Temporal trends of land-use favourability for the strongly declining little bustard: assessing the role of protected areas

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The Natura2000 network is one of the main biodiversity conservation tools of the European Union, aiming to protect areas hosting species of conservation concern from unfavourable land-use changes. The network, covers many landscapes across the continent, including farmland ones. In the present study, we use the little bustard, one of the farmland birds most negatively affected by agricultural changes in Europe, to assess whether habitat favourability based on the availability of land-uses explaining the species' presence vary among areas with different degrees of protection in North-western Spain. Moreover we examine the relationship between land-use favourability and population trends over a decade in the Nature Reserve of Villafáfila, a protected area under both Natura2000 and Nature Reserve designation. In that area under an active conservation-oriented management, favourability was far higher than in other protected and non-protected areas, which highlights the need to increase the level of conservation-oriented farmland management areas across the Natura2000 network, promoting the cover of natural habitats and traditional farming practices to maximise land-use favourability for little bustards. Though land-use favourability was positively related to little bustard abundance at a local level, conspecific attraction was the most relevant variable explaining it. Land-use favourability increased slightly during the study period both within and outside protected areas, while little bustard populations declined sharply, even in the Nature Reserve, indicating that additional factors are related with this decline. Factors such as field-level agricultural management and Allee effect processes need to be examined to better understand the drivers of little bustard regression.

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Abstract

The Natura2000 network is one of the main biodiversity conservation tools of the European Union, aiming to protect areas hosting species of conservation concern from unfavourable land-use changes. The network, covers many landscapes across the continent, including farmland ones. In the present study, we use the little bustard, one of the farmland birds most negatively affected by agricultural changes in Europe, to assess whether habitat favourability based on the availability of land-uses explaining the species' presence vary among areas with different degrees of protection in North-western Spain. Moreover we examine the relationship between land-use favourability and population trends over a decade in the Nature Reserve of Villafáfila, a protected area under both Natura2000 and Nature Reserve designation. In that area under an active conservation-oriented management, favourability was far higher than in other protected and non-protected areas, which highlights the need to increase the level of conservation-oriented farmland management areas across the Natura2000 network, promoting the cover of natural habitats and traditional farming practices to maximise land-use favourability for little bustards. Though land-use favourability was positively related to little bustard abundance at a local level, conspecific attraction was the most relevant variable explaining it. Land-use favourability increased slightly during the study period both within and outside protected areas, while little bustard populations declined sharply, even in the Nature Reserve, indicating that additional factors are related with this decline. Factors such as field-level agricultural management and Allee effect processes need to be examined to better understand the drivers of little bustard regression.

Keywords: Cereal steppes, conspecific attraction, farmland birds, Nature Reserves, population trends.

Introduction

Land-use change is likely the main driver of biodiversity loss (Sala et al., 2000) due to the associated loss of habitat suitability for many species (Thuiller, 2007). In agricultural landscapes, land-use changes include changes in the total area devoted to farming, as well as in the relative surface dedicated to different crops and in farming practices within crops. Agriculture intensification aiming at increasing yields is a main driver of these changes, although abandonment in less productive areas also contributes to variation in habitat quality for farmland wildlife (Emmerson et al., 2016).

Protected areas are one of the main conservation policy tools used to tackle land-use change impacts on biodiversity around the globe. The Natura2000 network, for example, is the main land-planning tool for biodiversity protection in the European Union, covering many landscapes across the continent with the aim to protect important biodiversity areas and make their conservation compatible with existing land-use (European Commission, 2022).

Extensive cereal farmland is home to important populations of threatened steppe birds in Europe, particularly in the Iberian Peninsula (Santos & Suárez, 2005). Consequently, the Spanish Natura2000 network (which protects 20.25% of the country's land surface) includes farmland landscapes hosting important populations of steppe bird species included in the Annex I of the Birds Directive (Ministry for Ecological Transition MITECO, 2021). However, Natura2000 sites such as Special Protection Areas (hereafter SPAs) are proving inefficient to protect farmland biodiversity against land use changes and agriculture intensification (Gameiro et al., 2020). On the other hand, Natura2000 areas coexist (and in most cases overlap) with Member State-level protection sites, such as Nature Reserves. Rodríguez-Rodríguez et al. (2019) found that Nature Reserves in Spain are more effective designations against land use and cover changes than SPAs, due to their legally stringent and conservation-oriented management, which contrast with the less effective conservation measures of Natura2000 network (Rodríguez-Rodríguez, Martínez-Vega & Echavarría, 2019). Further, SPAs frequently lack regular or systematic biodiversity monitoring and assessment of management results, which are paramount to develop evidence-based conservation programs (Kleijn & Sutherland, 2003; Trochet & Schmeller, 2013).

There are various approaches to analysing the effectiveness of protected areas, such as directly measuring changes in population abundance or land use. An alternative option is to measure changes in habitat quality or suitability for a given species. The latter is particularly relevant when species may use a variety of land uses, so that changes in one of them do not necessarily lead to an overall loss or gain in habitat quality. Habitat suitability may be calculated from occurrence modelling, assessing the variables that increase the probability of presence of a given species (Guisan & Thuiller, 2005; Miller, 2010). Of particular interest in this context is the calculation of the favourability function, which has been widely used in species distribution modelling, habitat selection or epidemiological studies among others (Manly et al., 2007; Pfeiffer et al., 2008; Franklin, 2010). Its main advantage is that it allows direct comparison between different samples (years, areas or species) regardless of species prevalence (Acevedo & Real, 2012). In addition, favourability indices may be extrapolated in space and time, thus allowing for the assessment of changes over time or across areas with a single indicator (Acevedo & Real, 2012).

