Spatial analysis of habitat quality in a fragmented population of little bustard 1 2 (Tetrax tetrax): implications for conservation 3 4 5 Javier GARCÍA 6 24392, Villadangos del Páramo, León, Spain 7 8 Susana SUÁREZ-SEOANE* 9 Área de Ecología, Departamento de Ecología, Genética y Microbiología, Universidad 10 de León, Campus de Vegazana s/n, León 24071, Spain. degsss@unileon.es 11 12 David MIGUÉLEZ 13 Departamento de Biología Animal, Universidad de León, Campus de Vegazana s/n, 14 León 24071, Spain 15 16 Patrick E. OSBORNE 17 Centre for Environmental Sciences, School of Civil Engineering and the Environment 18 University of Southampton, Highfield, Southampton SO17 1BJ, UK 19 20 Carlos ZUMALACÁRREGUI 21 C/Lucas de Tuy, 5, 24002 León, Spain 22 23 * Address for correspondence

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2 implications for conservation

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3 Abstract: Little bustard populations have suffered reduction and isolation as a 4 consequence of landscape transformations resulting from changes in traditional agricultural systems. Consequently, the species survives within reduced and 5 6 fragmentary habitats, like islands isolated in a modified matrix. In this paper, we 7 analyze the spatial variations in male density and habitat quality in a fragmented 8 population located at the limit of the species' Iberian range, which is affected by 9 agricultural intensification, using a regional modelling approach. Habitat quality 10 (quantified according to the species perception) and bird density decreased along the 11 intensification gradient. However, in the most intensive agricultural zone, the quality of 12 habitats selected by little bustard males increased, while density decreased, against the 13 expected. In possible explanation, we suggest: (1) density is not necessarily a good 14 indicator of habitat quality, (2) population could be under-saturated in this zone, (3) 15 interannual variations in species distribution, or (4) other relevant variables related to 16 the agricultural intensification process not included in this analysis, such as small-scale 17 disturbances. Analysis of population distribution pattern showed a spatial configuration 18 in which the most densely populated squares were located at the core of the biggest 19 population patches, in contact with mid-density squares, and all surrounded by low-20 density squares. Fragmentation negatively affected habitat quality and male density. 21 Largest population patches, containing higher density values, were located at the 22 beginning of the intensification gradient. Preservation of little bustard densities is 23 related to an adequate management of the farming system. Habitat fragmentation 24 requires an urgent conservation strategy to prevent local and regional scale habitat

- 1 deterioration, by reducing patch isolation to maintain genetic diversification and
- 2 functional connectivity. **Key words:** population saturation, agricultural intensification,
- 3 density

1. Introduction

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The European Union, via its old Common Agricultural Policy (CAP), encouraged agricultural intensification through direct payments to more productive farms, maintaining prices artificially; nevertheless, at the same time, it offers subsidies to farmers for the abandonment of crop fields in less productive areas (Pain and Pienkowski, 1997). These two opposite tendencies are the main threats affecting farmland bird species in Europe (Farina, 1995, 1997; Preiss et al., 1997; Sanderson et al., 2005; Suárez-Seoane et al., 2002a; Tucker and Heath, 1994). In Spain, this has been the cause of the decline of many key steppe birds. Of 42 species considered to be of conservation priority (SPEC "Species of European Conservation Concern"; Tucker and Heath, 1994) in steppe or "pseudo-steppe" habitats, 71% are declining (Suárez et al., 1997). Half of the total population of little bustard *Tetrax tetrax*, which is considered a "Near Threatened" species (Hilton-Taylor, 2000), resides in the Iberian Peninsula (De Juana and Martínez, 2001), where it is endangered by agricultural change (i.e. intensification) (Díaz et al., 1993; Goriup, 1994; García de la Morena et al., 2003). Since the 1950's, socio-economic changes have been important in the study area, León province, a target region of NW Spain located at the limit of the species' Iberian range. Following the integration of Spain into the European Community, land abandonment and reforestation have took place in large tracks of traditional agricultural lands, besides a big process of intensification, which include irrigation, mechanisation, land consolidation, increasing use of biocides and fertilizers, crops shift (decrease in legumes and cereals, such as wheat or barley, massive increase in maize) and fallow reduction. As a consequence of those land transformations little bustard populations

1 have suffered reduction and fragmentation, surviving in more or less reduced pieces of 2 habitat, like islands isolated in a highly modified matrix. The question is how the 3 quality of these remaining suitable habitat patches will affect little bustard population. 4 In forestlands, patch quality depend mainly on size and isolation (Van Dorp and 5 Opdam, 1987). However, in the Mediterranean agricultural landscapes, which are 6 mosaics of different land uses (Bennett et al. 2006), the contrast among patches and the 7 surrounding matrix is lower that for other kind of landscapes. Therefore, habitat quality 8 depends not only on the spatial configuration and arrangement of patches (Sötherström 9 and Pärt, 2000; Wolff et al. 2001), but also on its intrinsic quality, which is related to 10 other factors, like intensification (Benton et al., 2003). This could be the responsible for 11 the connectivity (i.e. species movement) across habitat patches (Baudry et al., 2004). 12 Habitat quality is expected to influence both species distribution and density. 13 Earlier studies have analyzed the relationship between land uses, agricultural practices 14 and management (which strongly determinate habitat quality in agricultural landscapes), 15 and little bustard male abundance (Wolf et al., 2001; Martínez and Tapia, 2002; Brotons 16 et al., 2004; Morales et al., 2005) at a landscape scale and, also, breeding habitat 17 selection at a local scale (e.g. Martínez, 1994, 1998; Campos and López, 1996; 18 Salamolard and Moreau, 1999). However, there are only a few papers dealing explicitly 19 with little bustard densities in fragmented populations (Wolf et al., 2002) (note that 20 density could be an indicator of habitat quality, helping in predicting population trends 21 and designing effective conservation measures) and analysing distribution and habitat 22 quality variations at a regional scale (Suárez-Seoane et al., 2002b, 2004). 23 The main aim of the present manuscript is to study spatial variations in male density and habitat quality available for a fragmented population of little bustard 24

