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BREEDING HABITAT SELECTION BY STEPPE BIRDS IN CASTRO VERDE: A REMOTE SENSING AND ADVANCED STATISTICS APPROACH

SELECCIÓN DE HÁBITAT DE REPRODUCCIÓN DE AVES ESTEPARIAS EN CASTRO VERDE: UNA APROXIMACIÓN CON TELEDETECCIÓN Y ESTADÍSTICA AVANZADA

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SUMMARY.—*Breeding habitat selection by steppe birds in Castro Verde: a remote sensing and advanced statistics approach.*

The Castro Verde SPA is the main pseudo-steppe area in Portugal, holding populations of several threatened steppe bird species of national and international importance. A specific agri-environmental scheme has been put in place in the area to support these populations. While the local steppe bird community is relatively well studied, existing knowledge about habitat selection is mostly based on limited datasets or restricted statistical methods, which could hinder the of recommended management measures. In this study, we used data from several different remote sensing sources (e.g. SPOT VGT, Landsat TM, LiDAR) to characterise landscape features at different spatial scales, while multi-date imagery captured agricultural crop dynamics. A large dataset of steppe bird occurrence was collected through a combined stratified random field sampling design. The species-habitat associations were quantified using a non-linear regression approach (MARS) within a robust methodological framework. The methodology showed consistent results with what is known, confirming most of the existing knowledge on habitat use by the local steppe bird community, while adding further information. The approach is thus reliable and could potentially be used to investigate less well known communities. It is further suggested that the findings of this study be incorporated into appropriate management prescriptions.

Key words: habitat models, habitat selection, model inference, multivariate adaptive regression splines, remote sensing, steppe birds.

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RESUMEN.—*Selección de hábitat de reproducción de aves esteparias en Castro Verde: una aproximación con teledetección y estadística avanzada.*

La ZEPA de Castro Verde es la principal área pseudo-esteparia de Portugal, con poblaciones de varias especies de aves esteparias amenazadas de importancia nacional e internacional. En esta área se ha desarrollado un programa agro-ambiental para mantener dichas poblaciones. Mientras la comunidad local de aves esteparias ha sido estudiada relativamente bien, el conocimiento sobre su selección de hábitat está basado principalmente en bases de datos limitadas o métodos estadísticos restringidos, lo cual podría obstaculizar la efectividad de las medidas de manejo recomendadas. En este estudio se usaron datos de diferentes fuentes de teledetección (p. ej. SPOT VGT, Landsat TM, LiDAR) para caracterizar rasgos del paisaje a diferentes escalas espaciales, mientras que se usaron imágenes multi-fecha para capturar la dinámica de los cultivos agrícolas. Se reunió una gran base de datos sobre presencia de aves esteparias mediante un diseño combinado y estratificado aleatorio de muestreo de campo. Las asociaciones entre especies y hábitats fueron cuantificadas por medio de regresiones no lineales (MARS) en un marco metodológico robusto. La metodología usada mostró resultados consistentes con la información conocida, confirmando la mayor parte del conocimiento existente sobre uso del hábitat por parte de la comunidad local de aves esteparias, pero también añadió información adicional. La aproximación es por tanto fiable y podría ser usada para estudiar otras comunidades peor conocidas. Se sugiere además que los resultados de este estudio pueden ser incorporados entre las prescripciones de manejo apropiadas.

Palabras clave: aves esteparias, modelo de inferencia, modelos de hábitat, selección de hábitat, *splines* de regresión multivariada adaptativa, teledetección.

INTRODUCTION

In Europe, low-intensity farming systems have the highest bird diversity of all agricultural systems (Bignal and McCracken, 1996; Tucker, 1997). The cereal steppe landscapes (pseudo-steppes) of Iberia, created by the extensive cultivation of cereals on a rotational basis, which result in a mosaic of cereal fields, stubbles, ploughed and fallow land, hold significant numbers of several threatened bird species (Burfield, 2005; Santos and Suárez, 2005). Indeed, 83% of the steppe birds in Europe have unfavourable conservation status, which is twice the overall figure for all European birds (BirdLife International, 2004; Burfield, 2005). It is now widely acknowledged that agricultural intensification (through extensive monocultures and irrigation) as well as land abandonment and afforestation are responsible for the degradation of pseudo-steppe habitats, and have a direct impact on bird populations (Baldock, 1991; Tucker and Heath, 1994; Suárez *et al.*, 1997).

Specific agri-environmental programmes for farmers have been implemented in several steppe bird areas in Europe; however the effectiveness of these programmes is open to question (Kleijn and Sutherland, 2003; Astrain and Zaragüeta, 2006; Whittingham, 2007). In order to apply adequate management schemes for the conservation of steppe birds, a good understanding of their habitat and landscape requirements is required. According to several authors, vegetation structure (alongside climate) is one of the most important factors determining steppe bird occurrence and abundance, both in true and pseudo-steppe environments (Suarez *et al.*, 1992; Moreira, 1999). In agroecosystems such as the cereal steppes, vegetation structure is determined mainly by agricultural use. Several studies have investigated the patterns of habitat selection by steppe birds in agricultural areas in Iberia (Martínez and De Juana, 1996; Suárez *et al.*, 1997; Delgado and Moreira, 2000; Moreira *et al.*, 2007). In most of these studies, however, the methodological approaches implemented have been somewhat limited. Common problems are the lack of unbiased and systematic characterisation of habitat features (mostly based on field notes); or the use of statistical methods which do not allow for the fitting of complex responses or for the identification of critical thresholds in the predictor variables.

This study thus aims to describe the patterns of breeding habitat selection and species' landscape requirements in Castro Verde, the main steppe bird area in Portugal, while tackling the methodological problems referred above.

According to Moreira *et al.* (2007), the steppe bird community of Castro Verde can be characterised into four main groups or habitat guilds: one that includes species associated with pastures or fallow fields (little bustard *Tetrax tetrax* and calandra lark *Melanocorypha calandra*); a second group including species associated with cereal crop fields (corn bunting *Miliaria calandra*, zitting cisticola *Cisticola juncidis*, quail *Coturnix coturnix* and Montagu's harrier *Circus pygargus*); a third habitat guild including species associated with bare soil areas and ploughed fields (short-toed lark *Caladrella brachydactyla*, black-eared wheatear *Oenanthe hispanica* and black-bellied sandgrouse *Pterocles orientalis*); and a fourth, more heterogeneous and less well described group, which includes species with other associations such as to particular features which fragment the cereal steppe landscape (galerida larks *Galerida* sp., red-legged partridge *Alectoris rufa*, stone curlew *Burhinus oedicnemus*, stonechat *Saxicola torquata* and great bustard *Otis tarda*).

