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Influence of spatial heterogeneity and temporal variability in habitat selection: A case study on a great bustard metapopulation

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ABSTRACT

We modelled great bustard abundance patterns and their spatial structure in relation to habitat and landscape variables. We developed Generalized Linear Models (GLM) using long term data series – years 1997–2006 – during the breeding season in Madrid region, central Spain. Our main goal was to assess spatial and temporal variability effects on habitat selection in this species evaluating the impact of inter-annual variability on habitat selection, the consistency of model predictions among years and the effect of data accumulation in the model performance. We examined the predictive ability of our models using internal and external validation techniques. We built separate models for each year and different models using the addition of several year data. The model perfomance increased as more census data were included in the calibration. One-off temporal data was insufficient to predict great bustard abundance properly. The final model (calibrated with all period data) showed a reasonable accuracy, attending to the validation tests. The variability in habitat suitability predictions between annual models does not seem to be caused by changes in habitat selection between years because the global model had a better explanatory ability than annual models. As far as interannual variability in spring greenness is concerned, the most variable sites are preferred, suggesting a selection for sites with smaller land use units and with a traditional rotation system. The great bustard abundance in Madrid was affected by the presence of other conspecifics but this pattern was conditioned to the existence of a suitable habitat denoted by the other variables in the final model. Future persistence of great bustards in Madrid region depends on a sustainable economic development that maintains traditional land uses, at least in areas with high ecological value for great bustards, whether they are occupied or not.

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1. Introduction

Habitat loss due to global warming and other human alterations is considered the most important cause of species extinction worldwide (Parmesan and Yohe, 2003; Lewis, 2006). Consequently, understanding the qualitative and quantitative environmental factors related to the abundance and distribution of species is a priority in current biodiversity conservation.

Human-induced habitat changes are particularly marked in grassland and farmland habitats. Farmland and steppe species are indeed at present the most threatened bird group, with 83% of the species subject to unfavourable status (BirdLife International, 2008; Burfield, 2005). One of these species is the great bustard (*Otis tarda*), a globally threatened bird classified as vulnerable under current IUCN conservation criteria (BirdLife International, 2010; IUCN, 2010). The greatest part of the world's population (*ca.* 60%) is found at present in the Iberian Peninsula (Palacín and Alonso, 2008). Nowadays, this originally steppe species is adapted to cereal farmland habitats. This and other bird species linked to agro-steppe areas in Europe have suffered severe declines during the last century. These declines are associated with changes in land use and landscape structure mainly related to agricultural intensification and abandonment (Benton et al., 2003; Chamberlain et al., 2000; Heikkinen et al., 2004). Particularly, great bustard populations have experienced severe demographic declines during the last decades caused by habitat destruction (BirdLife International, 2010; Kollar, 2006). In spite of this fact, previous studies have shown that there are areas with suitable habitat for great bustards that remain unoccupied as consequence of a conspecific attraction pattern (Lane et al., 2001). Departures from an ideal

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free distribution of individuals among available habitat types have been attributed to strong social interactions, temporally unpredictable habitats (Van Horne, 1983), post-disturbance crowding effects (Schmiegelow et al., 1997), or ecological traps (Weldon and Haddad, 2005). Particularly in human-altered environments habitat cues have frequently become decoupled from historic outcomes (Robertson and Hutto, 2006). However, conservation management plans tend to preserve only areas where a species is present. In such cases, management policies based only on species abundance may be misleading. According to metapopulation theory, empty patches of suitable habitat ought also to be protected because they are potentially colonizable areas that can guarantee the long-term survival at the level of the whole metapopulation (Hanski, 1999). Therefore, empty patches of suitable habitat are a chance for the establishment of new populations and not only for the maintenance of pre-existing ones. Considering the current rate of habitat loss for great bustard and other species that show similar spatial patterns, it is of major importance to identify suitable areas including those that are currently not occupied.

In order to predict the effects of anthropogenic and other habitat changes on suitable areas for species we need reliable measures of the relationship between abundance and environmental factors. Habitat models based on GIS tools allow quantification of environmental variables at the landscape scale. They may assist in generating predictions about species distributions over large spatial extents at relatively fine spatial resolutions (*e.g.* Osborne et al., 2001; Suárez-Seoane et al., 2002; among others). However, the most frequently developed models are based on the presence–absence data whereas model building on the basis of abundance is less common. Abundance data are more difficult, costly and sometimes even impossible to collect. Nevertheless, the presence might be a poor indicator of abundance because factors influencing abundance can differ from those which limit species distribution. Abundance might be a good indicator of habitat quality, reflecting key factors about population persistence as breeding success, carrying capacity or extinction probability (Pearce and Ferrier, 2001). It therefore provides more information and a better comprehension of the habitat selection process than the mere presence–absence data. Moreover, models based on abundance are more accurate than the presence–absence ones when species detectability is high (Joseph et al., 2006) as is the case with great bustards. Some previous studies have modelled great bustards on a basis of the presence–absence data (Osborne et al., 2001, 2007; Suárez-Seoane et al., 2002, 2004). Nevertheless, to our knowledge, this is the first attempt to predict great bustard abundance patterns using a set of environmental predictors.

Additionally, environmental variability can be a factor *per se* selected by species. For instance, Suárez-Seoane et al. (2004) compared variability among patches with the presence or the absence of their studied species, the great bustard. They found that empty and occupied patches which were defined as suitable habitat at a local scale (Lane et al., 2001) and at a landscape scale (Suárez-Seoane et al., 2002; Osborne et al., 2001,), differed in their seasonal stability, even if they are seemingly identical.