affected by agricultural intensification, using an approach based on remote sensing and GIS at a regional scale. As agricultural intensification negatively affects farmland bird species (Donald et al., 2001), our hypothesis is that this land transformation will decrease intrinsic habitat quality for the little bustard, which will be negatively correlated to bird density. Since habitat quality of patches will be influenced not only by its intrinsic value but also by its spatial arrangement, we investigate the spatial variations in habitat quality within the population patches, testing whether bird density is negatively correlated with fragmentation. Complementarily, we were interested in explore the advantages of using the habitat suitability index, made up in previous studies (Suárez-Seoane et al., 2002b, 2004), as an integrated and spatially explicit index of habitat quality, which gives a more synthetic view of the territory. Finally, we discuss some conservation implications of our results, exploring how this could be related to the new Common Agricultural Policy.

3. Materials and Methods

3.1. Study area

The study area lies in León province (NW of the Iberian Peninsula), which is located at the border of the species Spanish distribution of the little bustard. It occupies approximately 15 000 km². Here, at present, little bustard populations live in steppe farm systems traditionally managed across a plateau particularly located in the southeastern quarter of the province. However, in order to identify other potential areas which should be considered in terms of conservation, we model little bustard

distribution for the entire León province rather than only the area occupied currently by the species. The agricultural lands occupied by little bustard were divided into four zones according to their farm system and a gradient of increasing agricultural intensification: zone 1- Parameras Altas, zone 2- Páramo Leonés, zone 3- Los Oteros and zone 4- Tierra de Campos (modified from Penas et al., 1995). In addition, we defined, as zone 5, areas where the species is absent (Fig. 1). Intensification level has been estimated according to the agricultural practices and land structure (note: we did not consider irrigated areas where the little bustard does not breed). Less intensive areas show lower vegetative growth in spring, higher crop-diversity, less cereal croplands, more natural vegetation, vineyards and pasturelands, and a smaller field size than the more intensive ones. Fallows associated to a one or two year-cereal rotation are less frequent in the less intensive areas. However, in relative terms, wastelands are more important.

3.2. Bird data census

We studied the little bustard population in spring of 2003, from mid-May to mid-June, coinciding with the peak of male sexual display in this region. We conducted a single count on each 1142 survey points distributed across the current and potential distribution area (according to our previous knowledge on the species distribution), which were homogeneously distributed on the top of the 1km-UTM grid (the basis of the sample design). Sample points were conducted along transects which were carried out by car, following secondary routes and pathways, stopping for 5 minutes (De Juana and Martínez, 1996; Jolivet, 2001; Wolf et al., 2001) in each of them. They were

separated by up to 600m This distance was chosen according to evidence that the male song can be heard at a distance of between 250m (Wolf et al., 2001) and a maximum of 500 m (Hellmich and Núnez, 1996) according to the topographic variability. Censuses were conducted during the first three hours after sunrise and the last two hours before sunset, coinciding with the male highest activity, and avoiding adverse weather conditions. Bird geographical positions were recorded using a global positioning system (GPS). No contact was considered to represent absence or an extremely low-density.

Density was calculated as the number of males within each 1-km UTM grid.

Presence records were rasterised into 1-km-pixels (resolution imposed by the satellite imagery). An equivalent sample of "non-occupied pixels" was obtained by plotting an equal number of 1km-pixels randomly distributed on the maps, avoiding the occupied places and the non-suitable habitat for the species, such as urban and forested areas, or mountains over 980 meters of altitude (the maximum altitude noted for presence).

3.3. Environmental predictors

Habitat was characterised by three groups of environmental variables: vegetation and farm systems, topographic features and human disturbances (Table 1). These variables were measured using Geographic Information Systems (GIS) and digital cartography from different sources.

The first group of variables (vegetation and farm systems) was obtained from: (1) AVHRR data at 1 kilometre resolution: vegetation was characterised using a twelvemonth time series of monthly Maximum Value Composite (Holben, 1986; Marçal and

Wright, 1997) of Normalised Difference Vegetation Indices (NDVI-MVC). The raw imagery for 1999 (the most recent available in our archive) was received by the NERC Satellite Receiving Station at Dundee, Scotland, and processed by the Remote Sensing Group at the Plymouth Marine Laboratory (for a more detailed description about the product, see Suárez-Seoane et al., 2002b). NDVI-MVC were combined into different variables to identify annual variations in vegetation (biomass) detected by the birds; (2) CORINE Land Cover Thematic Map at 1:100 000 from 2002; (3) aerial orthophotographs at 1:10 000 scale from 2002: to determine field size, we calculated the number of fields in a 1-kilometre transect measured as a diagonal within either occupied or random pixels; (4) data on farm statistics (irrigation crops, dry crops, fallow and uncultivated lands) obtained from the Regional Government at the scale of the municipality from 2002; (5) National Plan of Irrigated Lands 2002-2008.

The second group of variables, on topographic features, was measured on a digital terrain model at 200 metres (and then transformed into a derived variable calculated within windows of 5 x 5 pixels (equivalent to 1 km^2 , the resolution used on this study, imposed by the satellite imagery resolution).

Finally, human disturbance predictors were obtained from digital maps of linear features at 1:200 000 (National Geographic Institute). These data were overlapped into grids of 200 meters cell size and then converted into quantitative variables measured within windows of 1 km²: (1) as the average of the distances measured from the centre of every 200m-pixel to the nearest habitat features, which provides information about landscape structure; and (2) as the percentage of each feature within the 1-km pixels, which provides information about landscape composition. Analyses were performed using the commands "distance", "filter" and "contract" in IDRISI 32.2 (Eastman, 2000).