In our study we accurately characterise the landscape mosaic by using multi-temporal remote sensing data from different sources. By thoroughly and systematically describing the Earth's surface, these are an excellent source of detailed environmental data for use in species habitat modelling (Kerr and Ostrovsky, 2003). With the aim of best describing the species-habitat associations we apply MARS (Multivariate Adaptive Regression Splines; Friedman, 1991). MARS is a high performing statistical approach (Elith *et al.*, 2006), which is capable of fitting non-linear responses and is therefore suitable for describing complex patterns of habitat selection and landscape requirements, such as optimum-like responses or species tolerance thresholds to a disturbance feature. Spatial scale effects were investigated by fitting the habitat models at two spatial scales: in the Castro Verde cereal steppes ('fine') and in the wider Baixo Alentejo region ('coarse'), the latter aimed at providing a regional context.

METHODS

Study area

The Castro Verde SPA (Special Protection Area for birds), with ca. 80,000 ha, is the main pseudo-steppe area in Portugal and holds populations of several threatened steppe bird species of national and international importance (Moreira, 1999; Moreira *et al.*, 2007). Its rolling plains (100-300 m) have a Mediterranean climate, including hot summers (30-35ºC on average in July), fairly cold winters (averaging 5-8ºC in January) and over 75% of the annual rainfall (500-600 mm) concentrated in the October-March months (Moreira *et al.*, 2005). The cereal steppe mosaic is dominated by fallow fields (usually over 50% of the area) which are usually used as pasture for sheep and, more rarely, cattle (Moreira, 1999; Delgado and Moreira, 2002). Some areas of open (holm oak *Quercus rotundifolia*) Montado woodlands are also present. Shrub patches, mostly associated with the river valleys or interspersed with old fallows, result from agricultural abandonment and scrub encroachment, more common in the south-eastern part of the region (Delgado and Moreira, 2000; Moreira *et al.*, 2007). The area is crossed by three main roads and two seasonal rivers (figure 1). The wider Baixo Alentejo region, which includes the Castro Verde SPA, is approximately 8,500 km^2 and reflects the typical diversity and structure of semi-natural Mediterranean landscapes, with features such as open woodland, shrubs, olive-groves and vineyards (Neves, 1998). The cereal crop areas include both high-intensive (irrigated) cereal fields and low-intensive (pseudo-) steppe grasslands as described for Castro Verde. The main topographic features include the Serra do Caldeirão hill chain on the South-West and the Guadiana River and its valley which crosses the region. The area has a low human population density, and is served by a sparse road network, with one highway crossing its western edge.

Bird data

Two datasets (one for each spatial scale of analysis) were collected, according to specifically-designed sampling schemes. The data for the 'fine' models were collected during the spring of 2006, consisting on 1,293 circular-plots of five minute duration and 125 m distance limit (Fuller and Langslow, 1984), following a combined systematic and random scheme (figure 1): 1,076 data points were distributed on a regular grid within 11 high-intensity sampling squares, which were randomly allocated over the region's steppe mosaic; the remaining data points followed a low-intensity sampling regular grid, collected within the scope of a large-scale survey of the Castro Verde's steppe birds (CAE 2006; Moreira *et al.*, 2007). The 'coarse' models were built on a dataset collected

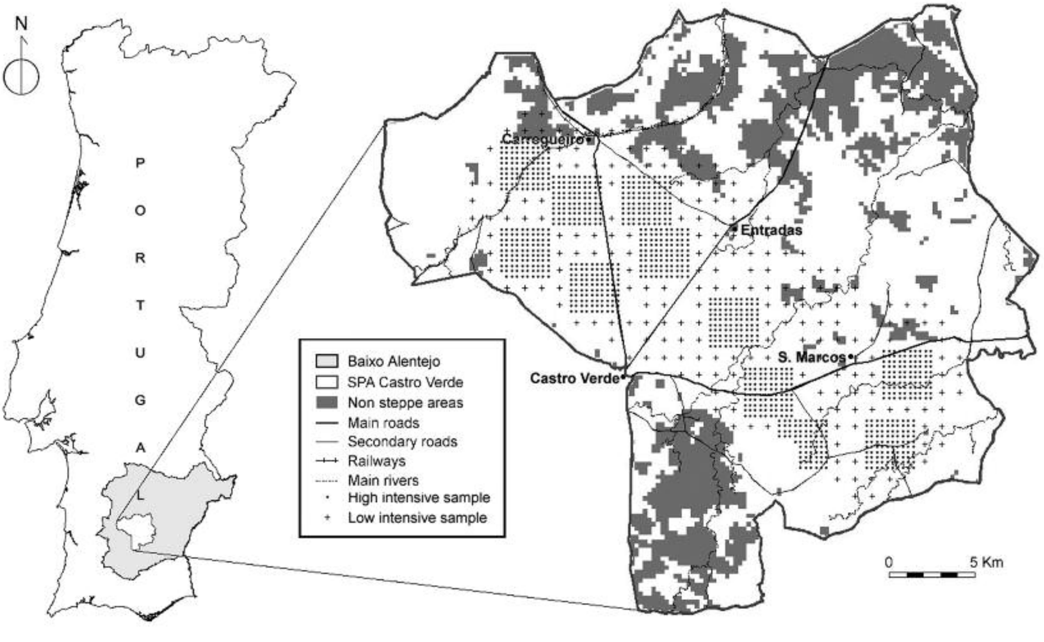

FIG. 1.—Study area and species data sampling points in the Castro Verde SPA.
[Área de estudio y puntos de muestreo de especies en la SPA de Castro Verde.]

TABLE 1

Prevalence of the studied species at both scales of study ('fine' and 'coarse'), and the predictive performance of the respective habitat models (cross-validated AUC).
[Prevalencia de las especies estudiadas a ambas escalas de estudio ('fina' y 'gruesa'), e interpretación predictiva de los respectivos modelos de hábitat (validación cruzada AUC).]