In the present study, we evaluated the abundance patterns of great bustards and their spatial structure in relation to habitat and landscape variables in central Spain. Our main goal was to develop a model to predict great bustard abundance during the breeding season (early spring) and to assess spatial and temporal variability effects on habitat selection in this species. Patterns of habitat selection in great bustards can be variable through the year (Palacín et al., 2012) but it could also be variable among different years due to temporal and spatial fluctuations on the availability or distribution of resources. However, few studies have attempted to assess the impact of temporal variability on species distribution (but see Boyce et al., 2002; Vernier et al., 2008). Using long-term data series,

we developed a set of models to predict great bustard abundance during the breeding season. With these models, (1) we evaluated the impact of interannual variability on habitat selection by great bustards; (2) we tested to what extent model predictions were consistent among years and (3) we assessed if the model performance increased with the accumulation of yearly abundance data (Boyce et al., 2002).

Validation is particularly important when models are used to guide conservation planning decisions because the distributions of habitat under which prediction is done may differ considerably from those where or when data were collected (Vernier et al., 2008). We examined the predictive ability of the models using internal validation (applying cross-validation techniques) and by means of external validation: (1) with a set of independent temporal data, and (2) using data collected within the same ecological region in a nearby area. Applying models to a new area or different time period results in changes in the availability of various habitats and this usually results in changes in the model apparent selection. Although, habitat models may be considered robust if they can be applied to other areas (Boyce et al., 2002), model validation have rarely been conducted using both k-fold cross-validation and geographically discrete independent data (but see Betts et al., 2006; Hirzel et al., 2006; Vernier et al., 2008).

2. Methods

2.1. Bird data

We used great bustard data collected through censuses conducted between 1997 and 2006. Censuses were carried out in early spring (mid March) when annual great bustard abundance in the study area reaches a maximum because birds aggregate at the breeding areas for reproduction. Details about the census protocol are described in Alonso et al. (2005).

2.2. Study area (spatial extent)

The study area was the Madrid autonomous region and surroundings, Spain, which extends over 7995 km^2 in the central plateau of the Iberian Peninsula. Our study area holds more than the 7% of the birds occurring in Spain. However, these populations are highly threatened because of traditional land use abandonment and urban and infrastructure development. We masked out non-suitable areas for great bustards in Madrid region, defining these as urban areas and sites with more than 1000 m in height.

2.3. Environmental factors

2.3.1. Spatial resolution

The grain size used must be a relevant scale for the studied organism, *i.e.*, its home range (Dunning et al., 1995). The daily distance moved by great bustards in our study area was on average 0.8 km (own unpublished data). Therefore, and following previous studies, the spatial resolution for our analysis were raster cells of 1 km^2. We measured great bustard spring abundance in 1 km × 1 km as dependent variable and different environmental factors (anthropogenic, climatic, topographic, land use, spatial and temporal heterogeneity variables) as predictors.

Original and derived GIS layers were used to model great bustard abundance. We used CORINE land cover data (CLC1990; CLC2000), which classify land use types on a 250-m grid basis. Data on infrastructures (including highways, roads, railways and trails) were obtained from vectorial maps (1:50,000) that were rasterized. Infrastructures included highways, roads, railways and trails. Monthly Normalized Difference Vegetation Index (NDVI) calculated from AVHRR images at 1–1-km resolution for the

1998–2005 period was used for temporal variability estimation. Climatic variables (temperature, insolation and rainfall) were based on interpolated data at 1 km × 1 km from weather stations for 30 years (Bustamante, 2003). Elevation and derived factors (slope, aspect, ruggedness and curvature) were determined from a Digital Terrain Model (DTM) with 50 m × 50 m resolution. Finally, data about human population were provided by annual censuses for each municipality in Madrid region between 1996 and 2005.

The set of predictor variables was selected on previous information about the ecology of great bustards. Variables included in the models (Table 1) have been used in previous studies or were assumed to correlate with the species abundance (Suárez-Seoane et al., 2002, 2004; Osborne et al., 2001; among others).

A "moving-window" GIS function was used to measure variables. Predictors based on surface percentages, such as land use classes, were measured as proportions of 100 m grid cells within the final grain of 1 km × 1 km pixels while continuous variables were calculated as a mean value of all 100 m pixels within the 1 km × 1 km grid (10 × 10 grid cells). Initially we measured 23 different predictors using raster grids in ArcGIS 9.1.

2.4. Statistical analysis

First, we used descriptive univariate analyses to test our data before entering them into the models. We compared rank differences on the explanatory variables between the presence and the absence great bustard sites with a non-parametric Mann–Whitney *U* test. Additionally, we avoided multicolinearity among the remanent significant predictors by removing strongly intercorrelated variables. We considered two independent variables to be strongly intercorrelated when Spearman rank correlation coefficient determined by the correlation matrix of the predictors was above a cutoff of 0.7 (Randin et al., 2006). All significant (Mann–Whitney *U* test) non-collinear variables (Spearman correlation) were included in the multivariant analysis. Among all correlated variables, those that could be considered more relevant according to our previous knowledge of the species' biology were retained for the GLM analyses.

We used Generalized Linear Models (GLM) (McCullagh and Nelder, 1989) to relate great bustard abundance to factors of the landscape. Habitat models using GLM are useful in formalizing the relationship between environmental predictors and specie's habitat requirements and in quantifying the amount of potential habitat. However, although parametric terms are preferable when developing a predictive model, non-parametric regression terms could be better for describing the shape of response curves due to their ease of use (Yee and Mitchell, 1991). We modelled abundance as a function of the explanatory variables using a non-parametric smoother for data inspection as this helped to visualize the type of relationships between abundance and the explanatory variables. The inspection results indicated that all variables had an almost linear effect on abundance and, therefore, a GLM was preferred to a Generalized Additive Model (GAM, non-parametric extensions of GLM) for all our analyses. All analyses were conducted using R version 2.10.1 and (R Development Core Team, 2009) 6.0 (StatSoft, Inc.).

