. 2002), which may explain the influence of nesting habitat suitability on male abundance. It has been previously shown that male distribution relates to high food abundance (Traba et al. 2008), but we did not find a relationship with foraging habitat suitability

Table 3. Results of generalized linear mixed models explaining variations in Little Bustard annual abundance in relation to habitat suitability and proportion of urban areas at the study area and subarea levels. Results of type III Anova tests for each variable and model are presented. The subarea model initially included two-way interactions between variables, but they were removed when not significant for assessment of the direct effects. The interaction between urban land and suitability without the direct effect of urban land in Model 2 indicates a common intercept at zero suitability, irrespective of urban area, but differing slopes for the relationship between abundance and foraging habitat suitability under different proportions of urban area.

	LR Chi ²	DF	P	Parameter estimates (± SE)	R ²
Model 1 (study area level)					90.7
				Intercept	-5.79 ± 1.098
Foraging habitat suitability	14.05	1	< 0.001		13.21 ± 3.48
Nesting habitat suitability	6.47	1	0.011		6.42 ± 2.52
Urban area	0.13	1	0.71		-0.04 ± 0.12
Model 2 (subarea level)					70.2
				Intercept	-2.17 ± 1.42
Subarea	40.93	3	< 0.001	A	-0.48 ± 0.33
				B	-1.30 ± 0.22
				C	-1.66 ± 0.39
Nesting habitat suitability	3.279	1	0.07		4.10 ± 2.29
Foraging habitat suitability	10.97	1	< 0.001		7.99 ± 2.43
Foraging hab. suitability*Urban	3.858	1	0.049		-0.45 ± 0.23

(assessed for the whole of the breeding season). Also, and in contrast to another study that showed that the presence of tracks and roads was negatively related to the probability of Little Bustard male occurrence (Martínez-Marivela et al. 2018), we did not find a significant effect of tracks and roads on the spatial distribution of males. In contrast, our results indicate a strong avoidance of built-up areas at the observation point level. A negative effect of building density (but not track density) on nest distribution was also found for Montagu's Harriers (*Circus pygargus*) nesting in farmland, modulated by female personality (Rabdeau et al. 2021). Negative effects of urban encroachment on Little Bustards have also been found in previous studies (Silva et al. 2004, Devoucoux 2014), although such effects have been absent or less marked in other studies (Martínez 1994, Faria and Rabaça 2004), which suggests that the relationship may be context dependent. Our results showed that the negative effect of urban areas at this spatial scale was additive, which indicates that this effect goes beyond that of habitat loss occurring from urbanization. Little Bustards have been shown to be sensitive to disturbance caused by human activities (Casas et al. 2009, Tarjuelo et al. 2015), which altered their short-term physiological stress, as well as their behavior and habitat use. Therefore, an avoidance of built-up areas may be associated with the presence of humans, but built-up areas in farmland are also often associated with the presence of cats and dogs, the former behaving in semi-feral ways, even when they are domestic pets. Therefore, avoiding the proximity of built-up areas may also be a way of reducing predation risk.

Variations in abundance at larger spatial scales through time were better explained by variations in habitat suitability than by urban encroachment. Annual male abundance trends at the study area level were explained by an additive effect of both nesting and foraging habitat suitability, although the effect size was stronger for foraging habitat suitability, which significantly declined through time, in contrast to nesting habitat suitability. A decline

in nesting habitat suitability could have been expected due to the decline in fallow land after the abolishment of set-aside within the European Union's Common Agricultural Policy in 2008 (Traba and Morales 2019). However, in the study area, the decline affected mainly ploughed (managed) fallow, which is not suitable for nesting, whereas the availability of fallow with vegetation cover remained relatively stable (Table A5). The fact that no long-term decrease in nesting habitat suitability was detected could be related to the simplicity in describing this type of functional resource, as if a certain structural plant cover is maintained, the functionality would remain according to our model. On the other hand, and despite the simplicity in our approach, our results suggest that feeding resources have declined more over time, and support that this is an important process behind observed declines. The additive effect of both variables means that even if nesting habitat suitability is maintained through time (as happened in our study area during the study period), a decline in foraging habitat suitability may lead to temporal declines. In our case, a 15% reduction in estimated foraging habitat suitability during the study period coincided with an approximately 60% decline in Little Bustard abundance over the years. Although other factors not considered in our study may have also contributed to the decline of the Little Bustard population, the additive relationship we found means that measures aimed at enhancing foraging habitat suitability could potentially be very effective in helping Little Bustard populations recover (e.g., Bretagnolle et al. 2011) if nesting habitat suitability is at least maintained.