Models	**Castro Verde ('fine')**		**Baixo Alentejo ('coarse')**	
Species	**Prevalence**	**Predictive performance**	**Prevalence**	**Predictive performance**
Corn bunting (*Miliaria calandra*)	0.780	0.735	0.903	0.739
Calandra lark (*Melanocorypha calandra*)	0.283	0.803	0.132	0.789
Galerida larks (*Galerida* spp.)	0.232	0.840	0.512	0.682
Little bustard (*Tetrax tetrax*)	0.160	0.683	0.285	0.793
Zitting cisticola (*Cisticola juncidis*)	0.115	0.806	0.637	0.738
Stonechat (*Saxicola torquata*)	0.108	0.738	0.440	0.590
Short-toed lark (*Calandrella brachydactyla*)	0.101	0.762	–	–
Red-legged partridge (*Alectoris rufa*)	0.077	0.683	0.519	0.682
Montagu's harrier (*Circus pygargus*)	0.062	0.630	0.188	0.780
Tawny pipit (*Anthus campestris*)	0.054	0.749	–	–
Great bustard (*Otis tarda*)	0.052	0.586	0.058	0.807
Black-eared wheatear (*Oenanthe hispanica*)	0.033	0.719	0.055	0.673
Stone curlew (*Burhinus oedicnemus*)	0.032	0.599	0.136	0.699
Quail (*Coturnix coturnix*)	–	–	0.461	0.756
Black-bellied sandgrouse (*Pterocles orientalis*)	–	–	0.022	0.836

during the spring of 2004, with 557 surveyed grid cells of 1 x 1 km^2 according to a geographically stratified random scheme (Leitão *et al.*, in press).

All bird censuses were carried out during the birds' period of peak-activity, i.e. the early mornings (first four hours after sunrise) and evenings (last two hours before sunset) during their breeding season (March-May). In total, data for 15 species were collected at both spatial scales (see table 1). The crested and thekla larks (respectively *Galerida cristata* and *Galerida theklae*) were categorised to the genus level due to difficulties in reliable field identification (Moreira *et al.*, 2007). All visual and auditory bird observations were registered and the occurrence status of the species determined.

Environmental data

Both direct (raw) and indirect (processed) remote sensing data products were used to describe environmental and landscape features related to vegetation, terrain and disturbance (Suárez-Seoane *et al.*, 2002). Key advantages of remote sensing datasets include their systematic recording (consistency over space and time), wide spatial coverage and varying spatial and temporal resolutions. By combining data from various sources it is possible to characterise topography, land use/land cover and vegetation patterns (such as vegetation type, vigour, phenology or agricultural crop dynamics).

At the fine scale, the main land cover classes in the Castro Verde area were characterised by using a two-image set of Landsat TM data (6th of March and 9th of May 2006), at a spatial resolution of 30 x 30 m^2. The temporal patterns of the spectral data allow for the description of the crop cycle and phenological changes in vegetation during the bird's breeding season (Reed *et al.*, 1994; Hill and Donald, 2003). After pre-processing the data (radiometric, atmospheric and geometric corrections), we applied a supervised multi-date classification – by simultaneously using both sets of spectral data – to describe the relevant spatio-temporal landscape mosaic patterns. For this purpose we used a SVM (Support Vector Machines) classifier, implemented in an improved version of the 'imageSVM' tool (available online at http://www2.hu-berlin.de/hurs/projects/imageSVM.php; Janz *et al.*, 2007). SVM is a machine learning algorithm based on statistical learning theory, effectively an optimal margin classifier which seeks the optimal separating hyperplane between different classes (Boser *et al.*, 1992; Cortes and Vapnik, 1995). It is considered to be a superior method for multi-class classification problems and is well suited to describe classes with complex and otherwise hardly separable spectral signatures (Huang *et al.*, 2002; Foody and Mathur, 2004). We used a soft classification approach – using the SVM decision values as measures of probability of membership of the pixels to classes – this way keeping the numerical heterogeneity of the spectral data while allowing for an ecological interpretation of the classification results. These probabilities can then be associated with proportions of cover of the different land cover classes (Foody, 1999). The SVM model was trained on 2,971 data points, distributed in a geographically stratified random manner, corresponding to visited locations where ground truth information was collected. The land cover classes considered were *Fallow*, *Cereal*, *Bare soil* and *Woodlands & shrubs* (see table 2), as well as one class related with the phenological gradient of herbaceous vegetation (*Phenology*), ranging from green to dry (senescent) – an indicator of soil water availability. By 'hardening' the image classification we extracted a map of all water bodies in the region, from which we derived the variable *Waterdist*, distance to the nearest water body. This variable constitutes a fragmenting element in the pseudo-steppe

TABLE 2

Full set of predictor variables used in the ‘fine’ models.
[Serie completa de variables predictoras usadas en los modelos ‘finos’.]

Variable	Description
Vegetation/Land Cover	
Fallow	Fallow fields
Cereal	Cereal or forage fields, possibly including some grass-dominated fallows
Bare Soil	Bare soil, mostly ploughed fields but also including dirt tracks and paved/built-up areas
Wood & shrubs	All areas of woodland and shrubs
Phenology	Phenological gradient (green to dry/senescent) of herbaceous vegetation
Terrain	
Slope	Surface slope (in percentage)
Terrainvar	Terrain variability: standard deviation of ‘*Slope*’
Disturbance	
Waterdist	Distance (in metres) to the nearest pixel containing water bodies
Roaddist	Distance (in metres) to the nearest pixel containing paved roads
Builtdist	Distance (in metres) to the nearest pixel containing built-up structures
Treedist	Distance (in metres) to the nearest pixel containing trees
Treedens	Tree density: proportion of 5 m pixels classified as ‘tree’ within each 30 m pixel

landscape, and was thus grouped together with the disturbance variables. Airborne laser scanning (LiDAR) data were collected over the Castro Verde study area by a purposely-planned air campaign (Steppebird) flown on the 18th and 19th of May 2006 at an altitude of ca. 2,000 m (equivalent to a vertical accuracy of 0.25 m). Dual-pulse laser return (point cloud) data were collected and further processed to extract useful topographic and cartographic information, converted into thematic raster images at a spatial resolution of 5 x 5 m^2. From these data we extracted altitude and slope information and mapped all vertical features in the landscape. The latter were systematically split into built-up features and trees, by thorough visual inspection and with the aid of supplementary data, such as simultaneously collected CASI-2 (Compact Airborne Spectral Imager) multi-spectral imagery at a spatial resolution of 5 x 5 m^2. Maps of distances from built-up areas and trees were calculated, as well as density of trees. Variables derived from these data were terrain slope (*Slope*), terrain variability (*Terrainvar*), distance to the nearest built-up structure (*Builtdist*) and to the nearest tree (*Treedist*) and tree density (*Treedens*). All roads in the area were mapped using a Global Positioning System (GPS), and the distance to these calculated in the variable *Roaddist*.