Abundance is usually best represented by a zero-inflated distribution, because species is either not present, or present at a moderate to high abundances. GLMs using Poisson or negative binomial probability distributions have been developed for modelling abundance. However, we used mean abundance values based on data from different years in each location, thus abundance became a continuous variable. Consequently, we chose gamma probability distribution, which can be considered the continuous analogue of the negative binomial (Ramachadran and Tsokos, 2009), and we used an appropriate link function (log link).

There were 320 different available 1 km × 1 km squares with great bustard's presence from spring censuses during 1997–2006. Their landscape features were compared to 350 additional squares selected using a random stratified sampling process to minimize spatial autocorrelation (Osborne et al., 2001). Both the presence and the absence cells covered 32% of total study area.

All models were developed using two approaches. First, to assess the temporal variability in great bustard–habitat relationships we developed separate models for each year (1997–2006) and recorded the direction, strength, and significance of the estimated coefficients using a backward stepwise regression and the Wald test. Secondly, to determine whether the predictive performance of the models increased with the number of years used to fit the model, we developed models using one year of data, 2 years of data, 3 years of data, and so on. For these last models, selection of the best-fit model was done using Akaike's information criterion (AIC; Burnham and Anderson, 2002).

2.4.1. Spatial autocorrelation

We suspected the abundance data to be spatially autocorrelated. To determine if our data were spatially autocorrelated we examined Moran's *I* correlograms (Legendre and Legendre, 1998) of dependent variable using ROOKCASE software (Sawada, 1999). We calculated values of Moran's *I* for 10 intersample lag distances, each of 1 km extent (*i.e.*, equivalent to a square in our study). For each correlogram, the significance of *I* for each lag distance was calculated using a Bonferroni correction for multiple tests (Legendre and Fortin, 1989). The statistical significance was assessed with 999 Monte Carlo permutation tests conducted for each distance class separately.

If autocorrelation was detected in any of the lag distances, we developed an additional model term to account for spatial dependency (an autocovariate; Lichstein et al., 2002). Predictive spatial models containing a locational covariate term (UTM easting and northing) are constrained to being used only within the study area. Moreover, its potential effect on abundance is difficult to interpret. We sought to overcome these limitations using an autocovariate term (Heikkinen et al., 2004). The autocovariate term represents the mean value of total number of great bustard flocks in the nearest neighbour grid squares in the vicinity of the target location (see spatial autocorrelation results below).

2.5. Model validation

We developed an internal evaluation of the models using data-partitioning techniques. Model accuracy for annual models was assessed using 80% of data for model calibration and other 20% for validation (Fielding and Bell, 1997). Additionally, we used each annual model (*e.g.* 1997) to calculate predictions that were tested against data from the following year (*e.g.* 1998) as an independent validation. Predictions from models calibrated using several yearly data also were independently validated using data from the following year of the serie and through data-partitioning (20% of data for validation). The model calibrated using all year data was validated through 10-fold cross-validation (data were randomly split into 10 roughly equal groups and we fitted models using 90% of the data and generated predicted values for the remaining 10%). Additionally, we tested our final model using independent great bustard distribution data collected in 2006 in a nearby landscape, Mesa de Ocaña, Toledo region (about 80 km south from our study area). This independent validation determined to what extent the model could be generalized to other areas different from our study area. We summarized our results using Spearman rank correlation

Table 1

Definition of variables used. The Mann–Whitney U test compares sites used by great bustards with unoccupied sites.

Variable	Variable type	Description	Source	Mann–Whitney U test
Climatic				
Rainfall	Quantitative	Mean annual rainfall		***
Insolation	Quantitative	Mean annual insolation	Weather station information for 30 years at a 1 km × 1 km resolution (Bustamante, 2003)	(n.s.)
tma	Quantitative	Mean annual temperature		(n.s.)
tjan	Quantitative	Mean temperature of January (temperature of the coldest month)		(n.s.)
tjul	Quantitative	Mean temperature of July (temperature of the hottest month)		(n.s.)
Topographic				
Dem	Quantitative	Average altitude in 1 km × 1 km	Digital elevation model (DEM) 50 m × 50 m; vectorial maps 1:50.000 (Regional Ministries for Environment of Madrid and Castilla La Mancha)	(n.s.)
Slope	Semi-quantitative	Slope as percentage (tangent of the angle of inclination times 100)		***
Ruggedness	Quantitative	Standard deviation in slope (based on 50 m × 50 m)		***
Curvature	Quantitative	Curvature measures following Pellegrini (1995) and based on 3 × 3 350 m^2		**
dist_riv	Quantitative	Average distance to rivers longer than 10 km in 1 km × 1 km		(n.s.)
Anthropogenic				
dist_highw	Quantitative	Average distance to highways in 1 km × 1 km	Vectorial maps 1:50.000 (Regional Ministries for Environment of Madrid and Castilla La Mancha)	**
dist_road	Quantitative	Average distance to local roads in 1 km × 1 km		***
dist_other	Quantitative	Average distance to other roads and trails in 1 km × 1 km		***
dist_railw	Quantitative	Average distance to railways in 1 km × 1 km		***
dist_urb	Quantitative	Average distance to urban sites in 1 km × 1 km		***
hum_dens	Semi-quantitative	Human population density in each municipality	Annual municipal censuses 1996–2005 (National Statistics Institute)	***
Land use				
non_irrig	Proportion	Proportion of non irrigated surface	CLC1990; CLC2000 (European Environment Agency)	***
ol_vi	Proportion	Proportion of olive and vineyard crop surface		***
dist_irrig	Proportion	Average distance to irrigated crops in 1 km × 1 km		(n.s.)
Temporal variability				
NDVImar	Quantitative	Averaged NDVI in march (1997–2005)	Remotely sensed satellite data from AVHRR) in a spatial resolution around 1 km (Ministry for Environment and Rural and Marine Affairs)	***
CVNDVImar	Quantitative	Coefficient of variation in NDVI in march (1997–2005)		***
CVNDVImar-may	Quantitative	Coefficient of variation in NDVI in spring (march to may; 1997–2005)		***
NDVIapr-jul	Quantitative	NDVI contrast: April 2000 minus July 2000 (Osborne et al., 2001)		***

** $p < 0.05$.
*** $p < 0.01$.

coefficients between predicted and observed abundance data as a measure of model accuracy.