Results at the subarea scale, which allowed us to test for interactions between variables, also showed that the presence of urban land modulated the relationship between habitat suitability and species abundance: when the proportion of urban land was high, abundance was much lower than expected from foraging habitat suitability. This means that the local-scale avoidance of urban land may lead to an overall reduction in abundance, an

effect particularly marked in good quality areas. The latter has marked relevance because those good-quality areas may be of utmost importance for maintaining the species (Inchausti and Bretagnolle 2005). Construction of built-up areas should therefore be regulated in the areas where Little Bustards are currently abundant in order to not accelerate the decline of this vulnerable species.

More generally, our results represent a validation for the use of resource-based models for inferring habitat suitability. Cardador et al. (2014) showed that describing the farmland landscape in the view of only two variables that described resources selected by a given species (vegetation height and food abundance) rendered habitat suitability values that correlated with occupancy probability for a suite of farmland bird species. We acknowledge that estimating availability of food resources based mainly on potential effects of management practices is a simplification, which should be re-assessed with information from future studies. For example, accumulated effects of agricultural intensification over the years may result in the homogenization of specific food resources across land uses (Tarjuelo et al. 2019). Regardless of this limitation, we showed that habitat suitability calculated with three simple variables (vegetation height, cover, and food abundance) allows for the production of habitat suitability indices that have biological meaning and explain variations in abundance of Little Bustards. Furthermore, this approach allows for the discussion of the relative importance of foraging versus nesting habitat suitability in explaining these variations in abundance, which will aid in the design of management measures that help reverse the species' population trend beyond the maintenance of favored specific land uses. Such an approach, however, may overshadow other important processes in the species' biology that are not related to resources used. Thus, our study shows the benefits of simultaneously assessing the influence of preferred resources with that of avoided elements of the landscape. Even if we have included the latter as an additive explanatory variable in our models, they could potentially be included in the resource-based suitability model as elements that modulate the use of the available resources in each plot. This way, it would be possible to use those models to explore the effects of different land use change scenarios (including urban or infrastructure development) on a range of species in a manner similar to that used by Cardador et al. (2015).

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Author Contributions:

All authors conceptualized the study and designed the methodology; FC and FM collected the data and performed data curation; BA, FM, AE, and LC analyzed the data; BA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix 1

Figure A1. Correlogram showing spatial correlation in little bustard abundance data. White dots represent little bustard abundance raw data, red dots represent the residuals of the non-spatial GLMM (see text for more details).