At the coarse scale, the temporal vegetation patterns in the Baixo Alentejo region were described by a 12 month series of (freely available) Normalized Difference Vegetation Index (NDVI) imagery from the Spot Vegetation sensor at a spatial resolution of 1 x 1 km^2 (www.spot-vegetation.com/vegetationprogramme/) following data processing methodology described by Osborne

TABLE 3

Full set of predictor variables used in the 'coarse' models.
[Serie completa de variables predictoras usadas en los modelos 'gruesos'.]

Variable	**Description**
Vegetation	
Summer	Vegetation senescence during the summer months: *Summer = NDVI (Sep)-NDVI (Jun)*
Winter	Vegetation growth during the autumn and winter months: *Winter = NDVI (Mar)-NDVI (Sep)*
Spring	Vegetation senescence during the spring months: *Spring = NDVI (May)-NDVI (Mar)*
Low	Mean NDVI during the months with low vegetation cover: *Low = Average [NDVI (Jun:Oct)]*
High	Mean NDVI during the months with high vegetation cover: *High = Average [NDVI (Jan:Apr)]*
Dec	NDVI value during the month of December: *NDVI (Dec)*
May	NDVI value during the month of May: *NDVI (May)*
Terrain	
Alt	Mean altitude in metres within a 5 x 5 array of 200 x 200 m pixels
Topov10	Variation in altitude in a 5 x 5 array of 200 x 200 m pixels, where altitude is re-classed to a 10 m vertical resolution. *TOPOV10 = (n-1)/(p-1)*, where n = number of different altitude classes in the array, p = number of pixels in the array, i.e. 25
Disturbance	
Urbandist	Distance (in metres) to the nearest pixel containing towns, settlements or constructed structures
Roaddist	Distance (in metres) to the nearest pixel containing paved roads
Riverdist	Distance (in metres) to the nearest pixel containing rivers

and Leitão (2009). This temporal series refers to the 12 month period preceding the end of the respective field season (June 2003-May 2004). The series was further reduced into seven uncorrelated variables (table 3) which describe the yearly vegetation phenological changes: three relating to vegetation vigour changes, such as senescence and growth in different periods (*Summer*, *Winter* and *Spring*); two relating to average vegetation vigour or biomass in peak periods (*Low* and *High*); and two single month NDVI averages, which were uncorrelated with all previous measures (*Dec* and *May*). The region's altitude (*Alt*) and topographic variability at 10 m vertical resolution (*Topov10*) were extracted from a DTM acquired from the Instituto Geográfico Português (IGP). Corine Land Cover 2000 raster data (from the European Environment Agency) were used to calculate a distance map to the nearest towns, urban settlements or other constructed structures (*Urbandist*). Distance to the nearest road (*Roaddist*) and nearest river or water body (*Waterdist*) were calculated, respectively, from a vector-based road map provided by the Instituto de Estradas de Portugal (IEP) and a hydrographical map from the Agência Portuguesa do Ambiente – Atlas do Ambiente Digital (http://www2.apambiente.pt/atlas/est/index.jsp). As described for the fine scale, the latter variable was grouped with the disturbance variables. All environmental data were compiled (averaged) to the respective grain of analysis, i.e. circular-plots with 125 m radius in the 'fine' models' predictors and grid squares of 1 x 1 km^2 in the 'coarse' models.

Habitat modelling and inference

A common methodological framework was implemented at both scales of analysis. The species occurrence data were fitted to the environmental descriptors using MARS models (Friedman, 1991) for the purpose of inference. These were implemented in R (R Development Core Team, 2010) using a modified version of code from the 'mda' package, to allow for binary data and n-fold model cross-validation (Hastie and Tibshirani, 1996; Elith and Leathwick, 2007). MARS, although fast and high performing, is known to be vulnerable to high dependency (correlation) in the predictor data, potentially resulting in performance loss as well as problems in model interpretability (De Veaux and Ungar, 1994; Morlini, 2006). Moreover, data multi-collinearity, by affecting model variable selection, is difficult to guard against in one-model approaches (MacNally, 2000). For this reason, we used a cross-correlation approach, by running three models per species (at each scale), with different subsets of predictor variables, based on different data dependency levels. We hence defined three thresholds of (rank) correlation between the variables – at Spearman *rho* values of 0.7, 0.6 and 0.5 – for all species, on both 'fine' and 'coarse' models. Using these defined thresholds, we generated three predictor subsets, from the original sets (see tables 2 and 3). In each case, the best fitting set of uncorrelated variables (below the respective *rho* value) was kept, the remaining variables being discarded. Model fine-tuning, relating to the use of interactions between variables and model backfitting penalisation, was done by grid search optimising for model performance (Jiménez *et al.*, 2008). The averaged ROC (Receiver Operating Characteristic) AUC (Area Under the Curve; Hanley and McNeil, 1982) scores were used as model predictive performance measures, following a 10-fold cross-validation procedure with five replicates. For inference of the species habitat preferences (at each scale of analysis), we considered only the responses which were consistently fitted across correlation thresholds (i.e. those that entered all models), and calculated their averaged model drop contributions (explained deviance loss when variable dropped). The responses were interpreted through inspection of the model partial plots, which represent the relationship between each variable and the probability of occurrence of the respective species, in the multivariate model context (Wintle *et al.*, 2005; figure 2).

As a result, the Castro Verde steppe bird community was characterised according to its habitat guilds and the individual species responses described, complementing and further improving the work already initiated by Moreira *et al.* (2007).