1 Multicolinearity among the predictors was avoided by calculating pairwise 2 Pearson correlations. Variables showing correlations greater than 0.7 (Tabachnick and 3 Fidell, 1996) were excluded from the subsequent analysis, retaining the strongest 4 explanatory variable. 5 6 3.4. Statistical analysis 7 8 In order to explore the relationships between habitat quality and little bustard 9 densities along an agricultural intensification gradient in León province, we performed 10 several analyses. 11 12 3.4.1. Univariate analysis 13 Firstly, we compared the mean values for the environmental variables (vegetation-14 farm systems, topography and human disturbances), discriminating: (1) between 15 occupied and non-occupied pixels for the whole of the study area; and (2) between the 16 occupied pixels within each of the four zones defined along the gradient. We applied a 17 univariate t-test with a Bonferroni adjustment to reduce the chance of Type I errors. 18 19 3.4.2. A habitat quality index 20 Subsequently, we ran generalised additive models (GAM) with logit link function 21 and binomial error term. Parsimonious GAM models were generated using backward 22 selection with an F-value of 0.05 for the variable to remain in the equation. For each 23 selected variable, we tested whether the smoothed term was significant over a linear

model and replaced non-significant smoothed terms with linear terms. Terms were then

dropped one by one from the final equation and their contribution to the model assessed using a likelihood ratio test (Venables and Ripley, 1999). We used S-plus 6.1 (Venables and Ripley, 1999) and the GRASP interface (Lehmann et al., 2002, 2003) to fit cubic splines with four knots to each variable. The response variables were the occupied and non-occupied pixels and, the environmental predictors used are presented in Table 1. The number of presences and absences included in the models were roughly equal within each zone (apart of zone 5, which has no occupied pixels) although they differ between them. We do not think that the small differences within zones significantly affect a GAM combining the data from all zones. The differences between zones may be more relevant: zones with few occupied pixels are under-represented in the model because we have tried to match the numbers of presences and absences within zones. In theory, this could make the model appear artificially good at classifying presences and absences, thus separating between zones rather than within zones. As a consequence, subsequent analyses could be an artefact of this limitation. In order to avoid this problem, we tested the effect of the modelling approach by doing an alternative analysis which has the opposite bias; we called it "stratified model" versus the original, "nonstratified one". We made the number of pixels approximately equal in each zone, irrespective of whether they are presences of absences (Table 2). This approach greatly increased the number of unoccupied pixels used in zones 3 to 5. It also breaks the link between the number of occupied-non occupied pixels and its representation in the model. Performance of final models was assessed through 10-fold cross-validation (Verbyla and Litvaitis, 1989; Fielding and Bell, 1997). Both final and cross-validated models were assessed using the area under the ROC curve (AUC) (Beck and Shultz,

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1986; Zweig and Campbell, 1993; Fielding and Bell, 1997), which is a convenient measure that does not require a threshold for presence and absence to be set.

With the purpose of testing if models (stratified or non-stratified) were significantly different, we compared the predictions made by both models for the sample points using a paired t-test. This indicates whether results depend on the sampling strategy and helped to decide which model we used for the subsequent analysis. If there are no significant differences, the stratified model can be considered as robust and be used as an integrated index of habitat quality (HQI). A value near 1 represents sites where the habitat is optimal for the bird; a value near 0 corresponds to unsuitable sites. To define an objective cut-off point above which to consider the species as present, we classified the HQI at all cut-off points between 0.0 and 1.0 with an interval of 0.1 into predicted presence and absence, and compared the result with the actual data. We chose to split the data at the cut-off point that maximised both the percentage of correct presences and absences (Pereira and Itami, 1991; Fielding and Bell, 1997; Brito et al., 1999; Suárez-Seoane et al., 2002b).

3.4.3. Relationship between habitat quality, agricultural intensification and bird density

Next, in order to analyse habitat quality for (1) selected habitat along the agricultural gradient, and (2) zones showing higher or lower little bustard densities, we ran univariate generalised linear models (GLM). Habitat quality was introduced (HQI) as the dependent variable, with agricultural gradient (zone) and density as a fixed factor and covariable, respectively.

1 Subsequently, we studied the ratio used/available habitat (obtained by 2 reclassifying the HQI map according to the cut-off point) to explore possible differences 3 in population saturation along the gradient. 4 5 3.4.4. Analysis at the scale of the occupied patches 6 Finally, we carried out another analysis at the scale of the occupied patches 7 (population nucleus), investigating their spatial structure: (1) In order to test whether 8 bigger nuclei showed higher quality and density than smaller ones, we ran a univariate 9 GLM introducing habitat quality and density as dependent variables and patch size as a 10 covariable. (2) With the aim of assessing whether pixels with similar densities were 11 contiguous, we calculated the connectedness (Eq. 1) (a structural parameter which 12 quantify relationships among landscape elements) between the three categories of bird 13 density (class 1: 1-3, class 2: 4-7, class 3: 8-11 birds/km²) identified for the four zones. 14 Eq.1. Connectedness: $C\{i\} = p_{(i,i)}$ (Baudry, 1985; Baudry and Merriam, 1987). 15 The parameter expresses the probability that two adjacent cells, x and y, belong to 16 the same landscape unit $\{A,B,...,i,...,T\}$. 17 18 4. Results 19 633 little bustard males were detected, with densities from one to 11 males/km². These 20 21 records were rasterised into 245 1-km-pixels 22 23 4.1. Univariate analysis

Birds were present in areas significantly flatter, showing lower values of green biomass (yearly values of maximum, minimum, mean and growing NDVI), and higher biomass loss by harvest (which indicates a cropland selection) than areas where the birds were absent. Little bustards preferred fallows and wastelands, avoiding irrigated lands. They tolerated less human disturbances associated to the proximity of roads and towns than absence points (Table 3a).