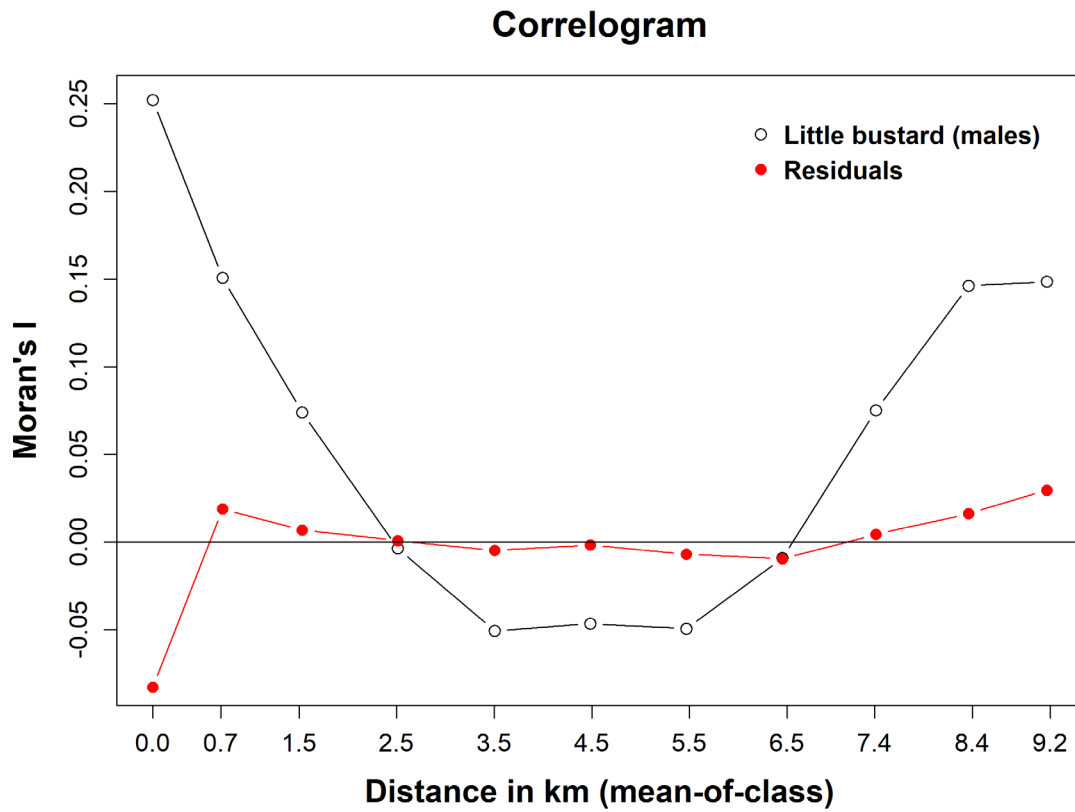


Table A1. Values for vegetation requirements (vegetation cover -C - and height - H) used in the resource-based model.

activity	foraging	foraging	nesting
Period	spring	summer	spring
C_0-5	0.5	0.5	0
C_5-25	0.5	0.5	0
C_25-50	1	1	0
C_50-75	1	1	1
C_75-100	1	1	0.5
H_1-25	1	1	0
H_25-50	0.5	0.5	0.5
H_50-100	0	0	1
H_>100	0	0	0

Table A2. Food requirement values used in the resource-based model.

period	seeds	plants	invertebrates	vertebrates
spring	0.5	1	0.5	0
summer	0.5	1	1	0

Table A3. Availability of vegetation height and cover categories in different land uses and months. A “0” indicates that a particular cover or height category is never present in that month for that land use. A “0.5” indicates that the category occurs sometimes. A “1” indicates that the category occurs frequently.