3. Results

Univariate analyses showed that only 17 environmental variables from the initial set were different between great bustard presence and absence locations (Table 1). Areas with lower rainfall, roughness, slope, curvature, olive and vineyard surfaces, and distance to highways were preferred by great bustards. Great bustard presence sites were also more distant to other roads, urban areas and railways and they encompass cells with lower human population. On the other hand, herbaceous non-irrigated surface, mean NDVI in March, yearly and spring variability in NDVI were higher in great bustard locations compare to sites where the species is absent.

No Spearman correlation coefficient between variable pairs was above the cutoff of 0.7, therefore all the 17 significant variables were included in the following GLM analysis Influential points accord to Leverage level and Cook's distance were removed from the analysis ($n = 3$). Full models were not overdispersed (overdispersion parameter for all the full models), hence indicating a good agreement between data and the selected link and error distribution (McCullagh and Nelder, 1989). Therefore we did not further consider overdispersion in the estimation of parameters.

3.1. Annual models

Backward stepwise regression results showed a moderate variability among years in the strength and significance of model coefficients, therefore the individual-year models were not a good indicator for the overall model (whole 1997–2006 period). However, the direction (sign) of the coefficients in the most significant variables (in terms of significance level and also in terms of number of significant annual models) was largely consistent across years (Fig. 1).

The estimated model performance was generally better when models were validated using the same data that were used to develop the models (Fig. 2). Annual model accuracy is better according to data-partitioning results (averaged r_s in-sample = 0.64; averaged r_s out-sample = 0.60). The predictive performance of models was more variable across years when assessed using data-partitioning than when using independent data. Generally, all models had relative good accuracy with r_s values higher than 0.55 for all years. In other words, when the prediction is the objective, the models appear to be robust, even though their interpretation may vary across years.

3.2. Several year data models

Significant variables (p-level lower than 0.05) in at least five of the annual models and with consistent sign in their coefficients
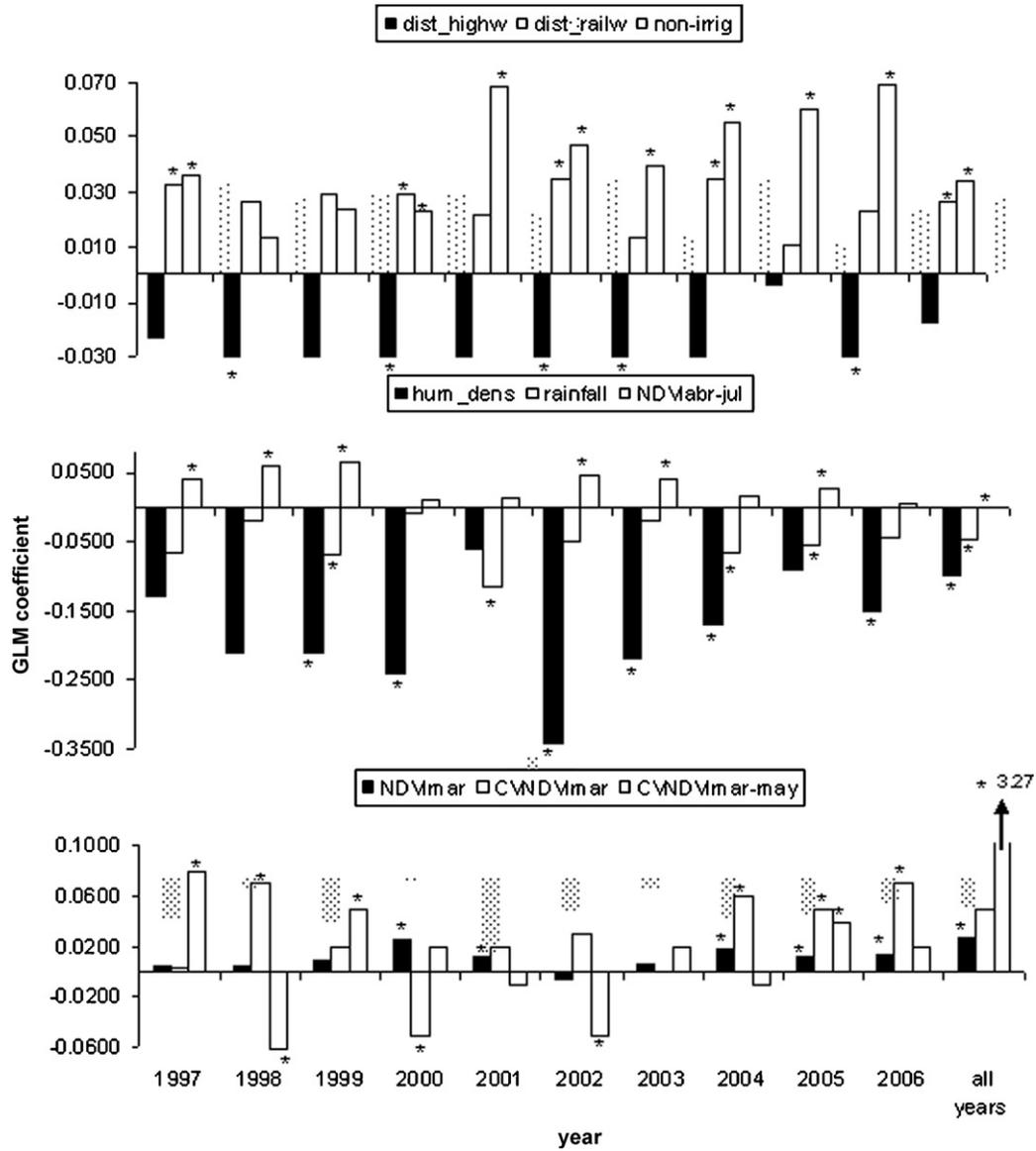
Fig. 1. Direction, strength, and significance of the estimated coefficients using a backward stepwise regression for annual models. Significance relationships (*p* < 0.05) according to Wald test are marked with (*). Only significant factors in at least five of the annual models are represented.
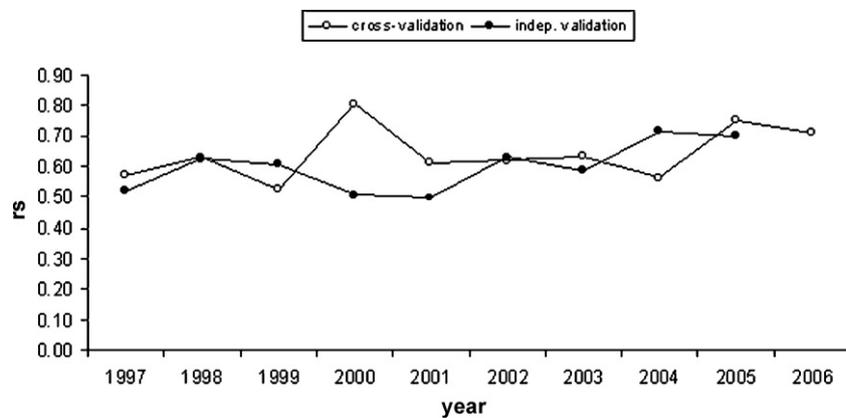