The little bustard (*Tetrax tetrax*) is a farmland steppe bird highly and negatively affected by agricultural changes in Europe (Morales & Bretagnolle, 2021). This steppe bird is linked to extensive heterogenous farmland landscapes which fulfil their breeding and non-breeding requirements (Morales, García & Arroyo, 2005; Faria & Silva, 2010) and can be considered an indicator of well conserved agricultural steppe ecosystems (Morales & Bretagnolle, 2021). Various studies have shown that the species is in strong decline all over Europe in recent decades (Morales & Bretagnolle, 2021), and this decline is associated with increasing agricultural intensification (Inchausti & Bretagnolle, 2005; Traba & Morales, 2019). Agricultural intensification typically involves land use changes such as reduced fallow surface, increased irrigation, and monocultures leading to landscape simplification (Matson et al., 1997; Emmerson et al., 2016), which are negative for the little bustard. Additionally, some farmland practices may also be detrimental for the species, for example fallow ploughing or night operations are a direct cause of nest loss, as well as nestling and adult mortality, leading to low productivity rates in little bustard populations (Morales et al. 2013; Bretagnolle et al. 2018, own unpublished data), and the use of agrochemicals such as fertilizers or pesticides may have effects on food abundance.

In the present study, we use little bustard data to analyse the effectiveness of Natura2000 areas and Nature Reserves in the conservation of this threatened species' habitat using the favourability function. More precisely, we (a) examine the land-use variables determining habitat favourability for the little bustard in extensive cereal farmland landscapes, and (b) we assess whether favourability values and trends differ between areas under different protection regimes: non-protected areas, SPAs, and a Nature Reserve that is also a SPA. Our prediction was that if Nature Reserves and Natura2000 policies are effective in preserving little bustard habitat, favourability values would be higher and population trends more stable in protected than in non-protected areas. Additionally, we also assessed (c) whether little bustard abundance varied across areas with different protection status. We expected little bustard abundance to be higher in areas with higher favourability and with higher protection status. Finally, we (d) use long-term little bustard data (10 years of breeding censuses) to evaluate whether little bustard abundance variation and population trends match those of habitat favourability in a protected area. Our prediction was that, if habitat quality loss is one of the drivers of little bustard regression, the population decline should be concomitant with a loss of habitat favourability.

Materials and methods

Study species

The little bustard is a medium-sized sexually dimorphic steppe bird that inhabits natural grasslands and farmland landscapes (Cramp & Simmons, 1980). Although it was widely distributed from Portugal to China until the middle of the last century, currently there are two disjoint subranges, a western one encompassing Iberia, France and Sardinia and an eastern one ranging from southwestern Russia to north-western China (Morales & Bretagnolle, 2021). It is classified as “Vulnerable” in Europe (BirdLife International, 2015) and as “Near Threatened” globally in the IUCN World Red List (Birdlife International, 2023). The Iberian Peninsula is the core of the western subrange and its population is experiencing a dramatic decline in recent years (ca. 50% from 2005 to 2016, García de la Morena et al. 2018; Morales and Bretragnolle 2021). Breeding little bustards depend on heterogeneous cereal farmland landscapes with presence of fallow fields (Morales, García & Arroyo, 2005), whose cover in Spain has markedly decreased due to agriculture intensification (Traba & Morales, 2019). Little bustards present an exploded-lek mating system (Jiguet, Arroyo & Bretagnolle, 2000) and thus they show a marked conspecific attraction, which largely explains the species’ patterns of abundance and distribution at different scales (Morales et al., 2014; Estrada et al., 2016; Arroyo et al., 2022). Therefore, not taking conspecific attraction into consideration may mask some ecological relationships relevant for conservation (Estrada & Arroyo, 2012).

Study area

The study was carried out in the central sector of the Duero basin in the region of Castilla y León (NW Spain, Fig. 1). Climate is continental-Mediterranean with marked oscillations during the year: hot and dry summers, cold winters and rainfall concentrated in spring and autumn. This region harboured important little bustard populations, which have experienced strong declines in recent years (García de la Morena et al., 2018).

The limits of the study area were defined in relation to the availability of little bustard data (see below), by adjusting a rectangle encompassing a total of 438 census points sampled in 2016 (12574.198 km^2; see below and Fig. 1). This area includes 15 SPAs (2395.743 km^2): according to the Natura2000 official forms published in 2005, 13 of them have steppe habitat potentially suitable for little bustards, but not the remaining two, which encompass mainly mountain and riparian habitats (Table A1). Two out of the 15 SPAs are also classified as Nature Reserve: the Nature Reserve of Lagunas de Villafáfila (N. R. of Villafáfila hereafter) and Riberas de Castronuño, but only the former one has potential habitat for little bustards, while the latter includes mainly riparian habitats. In our analyses, therefore, we only considered protected areas that were potentially suitable for little bustards: 13 SPAs, one of which was also a Nature Reserve (Table A1), whereas the other two were considered as non-protected areas. SPAs have Management Plans (Junta de Castilla y León, 2022) detailing guidelines and recommendations in order to reach their conservation aims but no specific restrictions in terms of farming practices, although farmers may sign voluntary agreements under Agri-Environmental Schemes (Orden FYM/775/2015). The measures promoted for little bustard conservation (as well as other steppe bird populations linked to long-term fallows, grasslands and shrublands) are the promotion of crop rotation between cereals, legumes and fallows, the reduction of agrochemicals and coated seeds, the maintenance of areas with natural vegetation (such as shrubs, field margins, wastelands and grasslands), the delay of mowing-harvesting until mid-July, and the reduction of mortality due to non-natural causes (e.g. limitation of night ploughing or harvesting). Plans also encourage monitoring programmes to assess the species' response to conservation measures (Junta de Castilla y León, 2022). Unfortunately, although all these areas have a common purpose, agricultural management is not homogeneous across SPAs: while most of them are experiencing strong agricultural intensification, some undergo a process of land abandonment with much lower cover of cereal crops (Table A1).

The Nature Reserve of Lagunas de Villafáfila occupies 325.49 km^2 of flat or gently undulated cereal farmland with a few seasonal semi-endorreic lagoons at an average altitude of 700 m.a.s.l. Although most terrain is devoted to cereal cultivation, nearly 10% of the reserve is cultivated with dry alfalfa crops for haying and sheep grazing (Rodríguez Alonso & Palacios Alberti, 2006). This area is actively managed for conservation according to its Natural Resources Management Plan (Decreto 7/2005) and any measure implying an intensification of farmland practices must be studied and approved by the park administration. In fact, some practices such as irrigation or afforestation are forbidden. Management carried out in the Nature Reserve has an important focus on cereal steppe habitats and their biodiversity (Rodríguez & Palacios, 2021), for example, most cereal fields are covered by Agri-Environmental Schemes (AES hereafter), and thus not harvested until mid-July to allow successful breeding of birds. Indeed, more than 60% of the Reserve´s extent was under AES in the 2000's (Rossel & Viladomiu, 2005).