In the more intensive areas ("Tierra de Campos" and "Los Oteros"), birds were present in agricultural areas showing higher vegetative growth, lower mean biomass, a stronger loss of "greenness" at harvest time, and a higher amount of fallow, than at the opposite side of the gradient ("Parameras Altas" and "Páramo Leonés"), where the birds also occupied more wastelands. Field size was smaller at the presence locations in less intensive areas, and this is related to a higher potential richness crop. Irrigated crops had less effect in more intensive areas because they are not present in these locations. According to the topographic features, we found no clear tendency. Little bustard males did not show significant differences in relation to the presence of roads along the intensification gradient. However, males were present further from towns in zones 1 (where housing is located near rivers) and 4 (where towns are bigger), probably because of the particular social organization of people in those areas (Table 3b).

4.2. A habitat quality index

Tables 4a and 4b show the summaries for both non-stratified and stratified GAM models, respectively. The stratified model (SM) had slightly higher predictive performance (AUC= 0.98) than the non-stratified one (NSM) (AUC= 0.94). The power

- of both models decreased in similar proportion when they were cross-validated; AUC
- 2 values decreased to 0.94 in the case of the SM model and to 0.90 for NSM.
- 3 Nevertheless, differences in the probability values predicted for both models for the
- 4 presence sites were not significant (t=0.086; gl=244; p=0.931). Consequently, as we
- 5 were particularly interested in evaluate differences between zones, we selected the non-
- 6 stratified model (NSM) for building the habitat quality index used in the subsequent
- 7 analysis.
- 8 Most of the selected variables in the NSM were related to vegetation/ farming
- 9 practices more than topography or human disturbances (six, one and three variables
- 10 respectively). Biomass growth from winter to spring and distance to irrigated lands were
- the variables which contributed more to the construction of the model (see drop values
- at the Table 4a).surface of probabilities (values 0 to 1, for unsuitable to highly suitable
- 13 habitat) which was used as a habitat quality index (HQI) in the subsequent analyses.
- 14 This index allowed for analysing available habitat quality, as perceived by the species.
- 15 The optimum cut-off point obtained for the model was 0.55. This cut-off point was used
- to identify areas where the species is predicted to occur (Fig. 2).

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4.3. Relationship between habitat quality, agricultural intensification and bird density

- 20 Male density decreased significantly along the gradient of increasing agricultural
- 21 intensification (F=9.45, DF= 3, p=0.00). Bird density (F=18.29, DF=1, p=0.00)
- increased with increasing habitat quality. The lowest values for the habitat quality index
- were noted in places showing lower little bustard densities (1-3 birds/km²), and the

- biggest values were for medium (4-7 birds/ km²) and high (8-11 birds/ km²) densities
- 2 (F=243.95, DF= 1, p=0.00) (see Fig. 3).
- In addition, significant differences (F=8.44, DF= 3, p=0.00) in habitat quality
- 4 occur among the four zones located along the intensification gradient (Fig. 4). Habitat
- 5 quality (as perceived by the species, measured through the HQI) decreased along the
- 6 gradient, following the same tendency as bird density. However, for zone 4 ("Tierra de
- 7 Campos", the most intensive area) we noted an increase in habitat quality selected by
- 8 little bustard males. This disagreement suggested to us the hypothesis that this area
- 9 could be under-saturated; therefore, birds may be using the optimal available sites.
- 10 Lower saturation values (i.e. used habitat/available) do occur in that zone, which
- supports this idea (Table 5).

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4.4. Analysis at the scale of occupied patches

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- Mean habitat quality increased with the size of the patches occupied by the bird
- 16 (F=228.75, DF= 1, p=0.00) (Fig. 5). In the same way, mean density increased with the
- size of patches (F=62.55, DF=1, p=0.00) (Fig. 6).
- The analysis of connectedness suggests that 1km squares (pixels) with higher
- 19 little bustard male density are core areas within big patches, located mainly in contact
- with pixels with medium density. Pixels with low density are the most numerous, and
- are mostly isolated, in small patches or at the periphery of big patches. The largest
- 22 population patches, containing higher density values, are located at the beginning of the
- 23 intensification gradient; in the more intensive areas, there are only small patches
- 24 enclosing low densities. (Table 6; Fig. 1).

5. Discussion

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4 5.1. Habitat quality, agricultural intensification and bird density

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A decline in both little bustard densities and distribution at a regional scale can be associated with farming changes which have occurred in Europe during the last decades, and which drive agricultural intensification in some areas (Díaz et al., 1993; Tucker and Heat, 1994). Our results show a direct negative relationship between agricultural intensification and little bustard male density, as highlighted by other authors (Wolff et al., 2001; Martínez and Tapia, 2002; Morales et al., 2005a). This seems to be related to a decrease in habitat diversity in intensive areas (in this case: "Los Oteros" and "Tierra de Campos"), as noted in previous studies (Martinez, 1994; Salamonard and Moreau, 1999; Suárez-Seoane et al., 2002b; Morales et al., 2005a, b). In fact, the variables with the highest explanatory power selected by our model are related to vegetative growth (crops), fallow and wastelands, with indicates a crop mosaic landscape. It is particularly relevant that in the most intensive areas, fallow could be the strongest determinant factor explaining little bustard presence. In another study carried out nearby (Díaz et al., 1993), the little bustard was absent from intensive dry croplands (cereal monoculture), while it was abundant (0.63 birds/10 ha.) in other, less intensive, areas characterised by the presence of a mosaic of land covers (cereals, legumes, vineyards, pastures, fallow). When fallow, pastures and wastelands vanish from the landscape, the little bustard is one the first species which disappears.

It could be considered surprising that the two less intensive sectors (zones 1 and 2) in the study area contain a small area of irrigated lands, when this is considered as one of the main intensification indicators. However, those lands are developed in a traditional manner, obtaining water from small wells.

