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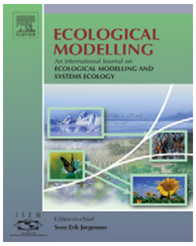

Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution

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ABSTRACT

The effects of habitat fragmentation on species may change seasonally mainly due to variations in resource availability and biotic interactions. In critical periods, such as winter, when the importance of intraspecific competition diminish, species may relax their environmental requirements widening their ecological niche to exploit the scarcer trophic resources more efficiently in comparison with spring. Those variations in niche width may implicate seasonal expansions/retractions in species distribution. In this sense, an integrated knowledge on the spatial arrangement of breeding and wintering suitable patches is essential to infer seasonal movements (migratory connectivity). This paper shows that little bustard environmental preferences were more predictable and complex (controlled by a larger number of environmental factors) in spring than in winter, when potential distribution and ecological niche width were slightly larger. In spring, habitat variables (i.e. percentage of dry crops and pasturelands and altitude) ruled species' distribution; while, winter pattern was driven by mixed criteria, based on both habitat and climate (i.e. percentage of dry crops and wastelands and winter rainfall). Suitable patches were more connected across spatial scales in winter than in spring, i.e. landscape was perceived as less fragmented. The overlap between potential breeding and wintering distribution areas was high. In fact, most of the predicted wintering areas coincided or showed high connectedness with predicted breeding patches. Conversely, there were significant breeding patches that were predicted with low suitability, showing little connectedness with potential winter areas. Spring habitat was a better predictor of little bustard's wintering range than vice versa, which has clear management implications (preserving breeding sites closer to wintering areas ensures the conservation of a larger proportion of the total distribution range). This is an example of how predictive large-scale modeling procedures can contribute to the optimization of land management aimed at species conservation.

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1. Introduction

The fragmentation of a habitat into discontinuous patches negatively affects population recruitment (Robinson et al., 1995; Smith and Hellmann, 2002), survival (Harris, 1984) and movement (Shirley, 2006) of terrestrial animal species. In poorly connected landscapes, where individuals have to move across the matrix to reach adequate pieces of habitat for different purposes (i.e. foraging, reproduction, dispersion and predator avoidance), the fitness cost of movement (Brooker et al., 1999) becomes higher than in continuous landscapes. This fact consequently influences the dynamics, spatial structure and persistence of populations (Turchin, 1991). Nevertheless, the importance of fragmentation for species may change through time, mainly seasonally, individual movements reflecting variations in resource availability (Blake and Loiselle, 1991) and biotic interactions. In this context, linking breeding and non-breeding populations (i.e. migratory connectivity) to infer movement patterns between seasons is one of the ultimate goals of animal movement studies in ecology (Rubenstein and Hobson, 2004).

As a result of the European Common Agricultural Policy, traditional agri-systems in southern Europe are particularly vulnerable to fragmentation due to management intensification in productive areas and land abandonment in marginal ones (Pain and Pienkowski, 1997). These systems are known to host a considerable diversity of birds and other taxa, most of which are currently experiencing marked population declines (Robinson and Sutherland, 2002; Sanderson et al., 2005). Among the valuable avian species (Suárez et al., 1997) held by these systems, the little bustard *Tetrax tetrax* is one of most seriously threatened by land use changes (Wolff, 2001; Wolff et al., 2002; García et al., 2007), disappearing from many European countries during recent decades (Schulz, 1985; Goriup, 1994; Del Hoyo et al., 1996). This Palaearctic, medium-sized steppe bird, from the *Otididae* family, is currently classified as 'Near Threatened' (Collar et al., 1994) in the world and 'Vulnerable' in Europe (BirdLife International, 2004), including Spain (García de la Morena et al., 2004b). Although Iberian little bustard populations have been regarded as sedentary or dispersive (Cramp and Simmons, 1980), many of them can actually be considered as migratory or partially migratory since they completely, or partly, disappear from their breeding grounds, performing regular medium or long distance movements and congregating in certain wintering sites (García de la Morena et al., 2004a, 2006). In Madrid region (the study area), it is considered a resident species (Díaz et al., 1994; García de la Morena, 2002), although it exhibits a partial migratory behaviour, as suggested by recent radiotracking data (with some birds leaving the region during the non-breeding season; own unpubl. data). During the spring (breeding season), birds do not move much, spending most of time in their territories (Schulz, 1985; Jiguet, 2001) but, from late summer through the autumn and winter, they gather in flocks and disperse from spring areas to exploit food resources in different zones, a common behaviour in most Iberian steppe birds (Suárez et al., 1997). As found in some of these species (Morales et al., 2000; Alonso et al., 2001), little bustards display interannual fidelity to certain wintering sites, where they stay for a variable period of time before returning to their breeding territories (García de la Morena et al., 2004b; own unpubl. data).