Finally, in unprotected productive regions management is relatively intensive with regular use of pesticides and fertilizers (Albiac et al., 2017), cereal harvesting may occur from early July onwards (Rodríguez-Teijeiro et al., 2009), fallow land is ploughed several times per year, and the overall area left as fallow is increasingly smaller. In these areas, the proportion of land under AES is much smaller than within SPAs.

Little bustard data

To address the aims of this study, we used little bustard data at different spatial and temporal resolution obtained from two different sources but in both cases the censuses were done during the breeding season following the same methodology.

On the one hand, we used data from the national little bustard census carried out in 2016 (García de la Morena et al., 2018). This census followed the methodology described in García de la Morena et al. (2018) and Cabodevilla et al. (2020): 20 census points were distributed in 5x5 km squares avoiding areas where the species is unlikely to be found due to the presence of large roads, villages or woodland patches. Each point was separated at least 600 m from the nearest one. In each point, all the individuals visually and acoustically detected in a 250 meters radius during a 5-minute period were recorded. Although females were also recorded when detected, most observations corresponded only to males due to their much higher detectability. Of all squares censused in 2016, we used those in central Castilla y León, totalling 366 points, none of which were within the N.R. of Villafáfila.

Additionally, little bustard censuses were carried out annually from 2011 to 2020 by regional wildlife officers within the N. R. of Villafáfila. A total of 72 points were censused each year, with the same methodology as described above. In the year of the national census, data from the N. R. of Villafáfila were also collected by the regional wildlife officers and added to observations outside the reserve. For 2016, therefore, we had data from 438 survey points (72 inside the Nature Reserve), but little bustards were only present in 30 of them (15 within the N.R.).

Land cover information

Land cover information was obtained from the Instituto Tecnológico Agrario de Castilla y León (ITACYL, 2021), which publishes annual raster maps (from 2011 onwards) with high resolution (20x20 meters, 10x10 since 2017) based on satellite imagery. The methodology used for the identification of different land covers is based on an automatic learning algorithm that uses additional information such as LIDAR data, terrain elevation and slope, or field data. ITACYL considers a high number (more than 25) of land cover categories, many of which are rare and/or not present every year in our study area (e.g. water bodies, trees, other cultures or horticultural areas represent less than 1% on average), although the accuracy of some of those categories has increased with time (so they are considered more often in later than earlier years). Therefore, we finally considered 6 land use variables for analyses, grouping several land-cover categories according to their functional meaning for little bustards (i.e. in terms of habitat selection, see review in Traba et al. 2022; Table A2). Irrigated crops were present only in some years and in less than 1% of 1x1 km squares of the study area during the period analysed, and thus we decided not to consider them separately, but were instead grouped with their respective rain-fed crop (Table A2).

We calculated the proportion of each of the 6 land cover categories within a 250 m radius buffer around each census point, as well as the Shannon index for land cover diversity as an indicator of landscape heterogeneity. A 250m buffer has been used in previous little bustard studies and represents the radius where detectability is highest (e.g. García de la Morena et al. 2018; Faria and Morales 2018).

Statistical analyses

Favourability modelling

To estimate land-use favourability, we computed a generalized linear model (GLM) with binomial distribution of little bustard male presence or absence as response variable using the data from 2016 (438 census points), which combined the data from the second national census with those obtained in that year's census of the N. R. of Villafáfila. We only used males because observations of females are scarce and, in fact, correlated to male observations (see results). In any case, there was just one female observation without males in the same point, so “male presence” and “species presence” was globally the same data set. We assessed multicollinearity of explanatory variables (i.e., the 6 land-use categories plus the Shannon index for land-use diversity) using the variance inflation factor (VIF) between the land cover percentages inside the 250 m radius and the Shannon index resulting from them (Table A2). Since all VIF values of the variables analysed were lower than 5 (Table A2), multicollinearity was not considered an issue and all of them were included in a stepwise model selection process based on AIC using the stepAIC function of the MASS R package (Venables & Ripley, 2002). In this procedure all possible combinations of explanatory variables are analysed, and the best model is selected based on its AIC value. In each step, a model is revised: its AIC value is calculated and compared with values from the models obtained by eliminating each variable already included and adding the ones not included. In a further step, the combination with the lowest AIC value was assessed. Explanatory variables were standardised prior to analyses as (value-mean)/SD. The best model, i.e., with the lowest AIC value, included the cover of seminatural areas, cereal, and legumes. To test for spatial autocorrelation, we computed Moran’s test on the residuals of this model, which rendered non-significant results ($p = 0.830$). Model performance was assessed by means of the area under the Receiving Operator Curve (AUC), whose values vary from 0 in completely inaccurate models to 1 in perfectly accurate ones (Manel, Ceri Williams & Ormerod, 2001; Mandrekar, 2010; Gonçalves, Cortez & Moro, 2020). We also considered including a spatial factor (resulting from a polynomial trend surface analyses, based on a logistic regression of the longitude and latitude of each census point and their combination up to the second power) in the model selection process, following the procedure in Estrada et al. (2016). However, the spatial factor had a very strong impact on probability of occurrence, while we were specifically interested in calculating land-use favourability (see below) without constraints imposed by the species’ current distribution (which may be influenced by historical rather than ecological factors). Therefore, we finally decided not to include the spatial factor in the model, which allows identifying favourable areas that may be colonized, thus improving model performance and outputs (Acevedo & Real, 2012; Chamorro et al., 2021).