Land use	Production system	Month	C_0-5	C_5-25	C_25-50	C_50-75	C_75-100	H_1-25	H_25-50	H_50-100	H_>100
Alfalfa	Irrigated	April	0	0	0.5	1	1	1	1	0	0
Alfalfa	Irrigated	May	0	0	0	1	1	1	1	0	0
Alfalfa	Irrigated	June	0	0	0	1	1	1	1	0	0
Alfalfa	Irrigated	July	0	0	0	1	1	1	1	0	0
Alfalfa	Irrigated	August	0	0	0	1	1	1	1	0	0
Alfalfa	Irrigated	Sept.	0	0	0	1	1	1	1	0	0
Fallow-ploughed	Rain-fed	April	1	0.5	0	0	0	1	0	0	0
Fallow-ploughed	Rain-fed	May	1	0.5	0	0	0	1	0	0	0
Fallow-ploughed	Rain-fed	June	1	0.5	0	0	0	1	0	0	0
Fallow-ploughed	Rain-fed	July	1	0.5	0	0	0	1	0	0	0
Fallow-ploughed	Rain-fed	August	1	0.5	0	0	0	1	0	0	0
Fallow-ploughed	Rain-fed	Sept.	1	0.5	0.5	0	0	1	0	0	0
Fallow-not ploughed	Rain-fed	April	0	0	1	1	1	1	1	0.5	0
Fallow-not ploughed	Rain-fed	May	0	0	1	1	1	1	1	0.5	0
Fallow-not ploughed	Rain-fed	June	0	0	1	1	0.5	1	1	0.5	0
Fallow-not ploughed	Rain-fed	July	0	0.5	1	0.5	0.5	1	0.5	0	0
Fallow-not ploughed	Rain-fed	August	0	0.5	1	0.5	0	1	0.5	0	0
Fallow-not ploughed	Rain-fed	Sept.	0	0.5	1	0.5	0	1	0	0	0
Cereal	Rain-fed	April	0	0	0	0.5	1	0	1	0.5	0
Cereal	Rain-fed	May	0	0	0	0	1	0	0.5	1	0.5
Cereal	Rain-fed	June	0	0	0	0.5	1	0.5	0.5	1	0.5
Cereal	Rain-fed	July	0	0	0.5	1	0.5	1	0.5	0.5	0.5
Cereal	Rain-fed	August	0	0	0.5	1	0	1	0	0	0
Cereal	Rain-fed	Sept.	0	0	0.5	1	0	1	0	0	0
Cereal-Vetch	Rain-fed	April	0	0	0	0.5	1	0.5	0	1	0
Cereal-Vetch	Rain-fed	May	0.5	0	0	0	1	0.5	0	1	0
Cereal-Vetch	Rain-fed	June	0	0	0.5	1	0	1	0	0	0
Cereal-Vetch	Rain-fed	July	0	0	0.5	1	0	1	0	0	0
Cereal-Vetch	Rain-fed	August	0	0	0.5	1	0	1	0	0	0
Cereal-Vetch	Rain-fed	Sept.	0	0	0.5	1	0	1	0	0	0
Cereal-no tillage	Rain-fed	April	0	0	0	0	1	0.5	1	0.5	0
Cereal-no tillage	Rain-fed	May	0	0	0	0	1	0	1	1	0.5
Cereal-no tillage	Rain-fed	June	0	0	0	0	1	0.5	0.5	1	0.5
Cereal-no tillage	Rain-fed	July	0	0	0	0.5	1	1	0	0	0
Cereal-no tillage	Rain-fed	August	0	0	0	0.5	1	1	0	0	0
Cereal-no tillage	Rain-fed	Sept.	0	0	0	0.5	1	1	0	0	0
Peas	Rain-fed	April	0	0	0.5	0.5	1	1	0.5	0	0
Peas	Rain-fed	May	0	0	0	0.5	1	1	1	0	0
Peas	Rain-fed	June	0	1	0	0.5	1	1	1	0	0
Peas	Rain-fed	July	0.5	1	0.5	0	0	1	0	0	0
Peas	Rain-fed	August	0.5	1	0.5	0	0	1	0	0	0
Peas	Rain-fed	Sept.	1	0.5	0	0	0	1	0	0	0