Habitat preferences and distribution of little bustards in spring have been extensively explored at both local (Martínez, 1994, 1998; Salamolard and Moreau, 1999; Wolff et al., 2001; Morales et al., 2005, 2008; Traba et al., 2008) and regional scale (Suárez-Seoane et al., 2002, 2004; Osborne and Suárez-Seoane, 2002; García et al., 2007). However, few authors have focused on winter season (Leitão and Costa, 2001; Silva et al., 2004; García de la Morena et al., 2006, 2007), even if this knowledge is essential for understanding the species' biological cycle, as well as in the design of adequate conservation strategies (Rappole and McDonald, 1994; Sherry and Holmes, 1996). In the Mediterranean region, as in other temperate and seasonally regulated areas, winter is a critical period for birds (Tellería et al., 1988), both at individual and population levels (Wiens, 1989; Newton, 1998), since availability in food and other resources decrease and may vary considerably in space and time. As a result, the distribution and abundance of wintering little bustards is closely dependent on the local variation of those resources (mainly provided by extensive cereal farmlands), which they must track actively (Wolff, 2001). During this limiting period, birds may therefore respond by relaxing the requirements associated to certain dimensions of their ecological niche to exploit more efficiently a larger amount of trophic resources, thus allowing the species' survival (Hutchinson, 1957) in a wider potential distribution range. As a consequence of this niche expansion, wintering populations are expected to become more heterogeneous in their environmental preferences, according to the niche variation hypothesis (Van Valen, 1965; Bolnick et al., 2007), which predicts that each individual might continue to use a narrow range of resources but diverge from its conspecific competitors to minimize resource use overlap and competition. At the same time, intraspecific interactions would become less intense than interspecific relationships (Morin and Chuine, 2006), such as competition or predation (birds have to aggregate in flocks as a defense strategy against predators), in comparison with spring, when the relevance of territorialism and sexual behavior is higher. As a consequence of this shift in the importance of inter/intraspecific interactions, the relevance of certain niche dimensions (e.g. climate conditions) would be relatively higher in winter than in spring.

To approach seasonal variations in species' niche dimensions and their influence in spatial distribution, we took advantage of using the Maximum Entropy Modelling (MaxEnt; Phillips, 2005; Phillips et al., 2006). This novel technique provides a general-purpose machine learning method whose performance has been evaluated as one of the best when compared to other modelling distribution methods, particularly at small sample sizes (Elith et al., 2006; Hernández et al., 2006; Pearce and Boyce, 2006; Pearson et al., 2007). The following are among the main reasons to use it in this study: (1) it is an envelope-method specifically applied on presence-only data (the link between absences and habitat suitability may be confusing); (2) it has a good ability to fit complex functions between response and predictor variables; and (3) model selection and fitted models are not too complex, being similar in expressiveness to a GLM or GAM. As other niche-based models, MaxEnt describes suitability in ecological space, which is projected into geographical space. Therefore, areas that satisfy the conditions of the species' fundamental niche represent its potential distribution, whereas the geographical areas that it actually inhabits constitute its realized distribution (Phillips et al., 2006). Nevertheless, Araújo and Guisan (2006) highlight several difficulties of using Hutchinson's (1957) concepts of fundamental and realized niches in species distribution modelling at large scale. In this sense, it is key to clarify the difference between "niche" and "area of distribution" (Soberon, 2007), distinguishing between niches as: (1) habitat or function; (2) characterized at local (when behavior and physiology are important) or at larger spatial extents (when distributional limits matter); and (3) defined by interactive variables such as resources (i.e. "Eltonian niches"), which can mainly be measured at local scales, or defined by non-interactive variables such as abiotic conditions (i.e. "Grinellian niches"), relevant to understand coarse-scale ecological and geographical properties of species. Both classes of niches are relevant to understand species' distribution, but the Grinellian ones are more appropriate at lower spatial resolutions and wider extensions, at which distributions are typically defined, as it is the case of the present study. Concerning the relevant niche dimensions to be explored at those large scales, climatic preferences can be used to predict areas where species could occur, since climate is the major driving factor of species' distribution (Thuiller et al., 2005), although Broennimann et al. (2007) showed that some climatic factors may only be indirectly related to niche shifts. Therefore, other non-climatic factors such as vegetation, soil or disturbances may become highly relevant to be included in the models (e.g. Acevedo et al., 2007), as they determine species presence at finer scales.

According to this background, the main objective of this paper is to analyse how little bustard's perceive landscape fragmentation in two critical periods (spring and winter), focusing on seasonal spatial variations in environmental (habitat and climate) preferences, niche width and connectedness of the predicted distribution patterns. In particular, we are concerned with the assessment of the importance of the spatial arrangement of suitable breeding patches for the selection of wintering sites and vice versa, which may influence seasonal movements across the landscape (and therefore migratory connectivity). More specifically, we explore the following hypotheses: (1) In winter, territorial behaviour becomes less important and resource availability decreases, therefore environmental preferences will relax and ecological niche will expand. This will allow birds to exploit the scarce resources across a broader range of conditions, reducing intraspecific competition. (2) Analogously, landscape suitability and its connectedness will be lower in spring, when birds will show more restricted environmental preferences as they will look for more particular resources/conditions to establish their breeding territories under higher conspecific competition. (3) Finally, the roles played by both habitat and climate factors on the species' distribution will change across seasons; in particular, we predict a greater importance of climate variables in determining wintering patterns. The results of this paper have important potential implications for improving the design of conservation measures addressed to protect this species by identifying key areas which ensure its connectivity across the year at a regional scale, the most pertinent for environmental and agricultural policies (Rounsevell et al., 2003).

2. Materials and methods

2.1. Study area

Madrid region is located in Central Spain (41°10′N, 39°53′N, 4°35′W, 3°03′W) and occupies about 8000 km^2. It can be broadly divided into two geographical units: (1) the mountains of the Spanish Central Range, which run along the north-east to south-west limit of the region, over 900–1,000 m.a.s.l. and (2) the plains which extend over the rest of the region as part of the Spanish Southern Plateau, between 430 and 900 m.a.s.l. (Fig. 1). This unit is, in fact, formed by a mosaic of different habitats, including extensive pastures, shrubs, forests and urban areas, although extensive cereal cultivation (with interspersed olive groves and vineyards) is dominant. It also holds the highest human population densities within the region (about 5.8 million people are concentrated in Madrid city and its surroundings). In spring, little bustards are widely distributed over this second unit (Díaz et al., 1994; García de la Morena et al., 2001), their presence and abundance being positively correlated with landscape heterogeneity and proportion of arable surface (Morales et al., 2005). In winter, the species principally occupies extensive cereal farms at the northeast and south of the region, but also uses other habitats, such as irrigated alfalfa (*Medicago sativa*) fields, open broom formations dominated by *Retama sphaerocarpa* and other shrublands (García de la Morena, 2002; García de la Morena et al., 2007).