The favourability function is preferred to simple probability of occurrence because it takes into account differences in prevalence (Acevedo & Real, 2012). Favourability values vary between 0 and 1; a value higher than 0.5 indicates a higher than random probability of occurrence given the prevalence, while in those areas with scores under 0.5 the probability of presence is lower than what is expected by chance for a given prevalence (Real, Márcia Barbosa & Vargas, 2006;

Acevedo & Real, 2012). Thus, favourability values are directly comparable across areas or years even if prevalence varies. Favourability scores were obtained from the logistic regression probabilities computed for 2016 as follows:

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}}$$

P is the probability calculated by the logistic GLM, n_1 is the number of census points with little bustard presence and n_0 is the number of census points with little bustard absences. Using the getModEqn function (modEVA R package; Barbosa et al. 2013) the favourability function was obtained for 2016, and then extrapolated annually from 2011 to 2020 with 1x1 km resolution according to each year's habitat composition. In order to validate the biological performance of our land-use favourability index, favourability values computed for 2019 were compared with accumulated locations of GPS-tagged little bustards in the same year (Fig A1).

To test for differences in favourability values and trends across areas with different protection levels, we computed a Gaussian generalized linear model with land-use favourability in each 1x1 km squares of the whole study area (Fig A2-A11) as response variable, and year (continuous standardized variable), level of protection and the interaction between both as independent variables.

Little bustard abundance and trend analyses

To test whether little bustard abundance varied significantly among the three protection categories in the study area (non-protected areas, SPAs and the N.R. of Villafáfila), we performed an GLM with data from 2016 censuses (438 census points), with the number of little bustard males in each census point as response variable (fitted to a Poisson distribution, with a log link function), and "protection category" as a categorical explanatory variable.

For the analysis of little bustard population trend and its relationship with changes in favourability, we used the census data carried out at the N. R. of Villafáfila from 2011 to 2020 (72 census points each year). We computed two generalized linear mixed models: one with the number of males in each census point as response variable and another one with number of females (both fitted to a Poisson distribution with a log-link function). In the case of the model explaining number of males, as explanatory variables we considered year (as a continuous standardized variable), the favourability values in the point buffer in that year, and the number of neighbouring males to account for conspecific attraction. The variable "number of neighbouring males" considers males counted in other census points within a 1.7 km buffer (mean distance between census points plus the standard error) around each census point. Under the appropriate visibility conditions, little bustard males could be detected by observers up to 1 km away during censuses (Wolff et al., 2001). However, presumably little bustards can detect their conspecifics from farther distances, so by using this radius we ensure that conspecific attraction is captured by this variable. In the model explaining the number of observed females, as explanatory variables we considered year, favourability, the number of neighbouring males and also the number of males in the same census point, given that females tend to visit areas with male presence (Jiguet, Arroyo & Bretagnolle, 2000; Morales et al., 2014). Census point identity was included as a random intercept in both models. In all models, we checked normality of residuals using q-q plots. We present Anova type III results for the significance of each variable. Means are presented ± SD. All analyses were carried out with R software version 4.0.1.

Results

Land-use favourability

The final model obtained included three significant land-use variables: seminatural areas, cereal crops and legume crops. The parameter estimates from this model indicate that male presence increased with the availability of all these three land uses; the effect size was higher for cereals, followed by seminatural areas and legumes (Table 1).

However, cereal crops alone never led to highest favourability values, whereas areas dominated by seminatural vegetation can reach highest favourability values (Figure 2). The AUC value for this model was 0.731, which indicates good model performance (Mandrekar, 2010; Gonçalves, Cortez & Moro, 2020).

The favourability function obtained was:

$$F = 1 - \left(\frac{1}{1 + exp^{-0.437 + 1.012 * seminatural + 1.287 * cereal + 0.741 * legume}}\right)$$

Using this function, we calculated the land-use favourability values each year for the whole study area for each 1x1 km square (Figures A1-A11). The comparison of favourability values and GPS locations from 2019 showed that little bustards use grid cells with high favourability values, which validate the biological significance of our final model (Fig A1).

A GLM analysis with Gaussian distribution showed that land-use favourability values in non-protected areas were lower than in protected areas (in fact, they were lower than 0.5, showing overall unfavourable conditions), but that values in the N. R. of Villafáfila were significantly higher than in other SPAs (Figure 3). Additionally, the analysis showed an overall increase of favourability values from 2011 to 2020 for the three protection categories, although the slope of increase was less pronounced in the N. R. of Villafáfila (Table 2 and Fig. 3).

Little bustard local abundance and population trends

The GLM test revealed a statistically significant difference in mean abundance of little bustard males per census point in 2016 between the three protection levels (Chisq= 16.799, df = 2, p=< 0.0001; Fig. 4). The male density found during the census was higher in N. R. of Villafáfila (mean ± SD = 1.49±3.25 males/km^2), than in non-protected areas (0.69±3.36 males/km^2) or other SPAs (0.32±2.50 males/km^2).

In the N. R. of Villafáfila, male and female abundance decreased during the study period (Fig. 4); in the case of males (far more detectable than females during the breeding season), this reduction was about 50% from 2011 to 2020.

Male local abundance increased with higher land-use favourability values in the census point, although the relationship was not significant. Variables significantly explaining male abundance at each point included the number of neighbouring males and year (Table 3 and Figure 5); male abundance in each census point was positively related to the number of neighbouring males, and overall declined during the study period (Table 3 and Fig 5). Female local abundance in each census point varied significantly with the number of males in that point, favourability values and year, but not with the number of neighbouring males (Table 3 and Fig 5).

Discussion

This study confirms the importance of traditional farmland landscapes where cereal crops are intermixed with legume crops and seminatural areas for little bustards during the breeding season, but also the relevance of conspecific attraction for the species. In fact, according to our results, in the case of males the latter component is even more important than habitat *per se* in explaining spatial variations in abundance within the Nature Reserve. On the other hand, favourability values based on land use, as well as little bustard abundance, were overall far higher inside the N. R. of Villafáfila than in other SPAs or non-protected areas (see Figures 3 and 4), which indicates the importance for the species of conservation-oriented land-use management carried out in areas under this protection category.