Fig. 2. Spearman rank correlation coefficients between predicted and observed abundance data as a measure of annual model accuracy. Results for both validation methods (in-sample – cross-validation data partitioning- and out-sample – indep.validation-) are shown. *Y*-axis shows the year data used to build each model.
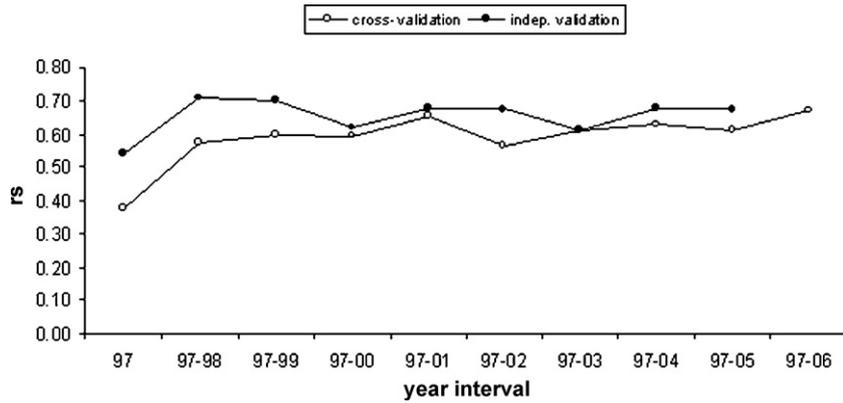
Fig. 3. Spearman rank correlation coefficients between predicted and observed abundance data as a measure of accuracy in models built adding censuses data. Results for both validation methods (in-sample – cross validation data-partitioning- and out-sample – indep.validation-) are shown. *Y*-axis shows the year interval data used to build each model.

Table 2
Summary of the most parsimonious models adding censuses data (from 1997 to 2006).

Year	Var. 1	Var. 2	Var. 3	Var. 4	Var. 5	Var. 6	Var. 7	d.f.	Deviance	AIC	R^{2a}
1997	disthighw	non_irrig	hum_dens		NDVI marCV	CVNDVImar-may	NDVI apr-jul	6	790.55	804.55	0.40
1997–1998	disthighw	non_irrig	hum_dens		NDVI marCV		NDVI apr-jul	5	1370.19	1382.19	0.45
1997–1999	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV		NDVI apr-jul	6	1671.44	1685.44	0.46
1997–2000	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV		NDVI apr-jul	6	2158.74	2172.74	0.46
1997–2001	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV		NDVI apr-jul	6	2392.77	2406.77	0.44
1997–2002	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV	CVNDVImar-may	NDVI apr-jul	7	2646.07	2662.07	0.46
1997–2003	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV		NDVI apr-jul	6	2885.02	2899.02	0.44
1997–2004	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV		NDVI apr-jul	6	3082.85	3096.85	0.42
1997–2005	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV	CVNDVImar-may	NDVI apr-jul	7	3271.47	3287.47	0.42
1997–2006	disthighw	non_irrig	hum_dens	NDVImar	NDVI marCV	CVNDVImar-may	NDVI apr-jul	7	3550.88	3566.88	0.44

[a] R^2 (Nagelkerke, 1991).