2.2. Bird data

Wintering data were obtained in early February (13th–16th) 2003 and late January (23th–26th) 2004 during surveys carried out by car over the species' regional winter range. We used the look-see counting and mapping method (Bibby et al., 2000) adapted for a large area to record the flocks (see García de la Morena et al., 2007 for survey details). Spring records corresponded only to breeding adult males and were gathered from an unpublished report on species distribution and population estimates in Madrid region (García de la Morena et al., 2001). Counts were carried out from the 18th April to the 1st June of 2000, coinciding with the peak of male sexual display (Schulz, 1985; Martínez, 1994). This survey followed the standardised census methodology recommended for breeding males by most species' experts (García de la Morena et al., 2006). For later analyses, all locations were overlapped in a grid at 1 km^2 to match the resolution of the predictors used for model development.

2.3. Environmental predictors

Habitat variables (topography, human disturbances and land covers) were considered as "static" or "non-variant" across the seasons during the study period (Table 1). For topographic features, a digital terrain model with a resolution of 200 m was built and then transformed into derived variables (mean altitude and topographic variability) calculated within a moving

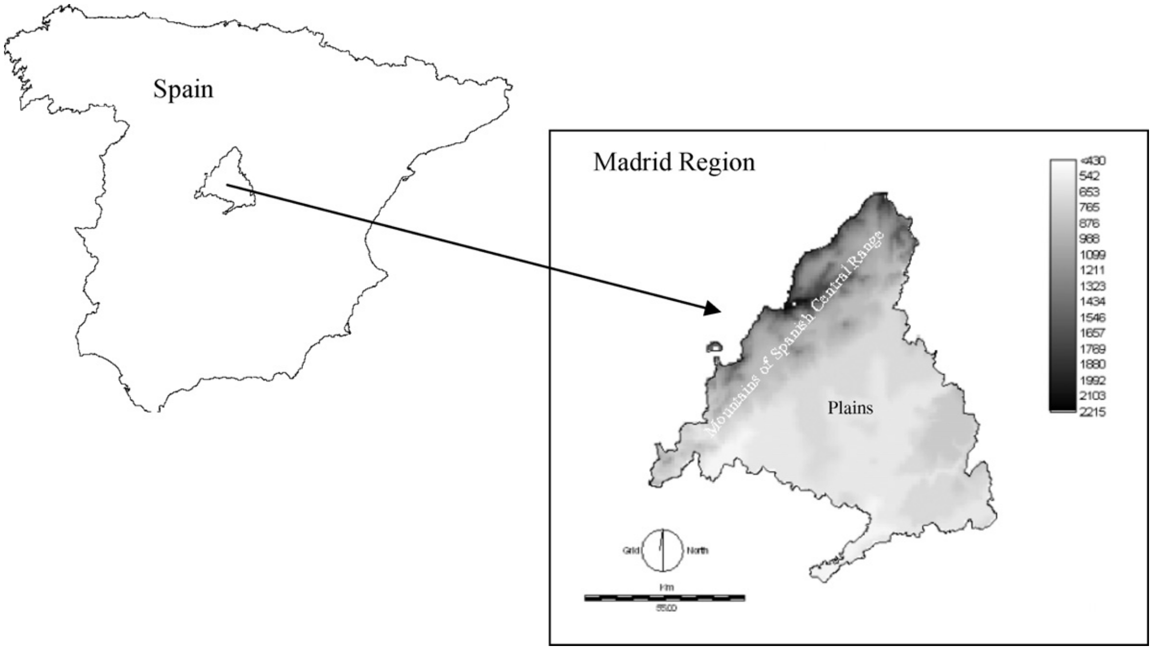

Fig. 1 – Location of the study area.

window of 1 km^2 (see Suárez-Seoane et al., 2002 for more details). Human disturbance variables (density of towns and roads) were obtained from vector maps at 1:200,000 (Spanish National Geographic Institute) and rasterised into grids of 200 m resolution, subsequently converted into quantitative variables at 1 km^2. Land cover classification was based on the official 1:50,000 habitat cartography of the Madrid Region (CAM, 1998), updated in the field in 2004. Relevant variables (percentage of irrigated lands, dry crops, pasturelands, olive trees and wastelands) were measured using the

Table 1 – List of habitat (topography, human disturbances and land covers) and climate predictors used for modelling seasonal species distribution in Madrid region

Code	Variable
Habitat variables	
Topography	
MDT	Mean altitude within a 5 × 5 array of 200 m pixels
TOPO10	Variation in altitude in a 5 × 5 pixel array of 200 m pixels, where altitude is measured to 10 m vertical resolution. Calculated as $TVx = (n - 1)/(p - 1)$ where n = no. of different altitude classes in the array, p = no. of pixels in the array (i.e. 25), and x = vertical resolution
Human disturbances	
TOWNDENS	Proportion of 200 m pixels in a 5 × 5 array containing towns, buildings or large structures such as airfields
ROADDENS	Proportion of 200 m pixels in a 5 × 5 array containing roads
Land covers	
IRRIGPERC	Proportion of 200 m pixels in a 5 × 5 array containing irrigated lands
DRYPERC	Proportion of 200 m pixels in a 5 × 5 array containing dry croplands
PASTPERC	Proportion of 200 m pixels in a 5 × 5 array containing pasturelands
OLIPERC	Proportion of 200 m pixels in a 5 × 5 array containing mosaic of cereal and olive trees
WASTEPERC	Proportion of 200 m pixels in a 5 × 5 array containing wastelands (old fallows, abandoned crops and suburban areas)
Climate variables	
EVPs/EVPw	Mean potential evapotranspiration value (calculated from the values per each 10-day periods) for the whole of the season (spring/winter)
RADs/RADw	Mean net radiation value (radiation balance calculated from observed albedo, temperatures and cloudiness according the time of the year and the position for each 10-day period) for the whole of the season (spring/winter)
RAINWs/RAINWw	Mean rainfall value during the last winter for spring bird data, and mean value of this parameter during the current season for winter bird data

1 km^2 moving window and then log-transformed to reduce collinearity caused by the unit sum constraint (Aebischer et al., 1993). Operations were performed using IDRISI Kilimanjaro14.01 (Eastman, 2003).