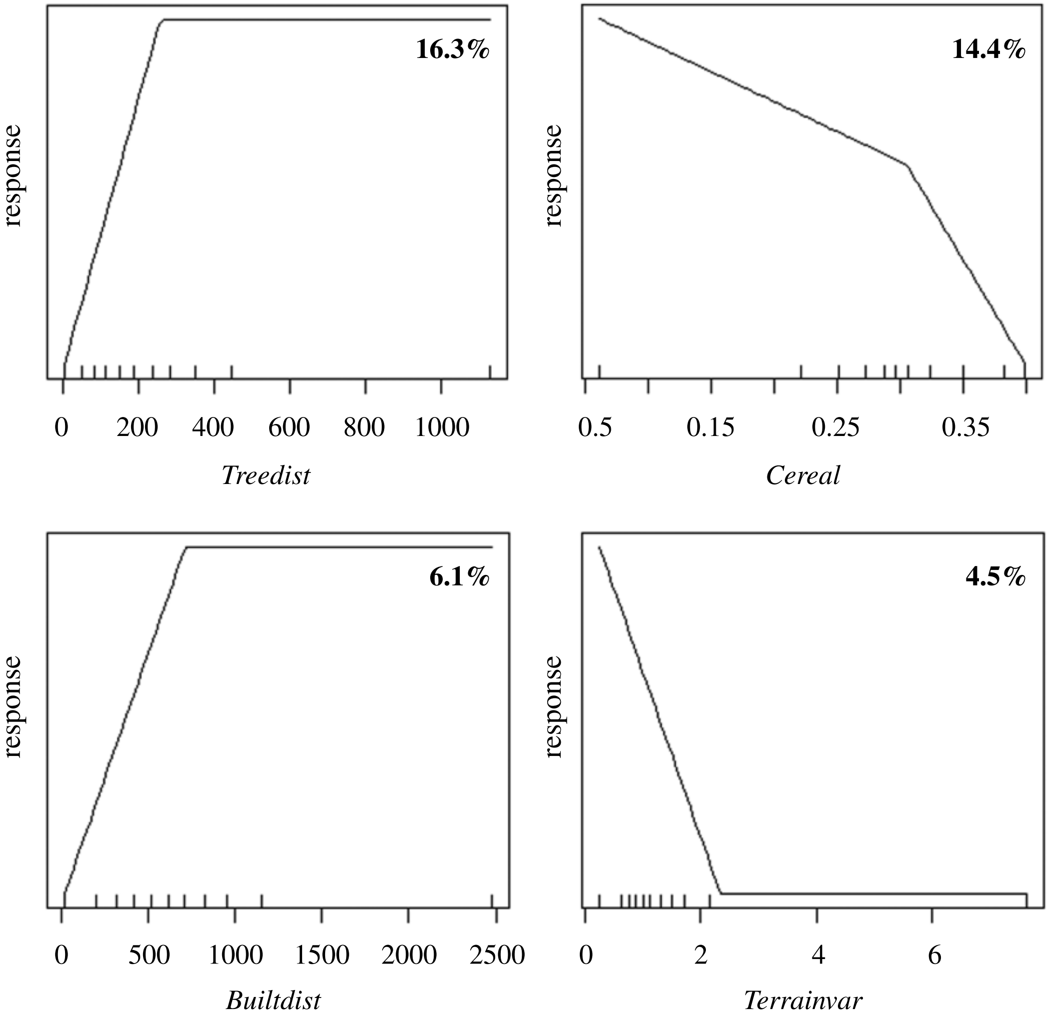

FIG. 2.—Example of model partial plots of the fitted responses used for inference: calandra lark responses in Castro Verde (fine-scaled models), with respective variable contributions in the upper right corner. *[Ejemplo de modelo de trazos parciales de las respuestas ajustadas utilizadas para la inferencia: respuesta de la calandria en Castro Verde (modelos de escala fina), con las contribuciones respectivas de las variables en la esquina superior derecha.]*

RESULTS

The corn bunting was by far the most commonly observed species at both scales of study (present on almost 80% of the circular-plots in Castro Verde and in over 90% of the sampled squares in the Baixo Alentejo). The prevalence of the remaining species ranged from 0.032 to 0.283 in Castro Verde and from 0.022 and 0.637 in the Baixo Alentejo (see table 1). The ranking of the most commonly observed species differed between the two study areas, denoting the particular characteristics of Castro Verde pseudo-steppes within the agricultural landscapes of the Baixo Alentejo. No data were collected for short-toed lark and tawny pipit at the 'coarse' scale and there were too few occurrences of quail and black-bellied sandgrouse to fit the models at the 'fine' scale.

The fit-to-purpose SVM classification of the Landsat TM imagery achieved an overall accuracy of 92.49%, with a respective Kappa of 0.88 as calculated from the confusion matrix resulting from a 10-fold cross-validation procedure (see appendix 1 for the respective class-wise accuracies). This further justifies the use of remote sensing data as sources of environmental data for habitat modelling.

The data were fitted using MARS, with predictive performance (average cross-validated AUC) ranging from 0.586 to 0.840 within the Castro Verde pseudo-steppes ('fine') and from 0.590 to 0.836 in the surrounding region ('coarse'; table 1). While more than half of the models achieved a reasonably good predictive performance (above 0.7 – *sensu* Hosmer and Lemeshow, 2000), some were considerably poorer, particularly the 'fine' models for great bustard and stone curlew and the 'coarse' model for stonechat.

The 'coarse' models were mostly useful for discriminating two main species groups (appendix 2). One group includes the species associated with areas with low vegetation biomass during the dry months of June to October (low values of variable *Low*: calandra lark, little bustard, Montagu's harrier, great bustard, stone curlew, and black-bellied sandgrouse). A second group includes the species selecting areas with higher vegetation vigour during the months of January to April (high values of variable *High* – or with little vegetation in December – low values of variable *Dec*: corn bunting, zitting cisticola, and quail). The 'coarse' models for the remaining species had lower predictive performances (below 0.7), resulting in less clear or more difficult-to-interpret responses. At this scale, only the quail responded to topographic features (by avoiding areas with rough terrain), and only the stonechat responded to a disturbance variable (distance to nearest water body, although with a difficult-to-interpret response).