among years were selected for calibrating models adding several censuses data. We also incorporated the coefficient of variation in spring NDVI although it did not fulfil the previous requirements because it was highly significant in the model for all period data (Fig. 1). According to in and out-sample validation tests, data from 2 year are enough for a reasonably accuracy of the models (Fig. 3). However, the greater the number of years used to build the model, the higher the model performance (Fig. 4). AIC weights increased sharply with the number of censuses included from 0.19 in the only 1 year data to 0.98 in the all data model. Delta AIC between the best-fit model and the other ones was also greater when more censuses data are added (Table 2). In-sample validation tests showed more variable results than independent data validation. In fact, independent tests appeared to be little affected by the number of years used to develop the models. Nevertheless, both
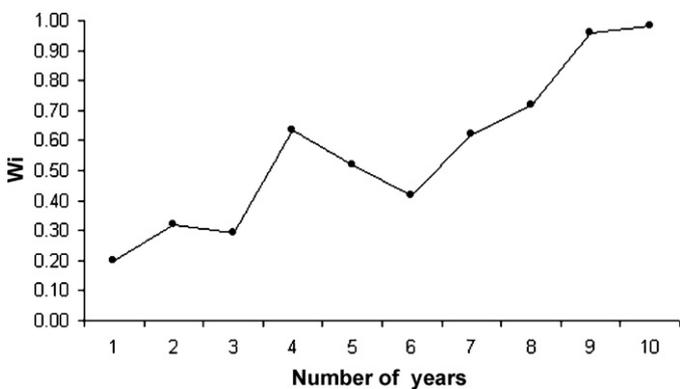
in-sample and out-of-sample model accuracy was usually greater than 0.6 indicating 'useful applications' and 'high accuracy' models (with the exception of only 1 year data model).

3.3. Spatial autocorrelation

The spatial correlation in great bustard abundance is initially high and decreases to nearby zero around 7 km. The Moran's correlogram as a whole was significant ($p = 0.01$), due to the statistically significant positive autocorrelation of great bustard abundance for the seven lag class (*i.e.*, at seven; Moran's $I = 0.3$; $p = 0.01$) but not for the other distance classes.

3.4. Final model

The summation of censuses data from additional years increased the model performance, hence we chose as final model the one built using all year data (Table 3). Factors included in the final model can be grouped in three different categories: (1) Variables that identify

Fig. 4. Performance for the most parsimonious models calibrated using several censuses data. w_i represents the AIC weights of the models.

Table 3
Final model including a spatial dependence term ("spatial term" = number of great bustards flocks registered between 1997 and 2006 in a radius of 8 km around each location).

Factors	Coefficients	S.E.	Wald-test	*p*-Level
Intercept	−0.857	0.304	7.944	0.004
spatial_term	0.007	0.0005	190.861	0.000
disthighw	−0.00002	0.00001	9.928	0.001
non_irrig	0.018	0.005	12.187	0.000
hum_dens	−0.086	0.035	6.149	0.013
NDVImar	0.003	0.002	1.807	0.178
CVNDVImar	0.041	0.009	19.584	0.000
CVNDVImar-may	0.070	0.012	35.947	0.000
NDVIapr-jul	1.392	0.498	7.824	0.005

Table 4
Final model including interaction terms (terms in bold).

Factors	Coefficients	S.E.	Wald-test	p-Level
Intercept	−1.784	0.369	23.432	0.000
disthighw	−0.00003	0.00001	15.527	0.000
non_irrig	0.093	0.020	22.343	0.000
hum_dens	−0.148	0.038	15.467	0.000
NDVImar	0.010	0.002	21.005	0.000
CVNDVImar	0.060	0.019	10.565	0.001
Non_irrig * CVNDVImar	−0.001	0.001	1.321	0.250
NDVIapr-jul	3.508	0.509	47.538	0.000
CVNDVImar-may	0.080	0.021	14.424	0.000
non_irrig * CVNDVImar-may	−0.003	0.002	4.416	0.035
hum_dens	−0.148	0.038	15.467	0.000

steppe-land sites in the study area (NDVI in March, NDVI April–July and non-irrigated crop surface); (2) Factors relative to human disturbance (distance to highways, human population density) and (3) Variables reflecting habitat stability (coefficients of variation in NDVI). Spatial dependence was included in this final model using an autocovariate based on the autocorrelation pattern found in the dependent variable. The spatial term was measured as the number of great bustards flocks recorded between 1997 and 2006 in a radius of 8 km around each cell with bird presence. The inclusion of the autocovariate term induced an increment in deviance model, suggesting that great bustard abundance is affected by the presence of nearby conspecifics.

We also tested the most probable interactions between environmental predictors in the final model. We assessed the possible interaction between non-irrigated crop surface and the inter-annual and annual variability in spring NDVI (*CVNDVImar* and *CVNDVImar-may*, respectively). Neither autocovariate nor interaction terms substantially modified significance or coefficients in the final model. Only interaction between annual variability and non-irrigated crop surface (*non_irrig * CVNDVImar-may*) was statistically significant according to the Wald test (Table 4). This significant interaction term means that great bustard prefer less variable sites in spring as the non-irrigated surface increases.

The final model included seven explanatory variables (Table 3). Great bustard abundance was negatively related to highway distance and to human population density. On the other hand, abundance showed a direct relationship with spring variability in NDVI (inter-annual or annual), with non-irrigated crop surface and with difference between NDVI in April and July (Osborne et al., 2001). Deviance explained by the model was 0.44 according to R^2 measure (Nagelkerke, 1991).

Averaged value for r_s Spearman correlation coefficient in the 10-fold cross validation was 0.64 (C.I. $r_s = 0.60$–0.68). A spatial dependence term reduces prediction accuracy for non-surveyed areas (Olivier and Wotherspoon, 2005) therefore we did not include this parameter in the independent validation process based on Mesa de Ocaña census data. Correlation between the out-sample observed data and those predicted by the final model was reasonably high with $r_s = 0.42$ ($p < 0.01$). Model over-estimated great bustard abundance (81% predicted values were higher than observed, particularly in the case of the absence sites). The final model was implemented in a GIS map that predicts great bustard abundance (density of birds per km²) in the study area (Fig. 5).