Climatic variables were considered as “non-static” or “variant” between spring and winter (Table 1). For each season, we created three time-dependent predictors related to rainfall, net radiation and potential evapotranspiration (as an indicator of soil moisture) from the European Energy and Water Balance Monitoring System EWBMS products (Rosema, 1993; Rosema et al., 2001), which are derived from the METEOSAT satellite, with a frequency of 10-days and a resolution of 5 km. This dataset has been evaluated before for modelling the distribution of little bustards in Spain by Suárez-Seoane et al. (2004), showing very good results. In particular, we extracted: (1) mean values of potential evapotranspiration for each season of bird data collection (spring: mid-April to beginning of June 2000; winter: beginning of October to mid-February 2002–2003 and 2003–2004); (2) idem for net radiation; (3) mean rainfall during the winter season for winter bird data; and, mean rainfall during the latest winter for spring bird data, according to Morales et al. (2002), who have shown a positive link between great bustard *Otis tarda* breeding productivity and winter precipitation.

2.4. *Statistical analyses*

Firstly, we explored the dataset by means of a univariate analysis (Mann–Whitney *U*-test), which provides a general picture of the importance of each environmental variable for characterizing both the distribution and the ecological niche of little bustard in Madrid region across seasons.

Then, we ran a collection of models using the MaxEnt 2.2 method by Phillips (2005) and Phillips et al. (2006). The approach of MaxEnt is to find the probability distribution of maximum entropy (closest to the uniform) subject to the constraints imposed by the information available regarding the observed distribution of the species and the environmental conditions across the study area. The method assigns a probability of occurrence to each cell grid in this area. Because the sum of the probabilities must equal 1, each probability is typically extremely small, making model output difficult to interpret. We therefore present the MaxEnt output (model predictions) as cumulative probabilities, where the value of a given pixel is the sum of that pixel and all others with equal or lower probability, multiplied by 100 to give a percentage. A high value (close to 100%) at a particular pixel indicates that it is predicted to have suitable conditions for the species. Note that using presence-only data, it is generally not possible to calculate probabilities of presence; instead, outputs are relative likelihood of presence (Pearce and Boyce, 2006). Regularization values, which reduce over-fitting, were selected automatically by the program. The recommended default values were used for both the convergence threshold (10^{-5}) and maximum number of iterations (500). The selection of environmental variables was also carried out automatically, following default rules dependent on the number of presence records. The default is to include all variables, i.e. no selection.

Spatial models were built separately for each season (spring or winter) and group of predictors (Table 1): (1) habitat variables, (2) climate, and (3) all together. In each case, occurrence locations (the dependent variable) were randomly partitioned into two sub-samples: 80% used as training data set and the remaining 20% reserved for testing the resulting models (partitioned models). In addition, for visual interpretation, the algorithm was run on the 100% of occurrence points (full models), taking advantage of all available data to provide the best estimates of the species’ potential distribution. The performance of both full and partitioned models was evaluated by means of an adaptation to presence-only data sets of the area under the receiver operating characteristic (ROC) curve (AUC; Beck and Shultz, 1986; Zweig and Campbell, 1993; Fielding and Bell, 1997). This measure can be interpreted as the probability that a presence site will be ranked above a random background site (by default MaxEnt generate a sample of 10,000 background “pseudo-absences” uniformly at random to represent the environmental conditions in the region) (Phillips et al., 2006; Phillips, 2008). A random ranking has a value of around 0.5, while a perfect ranking achieves the maximum possible AUC of 1.0. Models with an AUC value above 0.75 are considered as potentially useful (Elith et al., 2006).

As we are dealing with two occurrence datasets (winter and spring) of different size, we did a preliminary analysis (i.e. randomly making the spring sample size to be equal to the winter one) to test whether this fact affected MaxEnt final models.

Continuous model outputs (cumulative probability values ranging from 0 to 100%) can be transformed into Boolean maps of suitable–unsuitable areas through the application of different thresholds or “cut-offs” (i.e. all pixels showing values above a selected threshold are reclassified as “1” and the remaining pixels as “0”). However, as highlighted by Phillips et al. (2006), determining the optimal threshold still remains a little explored topic when MaxEnt is applied. In fact, no general purpose rule has yet been developed but, in general terms, it must be considered that as larger thresholds are selected, commission errors will decrease, but omission errors will increase (Fielding and Bell, 1997; Hernández et al., 2006). In order to accomplish further comparative analyses, we decided to use three alternative thresholds with different degree of restriction. In particular, we selected the corresponding cumulative value for an omission error of 10% (which maintain a high proportion of presences correctly predicted when compared with “the lowest presence threshold”; see Pearson et al., 2007), 5% and 15% (note that omission error values range from 0 to 100%). Results were assessed through changes in connectedness, which was measured on the suitable patches identified on the Boolean maps by applying the different thresholds. We used three indices: (i) a patch cohesion index (COHESION), which is computed from the information contained in patch area and perimeter and increases as the patch becomes more aggregated; and, two types of contagion indices which show the frequency of adjacencies between the same patch type on the map (they will take the minimum value when the class is maximally disaggregated and the maximum when the class is maximally clumped): (ii) CLUMPY, which it is corrected from random, and (iii) PLADJ, which does not account for random effects. Analyses were executed in Fragstat 3.3 (McGarigal and Marks, 1995).