Our main aim was to assess differences in land-use favourability values between areas with different degree of protection and thus of conservation-oriented management, namely non-protected areas, SPAs and Nature Reserves. We indeed found that land-use favourability for the little bustard was higher in protected than in non-protected areas, where values were overall lower than 0.5 (indicating lower probability of occurrence than expected from random given average prevalence). Additionally, land-use favourability values where higher in the N. R. of Villafáfila than in other farmland SPAs in the region, especially at the beginning of our study period. These results indicate that favourability is indeed related to the level of management oriented to conservation. Regulations regarding agriculture activities as well as land use changes are most restrictive in the N.R. of Villafáfila (see “Study area” section for more details). In the case of Castilla y León Natura2000 network, SPAs have management plans consisting of directives for preserving little bustard (and other steppe birds) populations, but their implementation depends on the will of farmers to enrol in Agri-Environmental Schemes. The N. R. of Villafáfila also has a Natural Resource Management Plan that specifically forbids certain intensive farming practices like irrigation or reforestation (Decreto 7/2005). Given that we only had one Nature Reserve in our study system, it is not possible to firmly conclude that the higher abundance of little bustards found in the N. R. of Villafáfila and other SPAs is related only to the protection regime and its associated higher land-use favourability, and not to other factors (e.g. historical events, philopatry), but our results strongly suggest that the significantly higher and constant values of favourability found there are likely due to the conservation management specifically carried out in the Nature Reserve, which includes the promotion of certain habitats favourable to steppe birds such as rain-fed legume crops (mean percentages of legume crops per 1x1 km square: N. R. of Villafáfila = 0.192%, SPAs = 0.127% and Non-protected =0.092%), and limitations to the expansion of other land uses known to be detrimental for them such as natural and cultivated tree cover (mean percentages per 1x1 km grid from 2011 to 2020: N. R. of Villafáfila=0.016%, SPAs=0.105% and Non-protected=0.166%).

These differences in land-use favourability between the three protection figures have been reported in previous studies (e.g. McKenna et al. 2014). In fact, Martínez-Fernández et al. (2015) described SPAs as half-way between non-protected areas and Nature Reserves regarding their conservation goals and legal stringency, a conclusion that matches our findings. Although the Natura2000 network has contributed to preserve European biodiversity (including steppe habitats), its effectiveness largely relies on the area covered by Agri-Environmental Schemes. Therefore, greater funding and legal support is required to avoid the so-called “paper park” effect in Natura2000 areas. According to Rodríguez-Rodríguez & Martínez-Vega (2018), Nature Reserves are the most efficient protection figure against land use changes due to their legal stringency and management regulations. Because of these restrictions, Nature Reserves in farmland regions present higher values of permanent natural habitats (such as pastures and meadows) than Natura2000 SPAs without additional protection status (Martínez-Fernández, Ruiz-Benito & Zavala, 2015). However, in order not to become isolated in a matrix of unprotected landscape and suffer deleterious edge effects, Nature Reserves should be surrounded by buffer areas where a similar management regime is implemented (Martínez-Fernández, Ruiz-Benito & Zavala, 2015; Rodríguez-Rodríguez & Martínez-Vega, 2018), especially those of small size, since they are more prone to edge effects from the management of surrounding areas. In the case of the N. R. of Villafáfila, which is surrounded by intensive farmland, its steppe bird conservation-oriented management (Rodríguez & Palacios, 2021) is likely counteracted by the more intensive management of immediately neighbouring farmland, which likely jeopardizes the efficiency of steppe bird conservation measures. Isolated reserves may fail protecting endangered species, particularly those exhibiting far reaching seasonal movements such as the little bustard (García de la Morena et al. 2015, own unpublished data). In fact, individuals tagged in our study area perform movements outside the protected areas, mainly during the non-breeding season, but always to squares with high favourability values (Figure A1), which validates the biological relevance of our land-use favourability results. However, the fewer high-quality areas available, the more difficult will be for little bustards to find them, which increases both individual (e.g. mortality) and population (e.g. Allee effect) risks associated to these movements. Thus, the management guidelines mentioned above and implemented in Nature Reserves like Villafáfila should be encouraged (e.g., with more voluntary contracts) in SPAs to overall increase land-use favourability and connectivity between areas with high quality little bustard habitat.

Regarding temporal trends, land-use favourability increased in the three protection categories from 2011 to 2020 (Table 2 and Figure 3). This result was unexpected considering the sharp decline of Iberian little bustard populations (Morales & Bretagnolle, 2021). However, it may be a consequence of the agricultural trends observed in Spain: in the case of our study area, the percentage of cereal crops has increased during this period in all the protection figures analysed, which may partly explain the observed trends. Moreover, areas with low crop yields have suffered abandonment (Oñate, 2005), which usually leads to an increase of natural vegetation habitat within the farmland matrix (long-term fallows, grassland, and wastelands). Although farmland abandonment is mainly taking place in areas with moderate to steep slopes, the flat farmland that dominates our study area does also present a certain cover of natural grasslands and wastelands in lower yielding sectors, which may have contributed to the favourability increase observed, given that these land uses weight positively on little bustard land-use favourability (Fig. 2). However, it is important to emphasize that global habitat quality is likely to be strongly affected by the agricultural practices implemented, beyond the cover of each specific land use type, something that we could not take into account (due to the unavailability of field-level information on management practices) but which would be important to include in future studies. For example, a potential increase in the use of pesticides in cereal crops leading to lower food availability and thus habitat quality for birds cannot be reflected in our analyses. Because of this, our land-use favourability trend results may be overoptimistic in terms of global habitat quality.

In spite of the high land-use favourability inside the Nature Reserve, and the positive trend in this variable throughout the study period also observed in this area, the species also markedly declined there (Figure 4). Therefore, although the large-scale decline of little bustards and other steppe birds has been found to be associated with the loss of key habitats in the agricultural landscape (i.e. fallow land, see Traba and Morales 2019), our result suggests that the decline in the study region may not right now be driven primarily by landscape changes, and underlines the need to develop finer-scale models of habitat quality accounting for agricultural practices at field level to better understand causes of mortality and breeding failure (see Bretagnolle et al. 2018; Cuscó et al. 2020). However, it is important to emphasize that the population reduction observed in the region was even higher outside the N. R. of Villafáfila (García de la Morena et al., 2018), which suggests that areas with high land-use favourability may attenuate the negative population trends observed at a larger scale.