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The habitat quality index, which allowed for an integrated view of the territory, decreased as intensification increased. However, in the most intensive zone (i.e. "Tierra de Campos"), where male density was the lowest, the value of the index increased. In this sense, Morales et al. (2005b) have shown before a non-linear response in little bustard male density to the agricultural intensification gradient in the Iberian Peninsula and France, moving from the linear theoretical pattern. There are several possible explanations to understand this apparent "incongruity" in our study: (1) density is not necessarily a good indicator of habitat quality, because a small number of dominant, reproductively successful, individuals could displace a larger number of young and other subordinate individuals into marginal areas, as warned Van Horne (1983) (2) the most intensive sector is less saturated: if density is low, few males may be using the better pieces of sub-optimal available habitat. (3) Interannual variations: climatic or land use changes at a local scale could produce fluctuations in abundance between sectors and years, as has been shown by Morales et al. (2005a) or De Juana and García (2005); consequently, this may reflect a snapshot characteristic only of a particular moment. (4) There are other relevant variables not included in the analysis that could be associated with the agricultural intensification process, such as small-scale disturbances, the use of pesticides and fertilizers, land consolidation (Suárez et al., 1997) and the leking system (Morales et al., 2005a). According to the first statement, Bock and Jones (2004) concluded that European and North American birds are usually able to aggregate in the

higher quality breeding locations, therefore in most cases density will be a reliable indicator of habitat quality. However, they highlight the need of further studies demonstrating that human disturbance can impair the ability of birds to recognize and occupy the best places. Our results support the second hypothesis (saturation was the lowest at zone 4), but personal observations also confirm the importance of the third argument (recording local extinctions or colonisations from year to year, particularly at this particular sector) and the forth criterion (this should be explored in future studies, but currently we do not have spatially explicit data). "Tierra de Campos" has received, during the last decade, agricultural subsidies which increased intensification and mechanisation. Paradoxically, this area has also obtained environmental funding to reduce the use of pesticides, to increase leguminous cropping and to delay the harvest time. The result of this policy has been favourable for great bustard (Alonso et al., 2003), but adverse for other species more sensitive to intensification, such as little bustard or black-bellied sandgrouse (personal data).

5.2. Population distribution pattern and habitat quality

The little bustard distribution pattern is very fragmented in León province, surviving in areas of habitat which are more or less reduced to islands isolated in a matrix of highly modified habitats (affected by new irrigation plans, shrubland colonisation after land abandonment, new large infrastructures and vineyard modernisation). Our analysis of population distribution pattern showed a spatial configuration where the most densely populated squares were located at the centre of bigger population patches in contact with mean-density squares, all of which were

surrounded by low-density squares. Those core areas correspond to optimal habitat quality (Wolff, 2001) resulting from a highly diverse mosaic of small crops, fallow and wastelands (Martínez, 1994); density decreases with the distance to that optimum, when the bird have to use a suboptimal habitat. Conversely, the mean density of the local population and patch size diminished in more intensive areas because of the negative effects of landscape homogenisation, the loss of fallow/wastelands (De Juana and Martínez, 1996) and disturbances due to agricultural practices. Smaller and more isolated occurrence groups have a higher probability of disappearing because local extinctions force increasing isolation of the surviving subpopulations, making recolonization more improbable and decreasing genetic diversification (Wolff et al., 2002). Another important fact is that the presence of other individuals (i.e. conspecific attraction), typical of "lek species", is the mechanism driving population concentration, preventing recolonization in empty patches, even if habitat quality is good (Reed and Dobson, 1993; Roland et al. 1998; Widemo, 1998).

It is also necessary to consider an important aspect of the reproductive biology of the species: aggregation in "leks", which is related to an increase in the reproductive success in central areas (Höglund and Alatalo, 1995). This fact amplifies the importance of patch structure to this species (Wolff et al., 2001; Incahusti and Bretagnolle, 2005), drawing a pessimistic future for more fragmented and spatially unstructured populated nuclei, more frequent in intensive areas. In fact, this question could explain the little bustard decline in fragmented areas as occurred in Southern France, where the population has decreased by more than 90% during the last 25 years (Inchausti and Bretagnolle, 2005).

6. Conclusions and conservation implications

In this paper we have demonstrated how, at a regional scale, agricultural intensification and the fragmentation of traditional habitats negatively affect habitat availability and quality for little bustards, as well as male density. It is particularly relevant to understand how a bird population is spatially organised in terms of its density.

Our findings show that the preservation of little bustard densities within local populations is related to an adequate management of farming systems through: (1) the promotion of extensive rather than intensive agriculture, (2) increasing fallow and wastelands, (3) the diversification of crop mosaics, (4) a reduction in the spread of irrigation plans and (5) the reduction of coniferous plantations. Agricultural sector policies need to be linked with non-agricultural policies and vice versa.

Land abandonment, promoted by the Common Agricultural Policy to reduce overabundant agricultural products, have been cited as the main cause of a decline in bird diversity in the Mediterranean Region (Farina 1995, 1997). A previous study by Suárez-Seoane et al. (2002a) carried out in zone 2 ("Páramo Leonés") of our study area, showed that land abandonment benefited Eurosiberian species from wooded habitats over the Mediterranean species from open areas. However, for the little bustard, this land change could be favourable at the initial succession stages, until colonisation by woody species, which is not tolerated by steppe species (Franco and Sutherland, 2004). The risk of land abandonment is elevated in zones 1 and 2, the most marginal (in terms

of topography and climate), with very low agricultural productivity but the highest bird densities. On the other extreme, zones 3 and 4, threatened by intensification, are characterised by several facts relevant to little bustard conservation: low saturation

4 related to low population densities, less than that expected according to habitat quality.