Finally, to look at the relationships between winter and spring patterns, we joint models in two different ways: (1)

We explored the advantages of including the final integrated spring model (continuous values) as a predictor to explain wintering distribution and vice versa. (2) Once the use of a particular threshold was decided, we combined Boolean integrated models for both seasons into a new layer showing wintering, breeding and resident areas.

3. Results

In winter, a total of 78 flock locations were gathered but, when these records were overlapped on the 1-km^2-resolution grid, only 53 pixels could be used as presence records for modelling. In spring, 417 records of males were collected and transformed into 211 occupied 1-km^2 pixels. The preliminary evaluation of the effect of the different sampling size in modelling seasonal distribution showed no significant differences (in both AUC and spatial pattern) when we randomly equalled the pool of presences for spring and winter.

3.1. *Seasonal changes in environmental preferences*

Exploratory univariate analyses of the input data showed seasonal differences between spring and winter (Table 2). Winter locations were significantly characterised by lower seasonal values (mean and variation) of both net radiation and evapotranspiration, indicating that, in general terms, birds tolerated a narrower range of climatic conditions than in spring. However, in this season, birds selected areas where winter rainfall remained more constant around medium values, at least for the study period. The analysis also showed that wintering, as well as spring habitats, corresponds to extensive landscapes (i.e. little bustards preferred dry croplands, as compared to, for example, irrigated lands in both seasons). However, in winter, the birds used a higher proportion of wastelands and were found at a lower altitude than in spring, when they selected pasturelands located at a higher altitude, in the northern part of the province.

Table 3 – AUC-values for habitat, climate and integrated seasonal models (random AUC is 0.5)

	Spring	Winter
Habitat		
Training (test) sets	0.933 (0.914)	0.923 (0.871)
Full model	0.932	0.921
Climate		
Training (test) sets	0.837 (0.805)	0.848 (0.837)
Full model	0.838	0.863
Integrated models		
Training (test) sets	0.944 (0.920)	0.923 (0.871)
Full model	0.945	0.940

All AUC values are significant at $p < 0.001$.

In general, both spring and winter models showed a good performance and predictive capability, although some differences can be noticed (Table 3). Dealing with habitat and climate independently, the spring models had a higher performance (see AUC values of training and full models) and predictive capability (see AUC values of test sets) when explaining habitat, but showed poorer explanatory power for climate than winter models. When climate and habitat were considered together in the integrated models, the spring model still was the most explanatory and predictable for the training/test sets, but seasonal differences became less important when full models were analysed (from 0.945 to 0.940). Table 4 shows that spring models were, in general, more complex because they explained the birds' distribution using a larger number of relevant variables (which greatly affected the models when they were dropped). In spring, the most significant variable for modelling the species' habitat preferences was the percentage of dry crops, followed by the altitude and the percentage pasturelands. For the climate model, the three climate variables included were all highly relevant for model construction, particularly net radiation. When both sets of

Table 2 – Comparison (means and standard deviations) between variables quantifying both spring and winter habitat for the little bustard in the study area

	Spring ($n = 211$)		Winter ($n = 53$)		Significance *U*-test
	X	S.D.	X	S.D.	
MDT	691.78	56.83	639.46	61.83	**0.000**
TOPO10	0.07	0.08	0.04	0.06	0.074
TOWNDENS	0.01	0.05	0.08	0.04	0.719
ROADDENS	0.07	0.11	0.07	0.11	0.786
IRRIGPERC	0.01	0.06	0.01	0.07	0.402
DRYPERC	0.54	0.24	0.80	0.27	0.632
PASTPERC	0.05	0.18	0.00	0.00	**0.024**
OLIPERC	0.02	0.11	0.01	0.04	0.693
WASTEPERC	0.01	0.05	0.07	0.19	**0.002**
EVPs/EVPw	28.49	1.18	5.84	0.27	**0.000**
RADs/RADw	51.02	1.86	10.18	0.41	**0.000**
RAINWs/RAINWw	8.90	0.80	17.44	1.14	**0.000**

The table shows the significance of the Mann–Whitney *U*-test between two independent samples (only significant values are in bold). Note that the climate data layers differed between seasons while those for the other variables did not.

Table 4 – Contribution of each environmental variable to the gain of the models

	Spring			Winter		
	Habitat	Climate	All	Habitat	Climate	All
MDT	**18.261**		**10.000**	3.846		0.858
TOPO10	2.174		1.739	2.137		0.429
TOWNDENS	0.870		0.435	0.427		0.429
ROADDENS	2.609		1.739	1.709		1.288
IRRIGPERC	2.174		1.304	0.855		0.858
DRYPERC	**33.043**		**15.217**	**31.624**		**18.455**
PASTPERC	**10.870**		**7.826**	0.427		0.429
OLIPERC	5.652		3.913	0.000		0.000
WASTEPERC	2.174		1.739	**7.692**		**5.579**
EVP		**19.535**	0.870		0.730	0.000
RAD		**32.558**	1.304		**31.387**	2.146
RAINW		**20.930**	1.304		**46.715**	**7.725**

Values represent the percentage of information dropped when each variable is omitted in each model (the highest values are in bold).

predictors were analysed together in the integrated models, the habitat variables above mentioned remained as the most relevant (even if their contribution to the model diminished in all cases), excluding any climate factors. In winter, after the percentage of dry crops (again the main variable in the model), the amount of wasteland was the most important predictor in the habitat model, while seasonal mean rainfall and net radiation were the most relevant variables in the climate model. The integrated winter models accounted for mixed-selection criteria, based on both habitat and climate variables; while spring models were based mainly in habitat variables.