The 'fine' models allowed the characterisation of the associations between species and particular land uses and or landscape features. In terms of species associations with vegetation/land use, it was possible to characterise the community in four main groups: one group constituting of species that avoided cereal fields (hence mostly selecting fallows) – calandra lark, little bustard and short-toed lark; a second guild of species that selected cereal cultivations (or alternatively avoided fallows and ploughed fields) – corn bunting, zitting cisticola, and Montagu's harrier; a third group of species that selected ploughed fields and bare soil areas – short-toed lark (also present in the first guild), tawny pipit, great bustard, black-eared wheatear, and stone curlew; and a fourth group comprised of species selecting areas with woodland/shrubs – stonechat, red-legged partridge and black-eared wheatear (also included in the third guild). At this scale only the calandra lark responded to topography, by avoiding areas with rough terrain. The disturbance/fragmenting features were found to be of great importance in the 'fine' models, sometimes the most contributing model variables, as was the case for the calandra lark, *Galerida* larks and stonechat models. We observed two main responses: the avoidance of fragmenting elements in the pseudo-steppe landscape, such as trees (calandra lark, little bustard, short-toed lark and Montagu's harrier), built-up structures (calandra lark and great bustard), roads (black-eared wheatear) or water bodies (little bustard and tawny pipit); and the selection of these elements - the *Galerida* larks selected areas close to trees and built-up structures, the stonechat selected areas close to trees and the zitting cisticola areas selected areas close to roads. The fitting of these features also often resulted in threshold-like responses (e.g. the calandra larks avoided areas closer than 250 m to the nearest tree and 650 m to the nearest built-up structure). The low occurrence of quail and black-bellied sandgrouse in Castro Verde (with respectively 27 and 12 observed occurrences) precluded the fitting of their responses at this scale.

DISCUSSION

Our study achieved the proposed aims by thoroughly characterising the steppe bird community of Castro Verde in terms of its habitat use. Nevertheless, our approach has some limitations such as the assumption that all birds were detected during our surveys, therefore not taking into account detectability differences (Diefenbach *et al*., 2003). We argue, however, that the detection or non-detection of a bird species during its peak period of breeding activity is still a good indicator of habitat quality/suitability. A second issue is that by dealing with measures of occurrence we cannot depict the effects of the environment on species abundance, although the positive relationship between occurrence and abundance is widely acknowledged (Gaston *et al*., 2000). Also, the pooling of the two *Galerida* lark species is expected to be an undermining factor in the fitted model performance and interpretation, particularly so because the species have been described as having distinct habitat preferences, as discussed below.

The SPOT VGT data provided vegetation variables, which were used to characterise the main (coarse scale) species habitat requirements. The variables *Low*, *High* and *Dec* were particularly useful. The first mainly identifies areas of extensive agricultural use, as low values of this feature represent non-irrigated crop areas with low vegetation biomass during the dry months of June to October. The other two variables were useful to identify cereal production areas. These areas have a high vegetation vigour during the months of January to April (with highly reflective cereal vegetation) - high values of *High*. During the month of December, recently sown (winter) cereal crops have little or no vegetation – and low values of variable *Dec*.

The use of Landsat TM satellite data to characterise land use, while being a great improvement to the use of field-based notes, still has its flaws. Landsat data, with six, wide spectral bands in the optical domain, are not sufficient to accurately discriminate woodland and scrubland areas, coupled in a single class in the current study. These two landscape features are expected to differ in ecological importance for several species and their differentiation could greatly improve the fitting of the steppe bird habitat responses. The advent of forthcoming hyperspectral sensors will solve this problem in the near future and allow improved landscape characterisation.

The relatively low predictive performance of some models can probably be explained by two main factors. First, the fact that the study area is generally suitable for the studied species (at both scales of analysis) diminishes the algorithms' capacity for discriminating between good and bad areas. Indeed, an increase in model performance could have been artificially achieved by increasing the extent of the study area (Lobo *et al*., 2008), but without improved knowledge of the species' habitat preferences. Second, performance could be limited by the non inclusion of relevant habitat variables such as food availability or spatial landscape configuration (Delgado and Moreira, 2002; Brotons *et al.*, 2005; Revaz *et al.*, 2008; Traba *et al.*, 2008). Nevertheless, we consider the current models suitable for inferring the main patterns of steppe bird habitat selection in the studied regions.

Our main findings relate to the description of the individual species' responses to the environment, categorised into vegetation/land cover, disturbance and terrain (Suárez-Seoane *et al.*, 2002). As a result, it is possible to characterise the steppe bird community of Castro Verde in terms of its habitat use (see figure 3), complementing the work by previous authors (Delgado and Moreira, 2000; Moreira *et al.*, 2007). Like Moreira *et al.* (2007) we identified four main species groups or habitat guilds. The first, species associated with extensive agroecosystems and fallow fields, comprises the little bustard and calandra lark. The fitted little bustard preference for fallow fields, and consequent avoidance of cereal crop fields is well known (Martínez, 1994; Delgado and Moreira, 2000; Wolff *et al.*, 2001). In our study, this species responded to tree density, rather than to distance to the near tree, denoting a certain tolerance to the proximity of trees. Also in the study by Moreira *et al.* (2007), the species was found to (negatively) respond to the proportion of Montado woodland cover in the vicinity rather than to the presence of this land use class. The calandra lark's association with fallow fields has been widely described (Mañosa *et al.*, 1996; Suárez *et al.*, 1997; Delgado and Moreira, 2000; Moreira *et al.*, 2007). Its avoidance of rough terrain areas