Maize	Irrigated	April	0.5	0.5	1	0.5	0	1	0	0	0
Maize	Irrigated	May	0	0	0.5	1	0.5	0.5	1	0.5	0
Maize	Irrigated	June	0	0	0	0.5	1	0	0.5	0.5	1
Maize	Irrigated	July	0	0	0	0	1	0	0	0.5	1
Maize	Irrigated	August	0	0	0	0	1	0	0	0	1
Maize	Irrigated	Sept.	0	0	0	0	1	0	0	0	1
Olive trees	Rain-fed	April	1	0.5	0	0	0	1	0	0	0
Olive trees	Rain-fed	May	1	0.5	0	0	0	1	0	0	0
Olive trees	Rain-fed	June	1	0.5	0	0	0	1	0	0	0
Olive trees	Rain-fed	July	1	0.5	0	0	0	1	0	0	0
Olive trees	Rain-fed	August	1	0.5	0	0	0	1	0	0	0
Olive trees	Rain-fed	Sept.	1	0.5	0	0	0	1	0	0	0
Pastures	Rain-fed	April	0	0	0.5	1	0.5	1	0.5	0	0
Pastures	Rain-fed	May	0	0	0.5	1	0.5	1	0.5	0	0
Pastures	Rain-fed	June	0	0	0.5	1	0.5	1	0.5	0	0
Pastures	Rain-fed	July	0	0	0.5	1	0	1	0.5	0	0
Pastures	Rain-fed	August	0	0	0.5	1	0	1	0.5	0	0
Pastures	Rain-fed	Sept.	0	0	0.5	1	0	1	0.5	0	0
Beetroot	Irrigated	April	1	1	0.5	0	0	1	0	0	0
Beetroot	Irrigated	May	0.5	1	1	0.5	0	1	0	0	0
Beetroot	Irrigated	June	0	0.5	1	1	0.5	1	0.5	0	0
Beetroot	Irrigated	July	0	0	0.5	1	1	1	0.5	0	0
Beetroot	Irrigated	August	0	0	0	0.5	1	0.5	1	0	0
Beetroot	Irrigated	Sept.	0	0	0	0	1	0	1	0	0
Vineyards-trellised	Irrigated	April	1	0.5	0	0	0	1	0	0	0
Vineyards-trellised	Irrigated	May	1	0	0	0	0	1	0	0	0
Vineyards-trellised	Irrigated	June	1	0	0	0	0	1	0	0	0
Vineyards-trellised	Irrigated	July	1	0	0	0	0	1	0	0	0
Vineyards-trellised	Irrigated	August	1	0	0	0	0	1	0	0	0
Vineyards-trellised	Irrigated	Sept.	1	0	0	0	0	1	0	0	0
Vineyards- not trellised	Rain-fed	April	1	0.5	0.5	0.5	0	1	0	0	0
Vineyards- not trellised	Rain-fed	May	1	0.5	0.5	0	0	1	0	0	0
Vineyards- not trellised	Rain-fed	June	1	1	0.5	0	0	1	0	0	0
Vineyards- not trellised	Rain-fed	July	1	1	1	1	0.5	1	1	0	0
Vineyards- not trellised	Rain-fed	August	1	1	1	1	0.5	1	1	0	0
Vineyards- not trellised	Rain-fed	Sept.	1	1	1	1	0.5	1	1	0	0

Table A4. Food availability values used in the resource-based model, and parameters used to calculate them. Specifically, we note for each land use and period (spring, Sp; and summer, Su) whether agricultural practices applied are likely to negatively influence food resources (seeds, plants, invertebrates and vertebrates) (✓) or not (empty cells) (the latter may reflect the practice not being applied, or not leading to loss of food supplies). We then summarize the total number of practices that may negatively affect availability of different food types (n), and the intensification scale used (f). Availability of seeds, plants, invertebrates and vertebrates is calculated as $1 / (n \cdot f + 1)$.