Habitat fragmentation requires an urgent conservation plan to prevent further deterioration at local and regional scales, including severe measures addressed at increasing and conserving habitat quality, reducing patch isolation and preserving the maximum number of subpopulations (even the smallest) to maintain genetic diversification and functional connectivity. 53 % of the population is under special protection (SPAs), the other half of the population is seriously threatened by land transformation and management.

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Table 1. Predictor variables used for modelling the occurrence of the little bustard along an agricultural intensification gradient. Habitat was characterised by three groups of environmental variables: vegetation and farm systems, topographic features and human disturbances

Variable	Description
NDVIMAX	Maximal value of a monthly series of Maximum Value Composite of
	Normalised Difference Vegetation Index (NDVI-MVC) based on a
	AVHRR imagery at 1 km ² resolution from 1999
NDVIMIN	Minimal value of a monthly series of Maximum Value Composite of
	Normalised Difference Vegetation Index (NDVI-MVC) based on a
	AVHRR imagery at 1 km ² resolution from 1999
NDVIMEAN	Mean value of a monthly series of Maximum Value Composite of
	Normalised Difference Vegetation Index (NDVI-MVC) based on a
	AVHRR imagery at 1 km ² resolution from 1999
NDVIGROW	NDVI-MVC for spring (maximum of April and May) minus NDVI-MVC
	for winter (minimum of November and December)
NDVILOSS	NDVI-MVC for spring (maximum of April and May) minus NDVI-MVC
	for summer (minimum of July and August)
CORINE	Land cover from the CORINE Thematic Map at 1:100 000 year 2002
MOSAIC	Number of fields in a 1-kilometre transect drown as a diagonal within
	either occupied or random pixels. Measured on aerial ortophotographs
	from 2002 at 1:10 000 scale
FALLOW	Percentage of year-fallow in dry crops per hectare. Data at the scale of the
	municipality from the Regional Government on Land Distribution for
****	2002.
WASTELAND	Percentage of wastelands (old fallows, abandoned crops and suburban areas)
	per hectare. Data at the scale of the municipality from the Regional
mp rop rom	Government on Land Distribution for 2002.
IRRIGDIST	Distance to the nearest irrigated land (in kilometres)
IRRIGPERC*	Percentage of irrigated land within each km ²
ALT	Mean altitude (in meters) within a 5x5 array of 200m pixels.
TOPOV10	Topo graphic variability: Variation in altitude in a 5x5 pixel array of 200
	m pixels, where altitude is measured to 10 m vertical resolution.
	Calculated as $TOPOVx = (n-1)/(p-1)$ where $n = no$ of different altitude
	classes in the array, $p = no.$ of pixels in the array (i.e. 25), and x is the vertical resolution.
ROADDEN	
ROADDEN ROADDIST*	Proportion of 200 m pixels in a 5x5 array containing roads Distance in km to the nearest 200 m pixel containing roads. Calculated at
KOADDIST.	200 m resolution and averaged to 1 km ² .
TOWNDEN	Proportion of 200 m pixels in 5x5 array containing buildings or large built
TOWNDEN	structures
TOWNDIST	Distance in km to the nearest 200 m pixel containing buildings or large
TOWNDIST	built structures. Calculated at 200 m resolution and averaged to 1 km ² .
* alimain atad fuam	the following GAM engly gog (they were highly correlated with other

^{*} eliminated from the following GAM analyses (they were highly correlated with other variables)

Table 2: Repartition of the pixels (presences and absences) within and between zones in both stratified and non-stratified model

Stratified model							
	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Total	
Presences	90	97	29	29	0	245	
absences	102	51	24	32	34	245	
Total	192	148	53	61	36	490	
		Non-stra	tified mode	el			
	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Total	
Presences	90	97	29	29	0	245	
absences	11	2	70	68	89	240	
Total	101	99	99	97	89	485	

Table 3a. Comparison (means and standard deviations) between 16 variables quantifying the little bustard habitat presence or absence at 1km resolution. The table shows the significance of Student t-test, with Bonferroni correction, for differences between the means with equal or different variances according to each case: *=P<0.05, **=P<0.01, ***=P<0.001. It includes the values of little bustard male density recorded in each of the four zones and the results of the t-test for comparing density and zone

	Abse	ences	Prese	ences	t	Sign
	X	SD	X	SD		
NDVIMAX	185.91	9.745	176.73	7.767	132.95	***
NDVIMIN	141.96	6.04	140.05	4.43	16.00	***
NDVIMEAN	163.79	7.67	157.40	4.17	131.50	***
NDVIGROW	31.64	9.98	27.79	11.35	15.92	***
NDVILOSS	10.83	21.50	20.97	15.25	36.29	***
MOSAIC	0.0120	0.006	0.0125	0.007	0.69	-
FALLOW	9.87	10.92	14.73	9.37	27.94	***
WASTE	6.55	9.68	12.80	10.47	46.95	***
IRRIGDIST	3.91	4.62	4.05	3.13	0.17	-
IRRIGPERC*	0.34	0.45	0.03	0.13	109.36	***
ALT	837.11	89.98	838.19	46.37	0.03	-
TOPOV10	0.04	0.07	0.03	0.05	4.79	*
ROADDEN	0.11	0.13	0.07	0.10	16.62	***
ROADDIST*	0.68	0.61	1.03	0.75	30.56	***
TOWNDEN	0.014	0.041	0.003	0.016	14.26	***
TOWNDIST	1.43	0.86	1.95	0.87	44.41	***
n	2-	45	24	15		

^{*} eliminated in the subsequent GAM analyses (they were highly correlated with other variables)

Table 3b. Comparison (means and standard deviations) between 16 habitat variables quantifying little bustard presences in four different zones established according to its farm practises. The table shows the significance of Student t-test, with Bonferroni correction, for difference between the means with equal or different variances according to each case: *=P<0.05, **=P<0.01, ***=P<0.001. It includes the values for little bustard male density recorded in each of the four zones and the results of the t-test for comparing density and zone