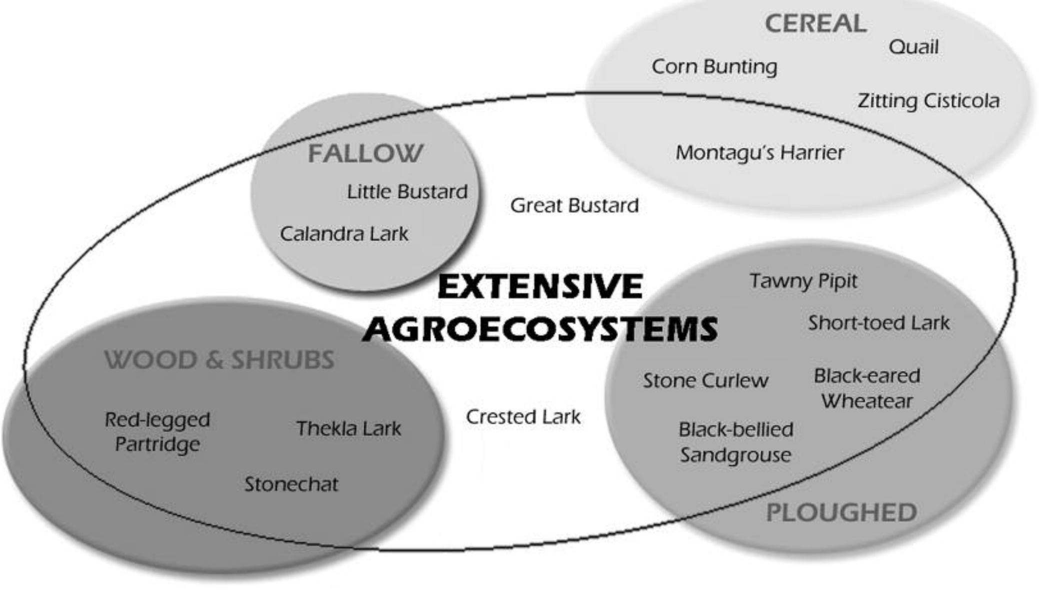

FIG. 3.—Main habitat guilds of the Castro Verde's steppe bird species community.
[Principales gremios por hábitat de la comunidad de aves esteparias de Castro Verde.]

is also known (Suárez-Seoane *et al.*, 2002; Brotons *et al.*, 2004). Our finding of this lark's avoidance of trees corroborates other studies reporting strong responses to the proximity of trees and afforestations (Reino *et al.*, 2009; Morgado *et al.*, 2010). We were able, however, to determine a particular threshold in the response, at 250 m distance to the nearest tree in the landscape, beyond which the species seems not to be affected.

A second habitat guild, species associated with cereal crop fields, includes the corn bunting, zitting cisticola, quail and Montagu's harrier, agreeing with previous knowledge (Moreira *et al.*, 2007). Within this guild, the latter was the species most strongly associated with extensive agroecosystems, by selecting the cereal steppe areas at the 'coarse' scale. Brotons *et al.* (2004) also associated Montagu's harrier with extensive cereal agricultural areas. Its fitted avoidance of areas closer than 600 m to the nearest tree constitutes, however, a new finding. While the corn bunting is known to be affected by agricultural intensification (Tucker and Heath, 1994; Brickle *et al.*, 2000; Stoate *et al.*, 2000), the species is so frequent within the Baixo Alentejo region (prevalences of 0.903 and 0.780, respectively the in 'coarse' and 'fine' scales of study) that these effects would possibly only limit species abundance, and thus are not detectable by models based on occurrence. Nevertheless, the species' selection of cereal fields in the region has been previously described (Delgado and Moreira, 2000; Moreira *et al.*, 2007).The associations of zitting cisticola and quail with cereal crop areas is also common knowledge (Delgado and Moreira, 2000, 2002). Brotons *et al.* (2004) found that quail occurred on irrigated crops as well as extensive agricultural areas. Furthermore, these authors also found a negative response of this species to areas with high slopes, consistent with our fitted response of avoidance of areas with rough terrain.

A third species group, composed of species associated with extensive agricultural systems and ploughed fields or bare soil areas, includes the short-toed lark, tawny pipit, black-eared wheatear, stone curlew and black-bellied sandgrouse. The short-toed lark showed a strong avoidance of trees, also previously described (Brotons *et al.*, 2004; Reino *et al.*, 2009). The black-eared wheatear responded positively to areas of 'Woodland & shrub', confirming other reports of the association of this species with shrubs (Tellería *et al.*, 1994; Suárez *et al.*, 1997). Although the black-bellied sandgrouse could not be fitted using our methodological approach, it occurred mainly in ploughed fields and was thus included in this group. The group differs from the one described by Moreira *et al.* (2007) by the inclusion of the stone curlew and tawny pipit. The stone curlew had been previously related to both ploughed fields and scrubland areas (Brito, 1996; Mañosa *et al.*, 1996) and included by Moreira *et al.* (2007) together with species associated with shrubs. Our fitted models for this species, however, were poorly performing, possibly due to the inadequacy of the field sampling methodology (as the species is mostly crepuscular). The tawny pipit, on the other hand, could not be successfully modelled in the study by Moreira *et al.* (2007), but was reported in highest densities on ploughed land. In our study it also showed a preference for areas close to water bodies, which to our knowledge has not been previously described.

The fourth habitat guild, formed of species associated with fragmenting landscape features such as woodlands and scrublands, includes the stonechat and the red-legged partridge. The stonechat, in fact, selected both areas with 'Woods & shrubs' and close to trees in the study area, thus corroborating existing knowledge (Moreira *et al.*, 2007; Reino *et al.*, 2009). The red-legged partridge also selected areas with high slopes, which in the study areas are mostly covered by shrubs.

As discussed previously, the fitted responses for the *Galerida* larks are probably the result of the pooling of two species with distinct habitat preferences. In our study area, however, the species cannot be reliably identified in the field and it is common procedure to pool them to the genus level (Delgado and Moreira, 2000; Moreira *et al.*, 2005, 2007; Reino *et al.*, 2009). This possibly explains the inconsistent and difficult-to-interpret responses fitted by the respective models. The thekla lark is known to be associated with sloping areas with shrubs and the crested lark with flat and human-disturbed areas (Tomé, 2008; Guillaumet *et al.*, in press). For this reason, and although our study could not confirm this, we included the former species into the fourth habitat guild, while the latter was kept outside these guilds although inside the sphere of the extensive agroecosystems (see figure 3).

The response of the great bustard to ploughed lands in our models is probably misleading, as the models showed poor performance. This is possibly due to an inadequate field sampling methodology for this species, and also due to higher detectability of the species in ploughed fields than in other habitats. The species is known to use the whole cereal steppe mosaic during spring, i.e. fallows, cereal and ploughed fields (Suárez *et al.*, 1997; Lane *et al.*, 2001; Moreira *et al.*, 2004). Our models, however, depicted the species' avoidance of human disturbed areas (closer than 500 m to the nearest built-up structures), which has been previously described. This species was thus included within the extensive agroecosystems, though outside any habitat guild.