Beyond agricultural management, little bustards are affected by different threats related to human activities, such as linear infrastructures that cause habitat fragmentation leading to isolated patches that are difficult to reach by dispersing individuals (García de la Morena et al., 2007) or power lines which generate mortality hotspots (Silva et al., 2014). These factors may be affecting the population dynamics at a larger scale, which may be reflected in the negative trends observed at the Nature Reserve despite its higher land-use favourability.

Our models also confirm the importance of conspecific attraction for the study species (Table 3 and Fig. 5), which has already been highlighted in previous studies (e.g. Morales et al. 2014). They also show that female abundance is explained by local male abundance, which supports the idea that results obtained from male abundance at landscape scale can be extrapolated to both sexes (Table 3 and Figure 5; Devoucoux et al. 2018). This overlap in male and female space use is consistent with the species' exploded lek mating system (Jiguet, Arroyo & Bretagnolle, 2000), in which males tend to aggregate over certain display areas to which females are attracted (Tarjuelo et al., 2013; Morales et al., 2014). Because of this tendency to cluster, little bustards may be absent from certain areas of good quality habitat, as shown by our positive but non-significant relationship of male abundance with land-use favourability obtained from the censuses at the N. R. of Villafáfila (Table 3 and Figure 5).

Furthermore, this result emphasizes how the ecology of the little bustard (from its breeding system to its wintering behaviour) is density dependent (Bretagnolle, Mañosa & Morales, 2022) and therefore extremely sensitive to local extinctions. As they tend to aggregate in areas where their conspecifics are present, it is difficult for them to colonise new areas even if they have high favourability values. Local population trends may be affected by processes occurring at metapopulation scale, since individuals spend most of the annual cycle out of breeding areas (Morales et al., 2022). Not only migration, but also other features such as habitat quality or mortality in the non-breeding quarters have an impact on breeding populations. It is therefore crucial to develop conservation strategies that protect summering and wintering quarters and distribution ranges as a whole in a more geographically integrated manner.

Conclusions

Our results confirm a sharp decline of little bustard breeding populations (Fig. 4; e.g. (García de la Morena et al., 2018; Morales & Bretagnolle, 2021), even in protected areas of relatively high land-use favourability for the species, such as the N. R. of Villafáfila. Furthermore, the population has declined despite the increase in land-use favourability estimated for the three protection categories. Although the latter may be partly related with the fact that models did not account for field-scale factors such as farming practices, these results suggest that the little bustard decline could be steepened by some behavioural traits of the species associated to lek mating, such as conspecific attraction or the density dependent space use shown by our models (Table 3 and Fig. 5).

On the other hand, the high land-use favourability values found in the N. R. of Villafáfila suggest that they are likely a consequence of its active management focused on steppe bird conservation (González del Portillo et al. 2021), in contrast with SPAs and, particularly, non-protected areas which, overall, cannot be considered favourable for the species (Figure A2-A10). Indeed, land-use favourability values obtained in non-protected areas were lower than 0.5, which means that habitat conditions there do not favour little bustard presence (Acevedo & Real, 2012), and individuals tagged with GPS since 2019 avoided these areas (Figure A1). This highlights the need to increase the level of conservation-oriented landscape management outside protected areas (ideally, at the level attained in Nature Reserves like Villafáfila), particularly in those sites where the species is still present, to ensure the preservation of the little bustard. Our results (Fig. 2) showed that the highest values of favourability can only be reached if seminatural areas are abundant in the farmland matrix. Therefore, promoting fallow fields and other land-uses with natural herbaceous vegetation cover would increase favourability, but also population productivity if adequately managed, as they are preferred by little bustard females as main nesting habitat (Morales et al., 2013).

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Table 1(on next page)

Results of the final model explaining the occurrence of male little bustards in sampling points in relation to habitat.

Dependent variable	*Explanatory variable*	*Parameter estimate*	*LR Chisq*	*Degree of freedom*	*Pr (>Chisq)*	*Sign*	*R2*	*AUC*
Presence of males	Seminatural	1.012	12.800	1	<2e-16	***	0.035	0.731
	Cereal	1.287	16.629	1	<2e-16	***		
	Legume	0.741	6.943	1	0.008	***		

Table 2(on next page)

Results from the Type III F tests from the model analysing little bustard land-use favourability trends during the study period.

Explanatory variable	*Sum Sq*	*Degree of freedom*	*F Value*	*Pr (>F)*	*Sign.*	*R^2*
Intercept	11192	1	132831.375	$<2.2e^{-16}$	***	0.128
Year	21.6	1	256.063	$<2.2e^{-16}$	**	
Protection	1563.9	2	9280.794	$<2.2e^{-16}$	***	
*Year*Protection*	3	2	17.759	$1.942e^{-8}$		
Residuals	11872.1	140904				

Table 3(on next page)

Anova type III results of the models explaining the number of little bustard males and females at sampling points within the Nature Reserve of Villafáfila.

Model	*Response variable*	*Explanatory variable*	*LR Chisq*	*Degree of freedom*	*Pr (>Chisq)*	*Sign.*	*R^2*	*Dispersion*
1	Number of males	Intercept	5.844	1	0.016	*	0.309	0.765
		Favourability	0.167	1	0.683			
		Neighbouring males	34.804	1	$3.646e^{-9}$	***		
		Year	7.170	1	0.007	**		
2	Number of females	Intercept	$5.607e^{6}$	1	$<2.2e^{-16}$	***	0.131	0.412
		Favourability	$1.381e^{6}$	1	$<2.2e^{-16}$	***		
		Males	$7.361e^{4}$	1	$<2.2e^{-16}$	***		
		Neighbouring males	$5.77e^{-1}$	1	0.448			
		Year	$1.576e^{4}$	1	$<2.2e^{-16}$	***		

Figure 1

Map of the study area. Census points are presented as dots and the rectangle represent the limits of the study area (see Methods).