Practice	Key impacts	Unmanag Fallow		Manag fallow		Dry cereal		Alfalfa*		Maize		Cereal+Legum		Legum.		Beetroot		Olive trees		Trell. Vine		Trad. Vine		Pastures		
		Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	Sp	Su	
Agro-chemicals	Loss of crop plant material					✓		✓		✓		✓		✓		✓	✓	✓	✓	✓	✓	✓	✓			
	Loss of seeds					✓		✓		✓		✓		✓		✓	✓	✓	✓	✓	✓	✓	✓			
	Loss of crop invertebrates							✓		✓						✓	✓	✓	✓	✓	✓	✓	✓			
Irrigation	Loss of crop plant material							✓	✓	✓	✓				✓	✓			✓	✓						
	Loss of crop invertebrates							✓	✓	✓	✓				✓	✓			✓	✓						
Ploughing	Loss of crop invertebrates			✓	✓		✓						✓		✓			✓	✓	✓	✓	✓	✓			
	Loss of crop plant material			✓	✓		✓						✓		✓			✓	✓	✓	✓	✓	✓			
	Loss of seeds			✓	✓		✓						✓		✓			✓	✓	✓	✓	✓	✓			
	Loss of crop vertebrates			✓	✓		✓						✓		✓			✓	✓	✓	✓	✓	✓			
Harvest	Loss of crop invertebrates						✓	✓	✓			✓	✓		✓											
	Loss of crop plant materia						✓	✓	✓			✓	✓		✓											
	Loss of seeds							✓	✓			✓	✓		✓											
	Loss of crop vertebrates						✓	✓	✓			✓	✓		✓											
Number of practices that negatively affect the availability of:																										
Seeds		0	0	1	1	1	1	2	1	1	1	2	2	1	2	1	1	2	2	2	2	2	2	2	0	0
Plants		0	0	1	1	1	2	0	0	2	1	2	2	1	2	2	2	2	2	2	3	3	2	2	0	0
Invertebrates		0	0	1	1	0	2	3	2	2	1	1	2	0	2	2	2	2	2	2	3	3	2	2	0	0
Vertebrates		0	0	1	1	0	2	1	1	1	1	1	1	0	2	0	0	1	1	1	1	1	1	1	0	0
Intensification Scale (Expert criterion)		1	1	1	1	2	2	3	3	8	8	2	2	2	2	8	8	3	3	6	6	2	2	1	1	
Seed availability ¹		1.00	1.00	0.50	0.50	0.33	0.33	0.14	0.25	0.11	0.11	0.20	0.20	0.33	0.20	0.11	0.11	0.14	0.14	0.08	0.08	0.20	0.20	1.00	1.00	
Plant availability ¹		1.00	1.00	0.50	0.50	0.33	0.20	1.00	1.00	0.06	0.11	0.20	0.20	0.33	0.20	0.06	0.06	0.14	0.14	0.05	0.05	0.20	0.20	1.00	1.00	
Invertebrate availability ¹		1.00	1.00	0.50	0.50	1.00	0.20	0.10	0.14	0.06	0.11	0.33	0.20	1.00	0.20	0.06	0.06	0.14	0.14	0.05	0.05	0.20	0.20	1.00	1.00	
Vertebrate availability ¹		1.00	1.00	0.50	0.50	1.00	0.20	0.25	0.25	0.11	0.11	0.33	0.33	1.00	0.20	1.00	1.00	0.25	0.25	0.14	0.14	0.33	0.33	1.00	1.00	

*In the case of alfalfa, negative effects of agricultural practices were only considered to affect seeds, invertebrates and vertebrates, but not plant material since the crop by itself could be consumed by plant-eaters.

Table A5. Proportion of the study area covered by different land uses in each study year, and suitability values attributed to each of them

	2002	2003	2004	2005	2006	2008	2009	2010	2011	Nesting suitability	Foraging suitability (April-August)
Cereal	42.93	52.73	53.26	55.71	53.60	62.07	52.91	49.77	48.57	0.363	0.322
Cereal mixed with leguminous crops	0.00	0.18	0.39	0.35	0.00	0.00	1.13	0.26	1.26	0.222	0.350
Ploughed Fallow	28.41	22.01	23.41	20.01	18.00	14.61	17.77	17.11	17.40	0.000	0.500
Unploughed Fallow	6.34	3.56	2.74	3.59	7.99	2.49	4.81	6.30	6.24	0.200	0.656
Olive groves	3.71	3.68	3.68	4.01	3.99	4.41	4.94	5.05	5.10	0.000	0.157
Trellis vineyard	2.40	2.37	2.85	3.10	3.17	3.17	3.20	2.16	2.16	0.000	0.000
Trad. Vineyard	2.61	2.29	2.08	1.96	1.80	1.58	1.28	0.90	0.90	0.000	0.271
Pastures	8.34	7.79	5.76	5.71	5.73	5.21	5.20	5.20	2.40	0.104	0.833
Alfalfa	0.12	0.12	0.08	0.08	0.06	0.05	0.05	0.03	0.05	0.175	0.750
Other leguminous crops	0.05	0.53	0.33	0.62	0.13	0.63	0.85	2.40	5.54	0.117	0.562
Maize	0.17	0.00	0.10	0.03	0.00	0.33	0.00	0.00	0.00	0.188	0.041
Beetroot	0.51	0.27	0.67	0.04	0.00	0.00	0.00	0.00	0.00	0.023	0.113
Riverine vegetation	0.53	0.53	0.53	0.48	0.48	0.48	0.48	0.48	0.48	0.000	0.000
Urban Land	2.29	2.32	2.53	2.71	3.11	3.34	3.34	3.34	3.34	0.000	0.000
Tracks-roads	1.57	1.57	1.57	1.57	1.57	1.57	1.57	1.57	1.57	0.000	0.000