3.2. *Spatial niche models and their seasonal variation*

Fig. 2 presents a geographical representation of the spatial niche and its seasonal variation as predicted by MaxEnt. In winter, little bustards disappeared from higher altitude areas, such as foot-hill pastures near the mountains or the high plateau of the eastern and southeastern rim of the region, instead occupying patches along the main river valleys (Jarama and Tagus). Moreover, the winter species distribution in the extensive cereal farmlands of the northeast (most of them included in the Special Protection Area of the Jarama and Henares valleys) was reduced, compared with spring, while it increased in the southern farmlands. According to the habitat models, predicted distribution (associated to niche dimensions) was slightly broader in winter than in spring. However, regarding climate models, conditions were better for the species all across the study area in spring and, therefore, the species was predicted to be more widespread. Boolean integrated seasonal models allowed to compute a slightly larger suitable area (associated to a wider niche) in winter (1058 km^2) than in spring (926 km^2) (Table 5). This table also presents the range of environmental predictors within suitable patches (removing the effect of the different sampling size on the input data) as a measure of the seasonal change in the niche width. These values again corroborated the general trend in the niche to be larger in winter than in spring. Note that birds supported similar town densities in both seasons, but could be found in areas with a higher proportion of roads in winter, when they tolerate more human disturbance. However, some land cover percentage values were small due to their reduced availability.

3.3. *Changes in landscape connectedness among suitable patches*

In the integrated models (based on both habitat and climate) the analysis of connectedness at different thresholds (Fig. 3) showed that: (1) in all cases, suitable patches for the species were more connected across spatial scales in winter; (2) when the threshold was increased (becoming more restrictive), connectedness decreased, more so for spring than for winter; (3) the three indices studied varied in parallel and linear manner for both seasons across scales, with the most similar responses for CLUMPY and PLADJ (both types of contagion indices). These comparable tendencies across thresholds indicate that the results for different indices varied in a proportional way. Therefore, the choice of a particular cut-off had similar effects on different indices.

3.4. *Prediction of suitable wintering areas from breeding patches*

The inclusion of the spring (breeding) model as a predictor in the integrated full winter model only slightly improved its performance (AUC value increased from 0.940 to 0.948 when this variable was considered), but made spatial patterns more realistic. More relevant was the fact that the spring distribution became the second most important variable (similar to the percentage of wastelands) in this model, behind winter rainfall and surpassing the importance of the amount of dry crops. On the other hand, the inclusion of wintering areas in the spring model also enhanced a bit its performance, although the increase was even smaller (from 0.945 to 0.950). In this case, winter distribution became a less important predictor, being ranked fourth, after dry crops, altitude and pasturelands. These results were consistent with the outcomes achieved when we repeated the models including