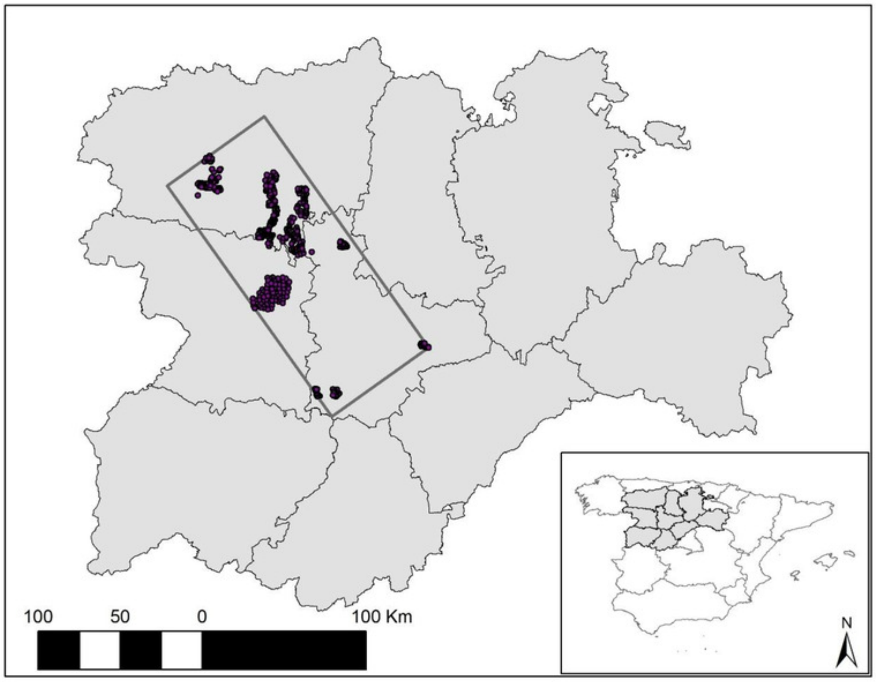

100
50
0
100 Km
N

Figure 2

Predicted male occurrence probabilities from the model detailed in Table 1 (mean and 95% confidence intervals are shown).

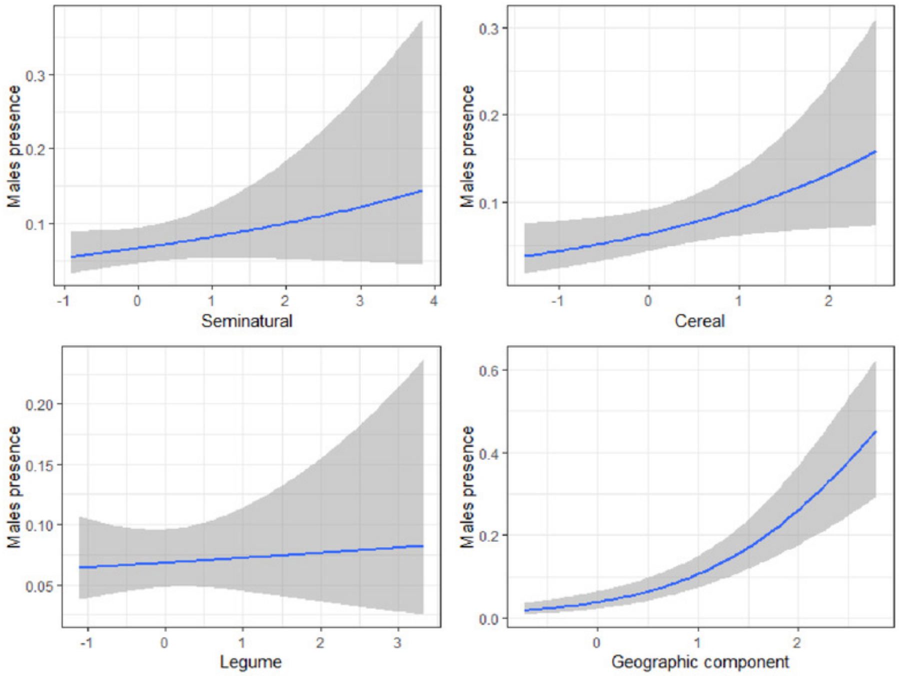

Males presence
Seminatural
Cereal
Legume
Geographic component
0.1
0.2
0.3
0.05
0.10
0.15
0.20
0.0
0.4
0.6
-1
0
1
2
3
4

Figure 3

Plot of values predicted by the final model analysing favourability trends in the three protection categories considered (Table 2, mean values and 95% confidence intervals are presented).

Note that “year” was standardized prior to the analyses, although the figure presents year labels for clarity.

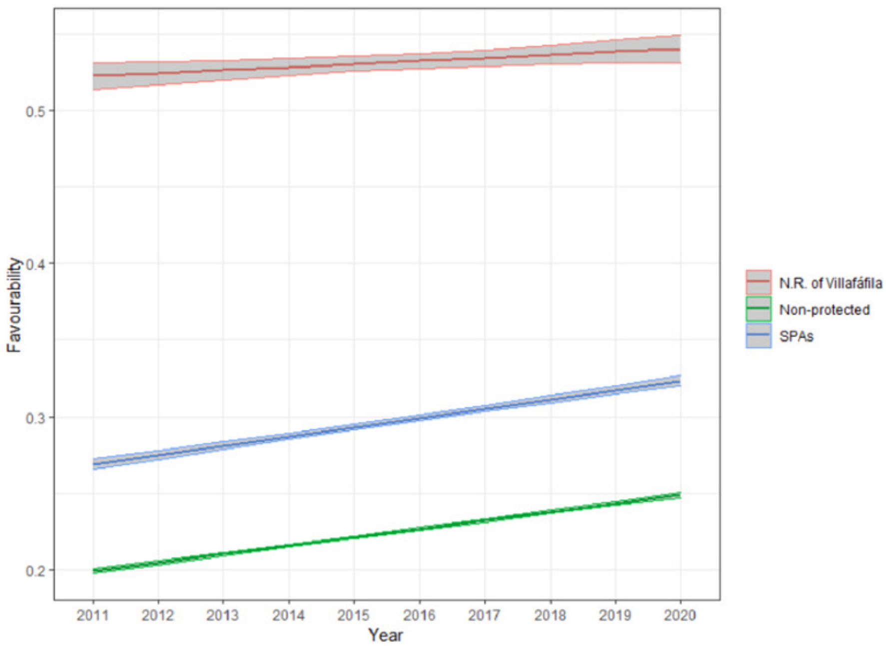

0.5
0.4
0.3
0.2
Favourability
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
Year
N.R. of Villafáfila
Non-protected
SPAs

Figure 4

Results from the generalised linear model analysing little bustard male abundance differences between protected area categories (mean and 95% confidence intervals are shown).