4. Discussion

Spatial modelling of great bustard populations has been performed in various studies using variables derived from GIS (Suárez-Seoane et al., 2002, 2004; Osborne et al., 2001, 2007). However, these models only tested presence–absence data, without considering species abundance, and they did not take into account
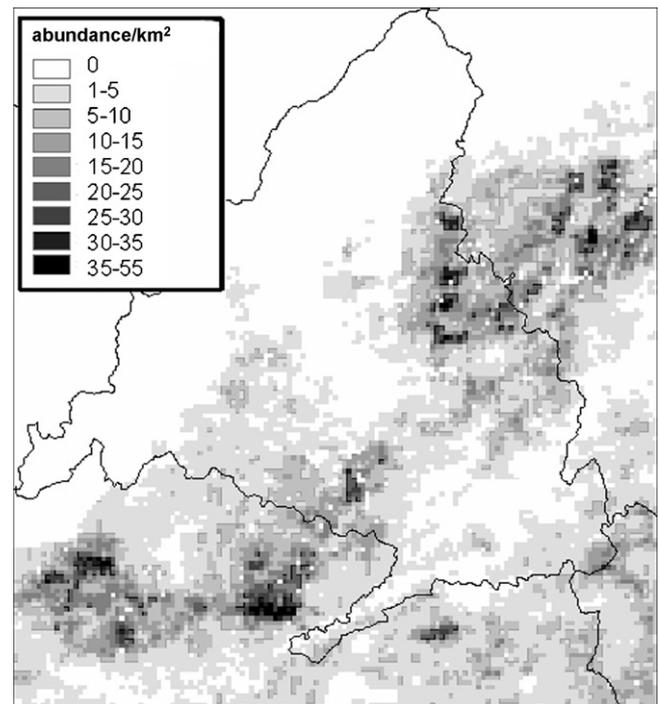

Fig. 5. GIS implementation of the final model. The model was calibrated with data from all census (1997–2006). The darkest squares indicate highest great bustard abundance (density per km²). The model was built with data from Madrid region (central area encompassed by the continuous line) and it has been extrapolated to Castilla La Mancha region (east and south).

yearly variation in great bustard distribution patterns. For instance, the model developed for Madrid region by Osborne et al. (2001) offers good results at a qualitative level (*i.e.*, which the suitable habitat is). However, according to our results, it is not useful in quantitative terms (how suitable the habitat is).

Our model predicts the spring density of great bustards in the study area with reasonable accuracy, attending to the validation tests, and is consistent with the habitat requirements for the species (Lane et al., 2001; Osborne et al., 2001). The application of models to a new area or to a different temporal frame results in changes on the availability of the different habitats, thus special care should be taken in interpreting model results beyond their original domain. Consequently, an internal model validation is not sufficient to guarantee model applications outside the original dataset. Nevertheless, model validation using geographically discrete data collected independently of the training data is still uncommon (but see Betts et al., 2006; Hirzel et al., 2006; Vernier et al., 2008). Our model was applicable with quite high reliability to an area not included in the present study, in spite of the fact that a model developed for a generalist species like the great bustard in a particular site is not easily generalizable to populations living in other areas. The explanatory ability of our model, however, was not particularly high. There is a tradeoff between the ability to detect broad-scale patterns and fine-scale details (Wiens, 1989). In addition, any inference made from a model is limited by the grain size because no pattern under this grain will be detected. Our models were built at the landscape scale with the subsequent loss in spatial resolution. If great bustards are responding to local habitat characteristics, these factors would not be detected in the present study.

4.1. Habitat stability

Not only average values of environmental factors are important in species habitat selection but variance experienced by these

factors is also relevant (*e.g.* Bautista et al., 2001). High quality areas are expected to be more stable than others (Osborne, 2005). For example, Sergio and Newton (2003) suggested that the best territories may be identified from degree of occupancy, that is, how often they are used. Spring seasonal variability presents a negative effect on great bustard abundance in Madrid region (after removing the confounding effect of the non-irrigated crop surface). Suárez-Seoane et al. (2002, 2004) also found similar results using presence–absence data. Empty and occupied sites can appear to be similar, but they are distinguished by their seasonal stability (Osborne, 2005). Therefore, sites with higher stability in vegetation biomass in spring are selected by great bustards in the study area. However, as far as interannual variability in spring grenness is concerned, the most variable sites are preferred. Several studies have found positive correlation between spatial heterogeneity and biodiversity in agricultural landscapes (Benton et al., 2003). Among other effects, agricultural intensification reduces landscape heterogeneity (Donald et al., 2001; Wolff et al., 2001). However, variability can occur not only at a spatial scale but also across a temporal scale, due to a higher degree of crop rotation in traditional agricultural systems. Therefore, a preference for higher interannual variability in vegetation biomass likely suggests a selection for sites with smaller land use units and with a traditional rotation system that characterize extensive agriculture regimes in the study area.

On the other hand, accurate detection of non-used sites by a habitat suitability model can be conditioned to sampling effort because data accumulation might result in sites initially identified as unused then being later reclassified as used sites (Boyce et al., 2002). Moreover, habitat quality can vary over time and space and, consequently, habitat preferences may reflect an optimal selection in the long term whereas they may appear neutral or maladaptive in the short term (Robertson and Hutto, 2006). Thus a single snapshot survey may not be enough to assess habitat selection. However, most models developed to predict species distributions are usually based on one-off data set (from only one survey). According to our own results, the model performance increase as more census data were included in the calibration. The variability in habitat suitability predictions between annual models does not seem to be caused by changes in habitat selection between years because the global model had a better explanatory ability than annual models. Additionally, the higher reliability of the model with more censuses shows that the use of one-off temporal data is insufficient to predict great bustard densities with accuracy. This is particularly important when variables relative to habitat stability are included in the models because a good estimation of temporal heterogeneity requires of at least 7 year data according to our results with great bustards in Madrid region. The higher the spatial and temporal variance in habitat selection, the greater increase should be expected in model performance with data accumulation.