	Zon	e 1	Zon	ie 2	Zon	e 3	Zon	e 4		
	Paramera	as Altas	Páramo	Leonés	Los O	teros	Tierra C	Campos	t	Sign
	X	SD	X	SD	X	SD	X	SD		
NDVIMAX	174.02	6.01	177.28	7.27	181.97	6.76	178.03	11.37	9.34	***
NDVIMIN	142.09	3.39	140.32	4.58	137.38	3.50	135.48	2.73	26.71	***
NDVIMEAN	157.71	3.45	159.03	4.02	154.93	2.71	153.45	4.33	21.57	***
NDVIGROW	21.51	7.17	26.27	9.06	40.03	5.88	40.10	14.00	53.17	***
NDVILOSS	21.92	9.83	12.41	15.7	36.31	7.35	31.31	14.45	34.71	***
MOSAIC	0.0139	0.009	0.0131	0.006	0.0097	.005	0.0092	0.005	5.28	**
FALLOW	13.58	7.82	9.79	5.95	26.09	9.58	23.45	7.47	52.25	***
WASTE	16.15	9.12	14.11	11.86	5.99	5.17	4.80	5.14	15.71	***
IRRIGDIST	3.22	1.56	2.7	1.8	8.97	3.85	6.25	3.60	66.38	***
IRRIGPERC*	0.01	0.07	0.06	0.19	0.00	0.00	0.00	0.00	3.41	*
ALT	861.60	51.42	827.94	42.96	832.14	23.07	805.86	15.09	16.83	***
TOPOV10	0.04	0.07	0.02	0.03	0.05	0.04	0.01	0.01	8.85	***
ROADDEN	7.20	11.35	5.32	8.85	6.62	9.21	11.17	12.21	2.46	-
ROADDIST*	1.01	0.75	1.06	0.73	1.15	0.86	0.84	0.71	0.91	-
TOWNDEN	0.36	1.66	0.37	1.64	0.28	1.45	0.28	1.45	0.05	-
TOWNDIST	2.09	0.91	1.68	0.78	1.82	0.79	2.50	0.81	8.55	***
MALE DENSITY	3.48	2.67	2.19	1.76	1.93	1.19	1.79	0.98	9.45	***
n	90)	9	7	29	9	29	9		

^{*} eliminated in the subsequent GAM analyses (they were highly correlated with other variables)

Table 4a: Summary of the non-stratified GAM model generated using backward selection with an F-value of 0.05 for the variable to remain in the equation. For each selected variable we tested whether the smoothed term was significant over a linear model and replaced non-significant smoothed terms with linear terms. Drop indicates the marginal contribution of each variable: values are obtained by dropping each explanatory variable from the model and then calculating the associated change in deviance (from Lehmann et al., 2003). Table includes ROC values for both final and cross validated models

Variable	Df	F	term	Drop
NDVIMIN	2.9	5.91	S	31.20
NDVIGROW	3.0	3.67	S	41.89
NDVILOSS	3.0	4.07	S	26.81
FALLOW	2.8	11.59	S	21.53
WASTE	3.0	7.35	S	17.68
IRRIGDIST	2.9	24.98	S	47.66
ALT	3.0	1.49	L	0.00
ROADDENS	2.9	2.08	L	6.53
TOWNDENS	2.9	1.33	L	6.29
TOWNDIST	3.0	3.96	S	34.37

Null deviance (df)	Residual deviance (df)	ROC (AUC)	cv ROC (AUC)
679.28 (489)	306.23 (449.48)	0.94	0.90

Table 4b: Summary of the stratified GAM model

Variable	Df	F	term	Drop
NDVIMAX	3.0	3.46	S	3.65
NDVIMIN	3.0	13.71	S	43.98
NDVIMEAN	2.9	3.37	S	11.95
NDVIGROW	2.9	18.07	S	39.86
NDVILOSS	2.9	1.65	L	23.11
FALLOW	2.9	6.57	S	10.66
WASTE	2.9	33.05	S	0.00
ALT	2.6	14.25	S	28.87
TOPO10	2.9	2.62	L	4.33
ROADDENS	2.8	2.81	S	4.02
TOWNDIST	2.9	3.37	S	35.08

Null deviance (df)	Residual	ROC (AUC)	cv ROC (AUC)
	deviance (df)		
672.30 (484)	196.81 (437.39)	0.98	0.94

Table 5: Percentage saturation of the little bustard habitat along the gradient. These values were calculated by dividing the number of pixels used by the number of suitable pixels (obtained reclassifying the habitat quality map according to the cut-off points: see Fig. 2)

Zone	Predicted suitable surface (Km ²)	used surface(Km ²)	% saturation
1	390	90	23.08
2	304	97	31.91
3	117	29	24.79
4	189	29	15.35

Table 6: Connectedness (%) between the pixels showing the three categories of density (1= low: 1-3 birds/km²; 2=medium: 4-7 birds/km²; 3=high: 8-11 birds/km²)

	Zone 1	Zone 2	Zone 3	Zone 4
1-1	33.03	59.14	66.67	92.31
1-2	29.36	31.18	33.33	7.69
1-3	8.26	3.23	0	0
2-2	13.76	3.23	0	0
2-3	11.93	3.23	0	0
3-3	3.67	0	0	0
Nb of occupied pixels	90	97	29	29