Letters indicate the results from Tukey post hoc comparisons, levels with the same letter showed no significant differences.

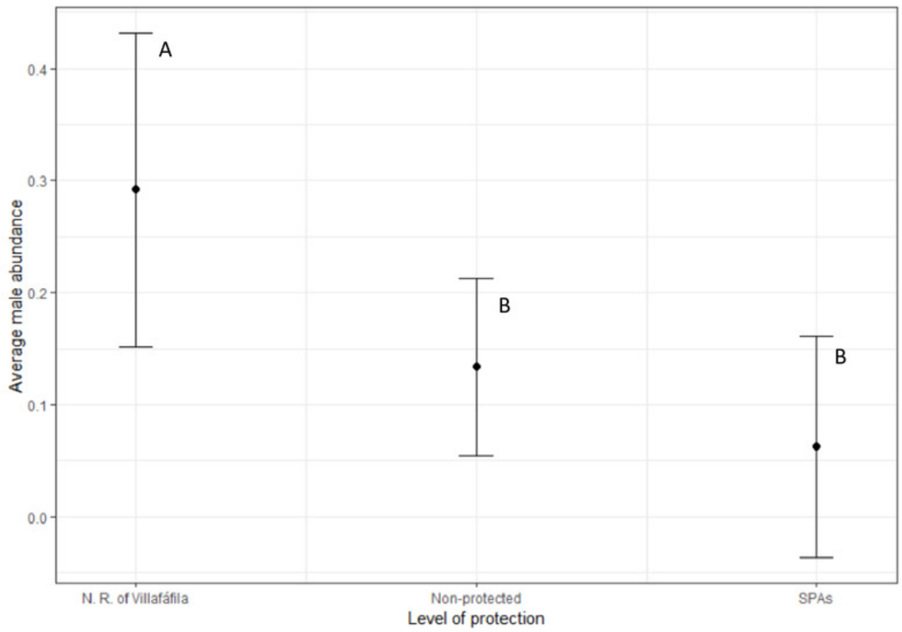
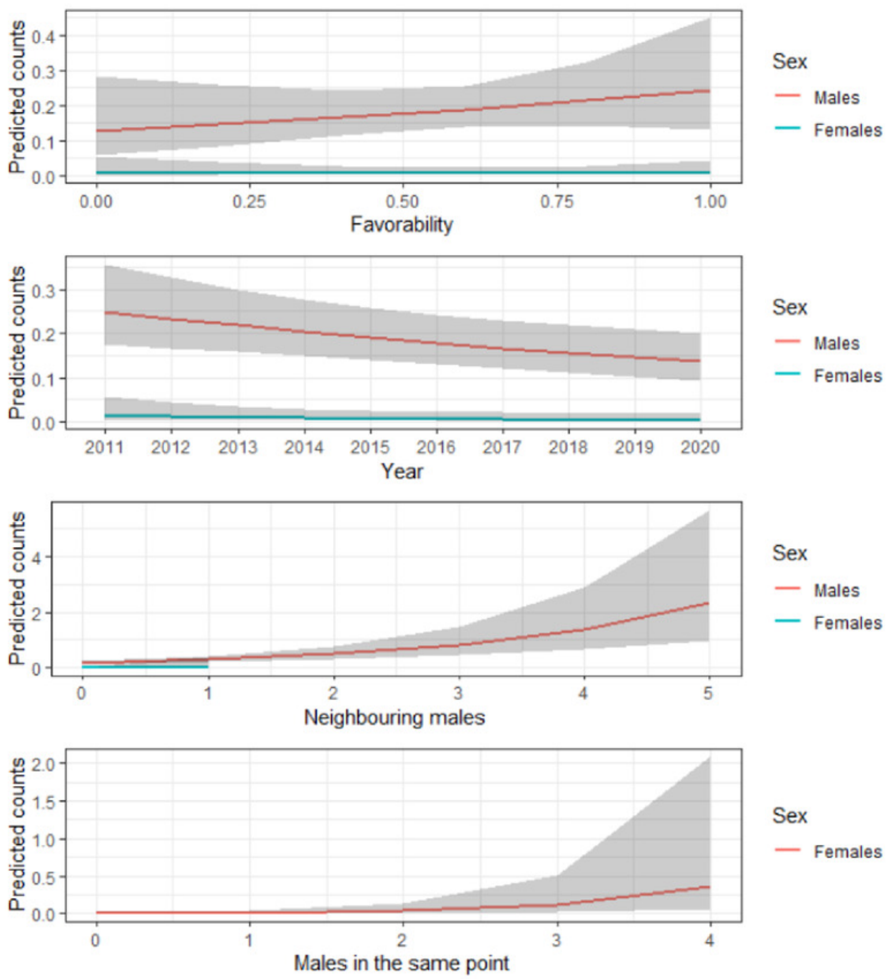

A
B
B
0.4
0.3
0.2
0.1
0.0
Average male abundance
N. R. of Villafáfila
Non-protected
SPAs
Level of protection

Figure 5

Predicted counts for little bustard males and females obtained from the model analysing census data from the N. R. of Villafáfila (Parameter estimates detailed in Table 3; mean values and 95% confidence intervals are shown).


Predicted counts
0.4
0.3
0.2
0.1
0.0
0.00
0.25
0.50
0.75
1.00
Favorability
Sex
Males
Females
Predicted counts
0.3
0.2
0.1
0.0
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
Year
Sex
Males
Females
Predicted counts
4
2
0
0
1
2
3
4
5
Neighbouring males
Sex
Males
Females
Predicted counts
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
Males in the same point
Sex
Females