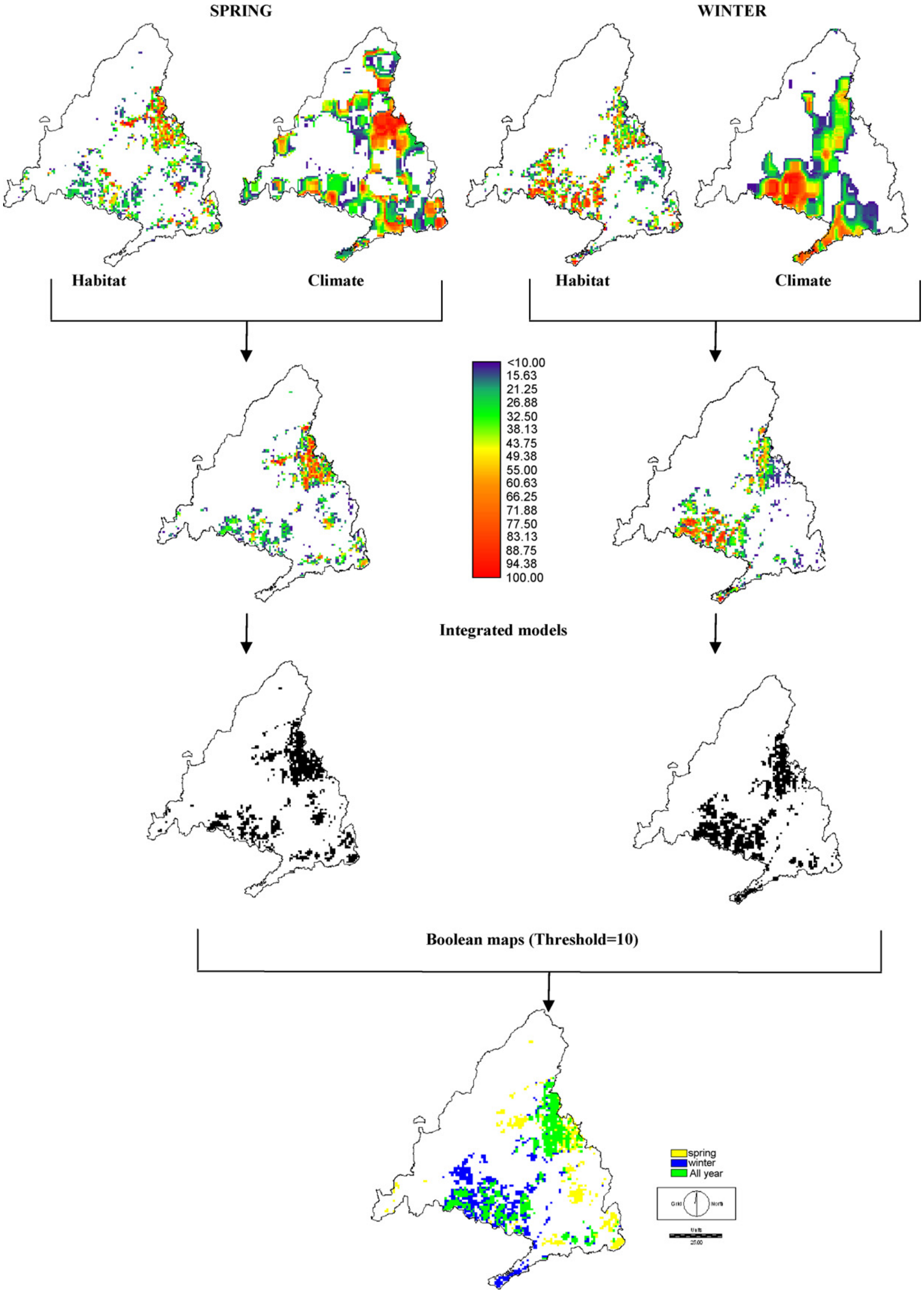

Fig. 2 – The figure shows habitat, climate and integrated models for spring and winter (values are cumulated probabilities represented by means of a palette from blue to red). Next, it includes Boolean maps of suitable areas obtained by applying a particular threshold (value of cumulate probability corresponding to a omission error of 10%) on the integrated models (palette black and white). Finally, those Boolean maps are combined to show the overlapping between winter and spring areas.

Table 5 – Percentiles of the environmental variables (i.e. niche dimensions) characterizing the predicted area suitable for the species obtained by applying a threshold of 10% to the full, integrated models (the highest values are in bold)

	Spring[a]				Winter[b]			
	P25	P50	P75	Inter-quartile range (P75 – P25)	P25	P50	P75	Inter-quartile range (P75 – P25)
MDT	626	700	700	74	600	630	700	**100**
TOPO10	0.00	0.04	0.12	**0.12**	0.00	0.00	0.08	0.08
TOWNDENS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ROADDENS	0.00	0.00	0.16	0.16	0.00	0.00	0.20	**0.20**
IRRIGPERC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DRYPERC	0.76	0.92	1.00	0.24	0.68	0.88	1.00	**0.32**
PASTPERC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OLIPERC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
WASTEPERC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
EVP	27.80	28.70	29.30	**1.5**	5.65	5.88	6.12	0.47
RAD	50.20	51.00	52.00	**1.8**	9.96	10.30	10.60	0.64
RAINW	8.33	8.89	9.44	1.11	16.40	17.00	18.20	**1.8**

[a] Available surface: 926 km^2.

[b] Available surface: 1058 km^2.

spring/winter distribution alone as the only variable explaining seasonal distribution: the spring pattern itself was a more relevant predictor for explaining wintering areas (AUC = 0.836) than vice versa (AUC = 0.769).

The extensive overlap (591 km^2) between spatial niches in spring and winter is shown in Fig. 3. Potential areas relevant only for breeding occupied 335 km^2, while only-wintering potential areas covered a larger area (467 km^2).

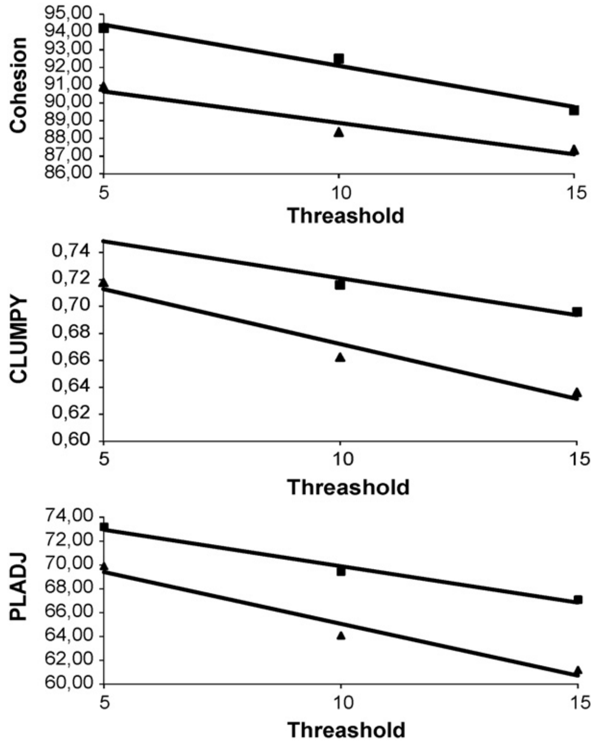

Fig. 3 – Variations in the three connectedness indices according to the three different thresholds used to create the Boolean maps. Triangles correspond to spring values and squares to winter data.

4. Discussion

4.1. *Can we use MaxEnt to predict seasonal changes in little bustard distribution, environmental preferences and spatial niche width?*

Although MaxEnt models do not predict the actual limits of a species' range, they can identify regions with similar environmental conditions to occurrence localities (Pearson et al., 2007). Models presented here provided a good approximation to little bustard distribution in the region of study, on the basis of climatic and habitat variables associated with the species' presence during either spring or winter. This result supports MaxEnt as an efficient tool to model species' occurrence when only small data sets are available, as already highlighted by previous authors (Elith et al., 2006; Hernández et al., 2006). On the other hand, ecological niche theory (Hutchinson, 1957; Chase and Leibold, 2003) predicts that a species' distribution should be largely determined by its specific environmental requirements and their spatial variation (Rosenzweig, 1987). In this sense, our models based on climatic conditions can be interpreted as the little bustard's potential distribution range within the region of study, based on simultaneous variations along different axes of the species' fundamental niche (Suárez-Seoane et al., 2004). Parallelly, the introduction of variables measuring human disturbances (i.e. town and road densities) in the habitat models, as a means of incorporating the species behavioural response (avoidance, attraction or neutrality) to strong landscape transformations, bring such models close to be interpreted as realized spatial niche models (Hutchinson, 1957). However, biotic interactions (i.e. competition) should be fully measured to obtain more realistic results. Thus the seasonal shift in the observed niche could result either from changes in the species' fundamental niche or from changes in the realized niche, as caused by the effect of those interactions (Broennimann et al., 2007). This framework may be used to assess seasonal variations in the species' habitat preferences and width niche through changes in its distribution ranges. Leaving apart the effect of biotic interactions, birds may respond to environmental stress by relaxing their requirements for habitat selection and thus widening their spatial niche, which allows them to expand their distribution range within the geographic limits imposed by the climatic niche. This fact was particularly observed in resident areas, where little bustard's potential habitat suitability slightly increased from winter to spring, even if this difference was lower than expected, probably because the seasonal loss of environmental suitability associated to certain niche factors can be compensated by positive changes in others.