List of Figures

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- Figure 3: Positive relationships between habitat quality and little bustard density. Low little bustard male density corresponds to 1-3 birds/ km², medium to 4-7 birds/ km² and high to 8-11 birds/km².
- Figure 4: Habitat quality values along the intensification gradient. 1: Parameras Altas, 2: Páramo Leonés: 3: Oteros, 4: Tierra de Campos. The figure includes the density values (in males/km²) recorded per zone
- Figure 5: Habitat quality characterising patches of habitat with different sizes where the little bustard is present. To make the graph easier to read, the size of the patches has been reclassified into three equal intervals: small (1-18 km²), medium (19-36 km²), large (37-53 km²)
- Figure 6: Little bustard densities within patches of habitat with different sizes where the bird is present. To make the graph easier to understand, the size of the patches has been reclassified into three equal intervals: small (1-18 km²), medium (19-36 km²), large (37-53 km²)

Fig. 1

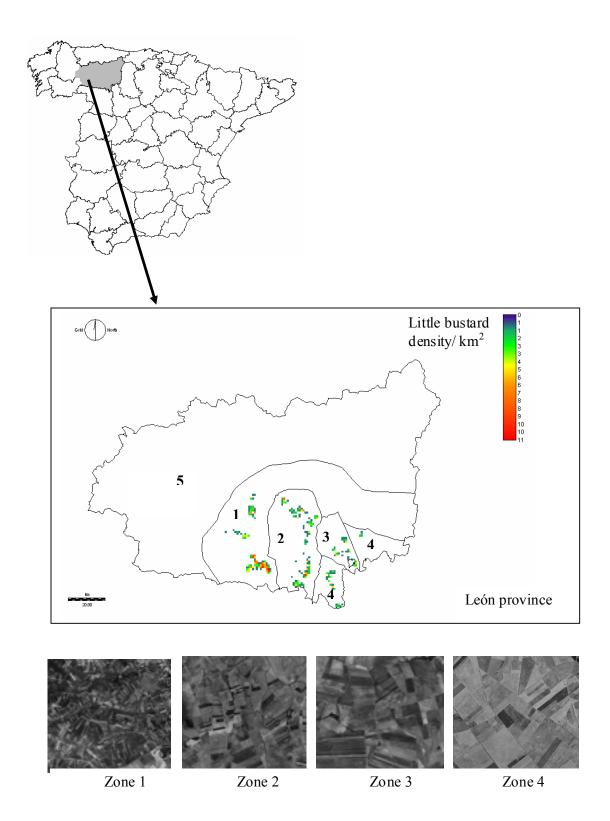


Fig. 2

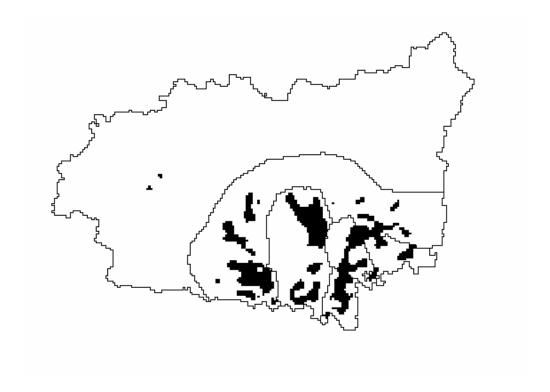


Fig. 3

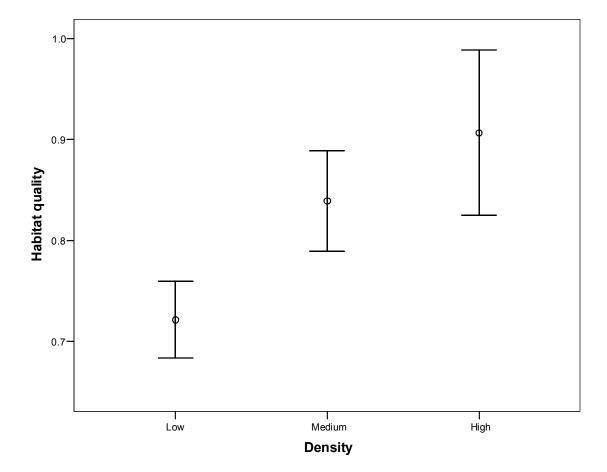


Fig. 4

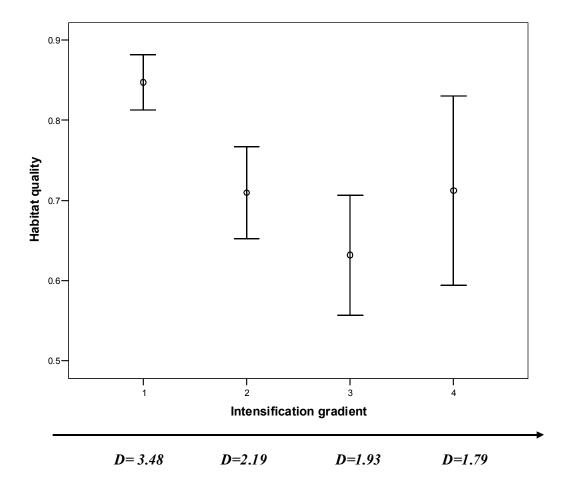


Fig. 5

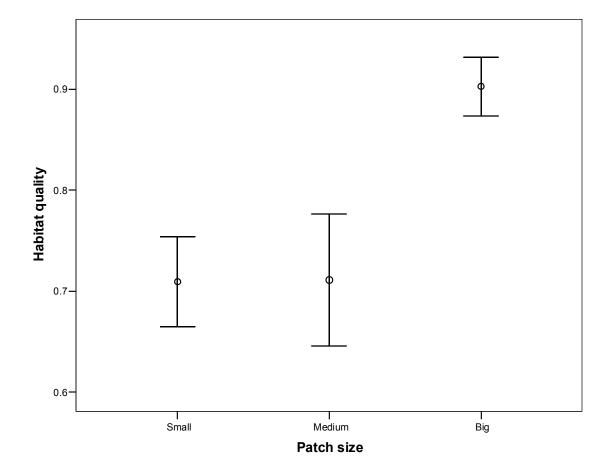


Fig. 6