By using predictor variables derived from remote sensing sources and applying a robust statistical approach, our methodology corroborated most of the existing knowledge of the local steppe bird community, while refining it further. This approach can therefore be considered reliable for characterising the patterns of habitat selection of faunal communities and could be applied to other, less well-known communities.

Finally, we recommend that the findings resulting from this work (e.g. the effects of individual trees in the landscape) be incorporated into future management prescriptions aimed at the conservation of steppe birds of Castro Verde.

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APPENDIX 1

Class-wise accuracy assessment of the Landsat TM image classification (user's and producer's accuracies refer respectively to the probability that a pixel included in particular image class is actually that habitat; and the probability that a pixel in a given habitat category is correctly classified on the image).
[Valoración por clase de la precisión de la clasificación de las imágenes Landsat TM (las precisiones del usuario y del productor se refieren, respectivamente, a la probabilidad de que un píxel incluido en una clase de imagen determinada sea realmente ese hábitat y a la probabilidad de que un píxel en una categoría de hábitat dado esté correctamente clasificado en la imagen).]

Classes	User's accuracy	Producer's accuracy
Fallow	92.69%	89.30%
Cereal	93.94%	96.18%
Bare Soil	96.45%	96.76%
Woodland & shrub	78.46%	73.91%
Water	100.00%	61.76%
Phenology	82.86%	82.68%

APPENDIX 2

Species responses to the predictor variables in the ‘fine’ models. For each species/variable pair, the respective variable model contribution (in percent) is indicated above the symbol. The species response shape is in the middle position (▲ for species preference for high values of the variable, ▼ for preference for low values, ▲▼ for optimum-like responses, and ● for high model contribution of the variable though with an unclear response). When applicable, the critical threshold values (in meters) is provided immediately below the symbol. The model predictive performance values are given in brackets under the species names.

[Respuestas de las especies a las variables predictoras en los modelos ‘finos’. Para cada par de especies/variables, la contribución respectiva de la variable al modelo (en porcentaje) se indica en la parte superior de la celda. La forma de la respuesta en cada especie aparece en posición media (▲ para preferencia de la especie por altos valores de la variable, ▼ para preferencia por bajos valores, ▲▼ para respuestas óptimas, y ● para contribución alta de la variable al modelo pero con respuesta poco clara). Cuando fue aplicable, los valores del umbral crítico (en metros) se muestran en la parte de abajo. Los valores predictivos del modelo se muestran entre paréntesis bajo el nombre de las especies.]

	Fallow	Cereal	Bare soil	Woodland & Shrubs	Phenology	Slope	Terrainvar	Waterdist	Roaddist	Builtdist	Treeddist	Treedens
Corn bunting (0.735)	23.7 ▼ –		39.6 ▼ –									
Calandra lark (0.803)		14.4 ▼ –					4.5 ▼ –			6.1 ▲ 650	16.3 ▲ 250	
Galerida larks (0.840)		9.6 ● –						7.3 ▲▼ 400		8.0 ▼ –	9.7 ▼ 250	
Little bustard (0.683)		49.9 ▼ –						18.7 ▲ 300				15.1 ▼ –
Zitting cisticola (0.806)		31.5 ▲ –							4.9 ▼ –			
Stonechat (0.738)				17.9 ▲ –							19.4 ▼ 300	
Short-toed lark (0.762)		22.1 ▼ –	18.4 ▲ –								20.3 ▲ 150	

APPENDIX 2 (cont.)

	Fallow	Cereal	Bare soil	Woodland & Shrubs	Phenology	Slope	Terrainvar	Waterdist	Roaddist	Builtdist	Treeddist	Treedens
Red-legged partridge (0.683)		16.6 ● –		17.7 ▲ –		24.0 ▲ –						
Montagu's harrier (0.630)	7.1 ▼ –	36.5 ▲ –									18.9 ▲ 600	
Tawny pipit (0.749)			74.1 ▲ –					20.5 ▲ –				
Great bustard (0.586)			40.0 ▲ –							12.6 ▲ 500		
Black-eared wheatear (0.719)	14.2 ● –		38.1 ▲ –	14.2 ▲ –					17.0 ▲ –			
Stone curlew (0.599)			76.9 ▲ –									

APPENDIX 3

Species responses to the predictor variables in the ‘coarse’ models. For each species/variable pair, the respective variable model contribution (in percent) is indicated above the symbol. The species response shape is in the middle position (▲ for species preference for high values of the variable, ▼ for preference for low values, ▲▼ for optimum-like responses, and ● for high model contribution of the variable though with an unclear response). The model predictive performance values are given in brackets under the species names.
[Respuestas de las especies a las variables predictoras en los modelos ‘gruesos’. Para cada par de especies/variables, la contribución respectiva de la variable al modelo (en porcentaje) se indica en la parte superior de la celda. La forma de la respuesta en cada especie aparece en posición media (▲ para preferencia de la especie por altos valores de la variable, ▼ para preferencia por bajos valores, ▲▼ para respuestas óptimas, y ● para contribución alta de la variable al modelo pero con respuesta poco clara). Cuando fue aplicable, los valores del umbral crítico (en metros) se muestran en la parte de abajo. Los valores predictivos del modelo se muestran entre paréntesis bajo el nombre de las especies.]

	Summer	Winter	Spring	Low	High	Dec	May	Alt	Topov10	Urbandist	Roaddist	Waterdist
Corn bunting (0.739)					24.0 ▲ –							
Calandra lark (0.789)				60.0 ▲ –								
Galerida larks (0.682)				36.9 ● –	32.5 ▼ –							
Little bustard (0.793)				40.8 ▲ –								
Zitting cisticola (0.738)					14.8 ▲ –							
Stonechat (0.590)					29.5 ● –							17.0 ● –
Red-legged partridge (0.682)							45.8 ● –					

APPENDIX 3 (cont.)

	Summer	Winter	Spring	Low	High	Dec	May	Alt	Topov10	Urbandist	Roaddist	Waterdist
Montagu’s harrier (0.780)				43.2 ▲ –								
Great bustard (0.807)				69.1 ▲ –								
Black-eared wheatear (0.673)			77.6 ● –									
Stone curlew (0.699)	25.0 ▲ –			21.7 ▲ –								
Quail (0.756)						13.6 ▼ –			16.3 ▼ –			
Black-bellied sandgrouse (0.836)				77.9 ▲ –								