Wintering niche models were, in general terms, less explanatory, predictable and complex than the spring ones, suggesting several facts. First of all, winter distribution was controlled by a smaller number of mixed environmental factors (related to both habitat and climate) than in spring, when birds are breeding and therefore show stricter environmental preferences (mainly related to habitat). This shift can be associated to the lower suitability of winter climate conditions in high altitude areas in combination with some differences in land management, such as the presence in river valleys of more permanent cultures (e.g. irrigated legume crops) or the more frequent set-aside land (e.g. fallows, wastelands) in extensive agricultural areas (see García de la Morena, 2002; Silva et al., 2004 for the species' winter habitat preferences). In this context, the high winter potential of southern farmlands and a considerable proportion of northeastern farmlands may reflect the joint effects of climate and land management. In those sectors, little bustards tend to select winter stubbles (unpubl. data), a habitat where environmental stress is reduced due to an increased biomass content (weeds and germinated unharvested cereal seeds; Suárez et al., 2004). Complementarily, our results revealed that winter habitat was less predictable than spring, finding the opposite situation for climate conditions. This fact may be related, according to Brotons et al. (2004), to a widening of the ecological requirements of the species, which become more generalist in winter, and therefore more difficult to predict.

On the other hand, spring models, as before mentioned, defined a narrower niche than in winter, a fact obviously related to strong biotic interactions, reproductive behavior and diet specialization. In this sense, Jiguet et al. (2000) explain that food availability is not critical for little bustard mating selection, as expected for species breeding in exploded leks, although Traba et al. (2008) conclude it is related to display site selection. Those authors also found that large carabids and, in general, large beetles played a relevant role as food resources for males and perhaps for females during the mating season. In this context, considering other niche dimensions (Peterson, 2007) and including demographic parameters into the modeling framework, the reproductive niche would be more realistic and even narrower than suggested by us, as founded by Titeux et al. (2007) for red-backed shrike.

At this point, it must be emphasized that despite the fact that distribution modelling (as developed here) provides relevant insights on the broad-scale environmental niche of species (Grinellian models) for conservation and biogeographical research, there are still important conceptual uncertainties which must be investigated, such as the identification of causal relationships between species distribution and predictors, and the effect of species' ecological characteristics on the performance of the models (McPherson and Jetz, 2007; Tsoar et al., 2007). In this context, besides the development of new algorithms, niche modeling is still hampered by inadequate consideration of critical ecological traits of species, such as dispersal and metapopulation dynamics (Araújo and Guisan, 2006), reproductive parameters (Titeux et al., 2007), biotic interactions and disturbance regime. Also a good knowledge on the ecology of the species is critical to adequately interpret models (Austin, 2002, 2007).

4.2. *Can we predict suitable wintering habitat from breeding habitat patches?*

The overlap between spring and winter potential distribution areas predicted by our models was high. In fact, most of the identified wintering areas coincided or showed high connectedness with spring patches. Conversely, however, there were significant breeding patches with low suitability which showed little or no connectedness with potential winter areas (foot-hill pastures, eastern rim highlands). On the other hand, we have shown that spring habitat was a much better predictor of the little bustard's wintering range that vice versa, which has clear management implications. In this sense, preserving breeding sites closer to wintering areas will ensure the conservation of a larger proportion of the total distribution range of the species. Similarly, preserving the largest possible proportion of the potential breeding range will also protect a higher proportion of the wintering range. This is a clear example of how predictive large scale modeling procedures can contribute to the optimization of land management aimed at species conservation. Moreover, we found that fragmentation was perceived differently across the seasons, i.e. suitable patches for the little bustard were more connected across the scales (different thresholds) in winter than in spring, which may have time-dependent implications for species' movement across the landscape. Therefore, we must preserve not only suitable patches, but also agricultural matrix quality (or restore it through, for example, farming extensification) to guarantee dispersion (Donald and Evans, 2006) and enhance its biological connectivity through the year. In particular, for species with seasonally variable food requirements, habitat complementarity may be required to permit movements between these patches (Henle et al., 2004; Donald, 2005) and therefore migratory connectivity across time. This appears to be a useful tool for conservation and management purposes.

5. Conclusions

The applied methodology has allowed us to model successfully little bustard seasonal distribution and environmental preferences starting from two input datasets with different sample sizes. Analogously, we have shown how these models can be interpreted as a representation of the species spatial ecological niche at large scale, and may be used to explore niche shifts over a species' annual cycle and their probable causes. In this sense, it must be noticed that even if climate models were only partial (we may not include all the important variables), they have been highly valuable, particularly when they have been integrated with habitat data. MaxEnt models have proved its efficacy in predicting little bustard winter occurrence from known patches of breeding habitat, which has clear conservation impact in this species, since allows identification of potential winter range and its consideration in large scale management. Additionally, the different relative importance of the areas predicted for each season may help allocating conservation efforts according to the species environmental requirements over the annual cycle.

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