An unexpected result was the great bustard's preference for sites that exhibit short distances to highways. Highways were *a priori* expected to be avoided due to their considerable traffic density and vehicle speed. We think of three not mutually exclusive explanations to this pattern. First, and perhaps most importantly, highways in Madrid region have been built in areas previously used by great bustards. Second, great bustards are long-lived species and very faithful to their traditional display sites (Alonso et al., 2004), and thus their response to some impacts are probably delayed. Accordingly, some of the highways included in our analyses are of recent construction. Greater abundance of this species close to highways might be a maladaptive response caused by the high year to year fidelity to breeding sites together with the conspecific attraction pattern described below. Consequently, areas near highways might be ecological traps that were suitable habitat for great bustards in the past but they might be of poor quality nowadays, although they are still occupied by the species as a result of a mismatch between the environmental cues used to identify suitable habitat (flat areas, the presence of conspecifics) and actual habitat quality (Battin, 2004). Therefore, anthropogenic changes in landscape such as new highways occur too quickly and great bustards may be not able to respond because individuals are selecting the same habitats as their predecessors (Remes, 2000). Finally, the scale of our study might have prevented us from detecting small-scale avoidance effects near highways (see also Torres et al., 2011).

4.2. Conspecific attraction

The abundance of a species is typically spatially autocorrelated due to locomotory constraints (Abrahams, 1986), social organization (Stamps, 1988), or aggregative responses to cues from conspecifics (Turchin and Kareiva, 1989). The presence of a positive spatial autocorrelation (spatial dependency) may occur when (1) one fails to include an independent variable that is itself spatially autocorrelated (Haining, 1990) or (2) the target species exhibits an aggregative behaviour of species resulting from a variety of processes (Lichstein et al., 2002). If the latter was true, we would expect prediction success to improve with the inclusion of a spatial covariate (Betts et al., 2006). The low predictability of the model in areas where the species is absent reflects a process of conspecific attraction: areas without the presence of great bustards but with good quality habitat for the species persistence. Such avoidance of high-quality areas because they are less attractive has been termed a "perceptual trap" (Patten and Kelly, 2010). This effect is also expressed in the spatial autocorrelation pattern detected in great bustard density. Models that ignored spatial autocorrelation tended to show stronger habitat effects because space and habitat are confounded (Keitt et al., 2002; Lichstein et al., 2002). The conspecific attraction pattern is adaptive (Alonso et al., 2004; Osborne, 2005) because it facilitates coupling, and provides a rapid information about habitat quality for young individuals not yet established in an area (Valone and Templeton, 2002). As habitat stability is difficult to be evaluated by a young individual that arrives for the first time in an area, conspecific presence would be a rapid clue about habitat quality without no need of previous experience (Martín et al., 2008). Nevertheless, although great bustards density is affected by the presence of other conspecifics, this pattern is conditioned to the existence of a suitable habitat denote by the other variables in the final model.

4.3. Conservation implications

Patterns of conspecific attraction act as "perceptual trap" and limit the great bustard ability to colonize new areas. An attempt to attract great bustards to other high quality areas might be tried. Nonetheless, it is expected that, as the size of current populations increases a spatial expansion of the metapopulation will take place. Recent censuses have shown a positive demographic trend in the size of the great bustard metapopulation in Madrid region. Although social constraints may limit future colonization of distant areas, in recent years we have observed an expansion of the areas occupied by the species in some local populations with a positive demographic trend (Martín, 2009).

The models developed here, like others on steppe-land birds (*e.g.* Chamberlain et al., 2000; Benton et al., 2003; Heikkinen et al., 2004) show the impact of human activities on great bustard abundance. Human density is an indicator of poor habitat quality for great bustards in Madrid region. Traditional agricultural land-use practices are linked to great bustard presence (Palacín et al., 2012). These practices also involved a low intensity exploitation system and low-density human settlements. Additionally, urban development in the last years in Madrid region has caused the loss of suitable habitat for great bustard. Habitat destruction due to

land use changes amounted a 3% of the total surface for non-irrigated crops in the study area during the last 10 years (Corine Land Cover 1990, 2000; Corine Land Cover Changes, 2004). Steppe-land destruction is currently increasing according to recent urban development plans in most municipalities of the area. Future persistence of great bustards in highly humanized areas depends on a sustainable economic development that maintains traditional land uses, at least in those areas identified in the present study as being of high ecological value for the species, including those that are currently not occupied.

More studies are needed to determine if other indicators of habitat quality (*e.g.* food intake, survival rate) are worse in areas close to highways compared with other suitable areas for the species. Future information about spatial use of these areas will also enlighten whether great bustards will persist in these sites in the future or if they are sink sites where the species will disappear from.

5. Conclusions

We found that one-off temporal data was insufficient to predict great bustard abundance properly. Model predictions are not consistent among years and the model performance increased with the accumulation of yearly abundance data. Additionally, sites with higher stability in spring are selected by great bustards in the study area. However, as far as interannual variability is concerned, the most variable sites are preferred, suggesting a selection for sites with smaller land use units and with a traditional rotation system. Future persistence of this and other related species depends on the conservation of high ecological value areas, whether they are occupied or not.

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