



Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland

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Abstract. Research conducted in several Mediterranean areas indicates that most populations of steppe birds are currently experiencing population declines associated with intensification of traditional agricultural practices. By using habitat suitability modeling (HSM), our aim was to use available environmental data sets, including land use and relief, to model the current distribution of nine steppe bird species in the agriculture dominated areas of the Catalan Ebro basin (northeast Iberia). We then employ HSM to quantitatively assess the future impact of land use changes on the potential distribution range of these species under two scenarios following irrigation of present extensive cereal steppes in the area. HSM analyses showed a close association between steppe bird distribution and the extent of extensive cereal agriculture in flat areas. Although the sensitivity to planned irrigation schemes was species specific, we estimated significant decreases in distribution after irrigation for seven of the nine species examined, i.e. the Little bustard, the Montagu's harrier, the Roller and the Calandra lark, the species predicted to be more severely affected by predicted decreases in area exceeding 50%. Overall, core steppe habitats where most valuable steppe species may co-occur are expected to be mostly impacted and decrease by 74 to 81% after irrigation of only 28 to 36% of the cereal cropland in the region. Future maintenance and survival of viable populations of steppe birds will rely on our ability to enlarge the network of protected areas and to implement agri-environmental measures targeting current species core habitats in low-intensity farmland.

Introduction

Agricultural change is now acknowledged as having a profound impact on biodiversity, and is recognized as one of the main factors currently threatening bird populations in many areas of the world (Pimm et al. 1995). Low intensity farming systems in Europe have high bird diversity (Tucker and Heath 1994). These systems are under strong pressure due to large-scale socio-economic changes leading towards intensification of agriculture and to large-scale changes within traditional farming activities. Such radical changes in landscape structure may have critical impacts on bird populations (Donald et al. 2001), particularly in the Mediterranean

Table 1. Occurrence and conservation status of steppe and open habitat species currently maintaining breeding populations in the Lleida plain. The Great bustard (*Otis tarda*) disappeared from the study area as a breeder in the 1960s. The total number of 1×1 km squares included in the analysis was 313.

	SPEC ^a	Conservation status ^b	Occurrences in 1×1 km squares
Red-legged partridge (<i>Alectoris rufa</i>)	2	V	159
Quail (<i>Coturnix coturnix</i>)	3	V	123
Short-toed lark (<i>Calandrella brachydactyla</i>)	3	V	13
Thekla lark (<i>Galerida theklae</i>)	3	V	68
Montagu's harrier (<i>Circus pygargus</i>) ^c	4	S	14
Little bustard (<i>Tetrax tetrax</i>) ^c	2	V	39
Stone curlew (<i>Burhinus oedecmus</i>) ^c	3	V	67
Roller (<i>Coracias garrulus</i>) ^c	2	D	15
Calandra lark (<i>Melanocorypha calandra</i>) ^c	3	D	22
Black-bellied sandgrouse (<i>Pterocles orientalis</i>) ^d	3	V	1
Pin-tailed sandgrouse (<i>Pterocles alchata</i>) ^d	3	E	0
Dupont's lark (<i>Chersophilus duponti</i>) ^d	3	D	0
Lesser kestrel (<i>Falco naumanni</i>) ^d	1	V	1

^aSPEC category according to Tucker and Heath 1994. ^bEuropean Conservation Status according to Tucker and Heath 1994. ^cIndicator species of high-quality steppe habitat (see Methods). ^dSpecies for which a low number of presence squares prevented habitat modelling.

area (Blondel and Aronson 1999), where rapid transformation of agricultural practices occurs (Lavorel et al. 1998) in areas hosting many bird species of high conservation value and sensitivity to land use changes (Rocamora 1997). Among these are steppe and pseudosteppe species which have their European strongholds in the Mediterranean (Table 1), especially in the semiarid 'páramos' and in cereal steppes (extensive cereal farmland; Suárez et al. 1997; Tucker 1997).

Research conducted in several Spanish areas indicates that most populations of steppe birds may be declining in response to several factors (Tucker 1997), including habitat alteration and land transformation associated with the intensification of traditional agricultural practices (Suárez et al. 1997). Some of these species encounter their northeastern distribution boundary in Catalonia (northeastern Spain) within the Iberian Peninsula. Due to their location near the edge of their species ranges, these populations may be more sensitive to habitat alteration or modification, and their disappearance may lead to irreversible shrinking of the distributional range (Gaston and Blackburn 2002). In response to the decline of several steppe birds in Catalonia (Estrada and Curcó 1991), several studies have recently focused on their current distribution (Estrada et al. 1996; Mañosa et al. 1996). These studies indicated that population strongholds concentrate in the Catalan Ebro basin, in areas where several irrigation schemes are to be developed in the coming years (DARP 1999), raising the question of their impact on the survival of this group of birds in the region.

Although previous studies associate these birds with extensive habitat use (Mañosa et al. 1996; Delgado and Moreira 2000), a quantitative prediction of the

effects of large scale transformation of agricultural landscapes by irrigation on the regional distribution of steppe birds has never been attempted (but see Osborne et al. 2001; Suárez-Seoane et al. 2002). Habitat modelling of species distribution is a convenient methodology (Guisan and Zimmerman 2000) to assess the suitability of different locations to host focal species according to the prevailing environmental characteristics. Habitat suitability models (HSM) require simultaneous consideration of information on the current distribution of species within a given area and information on land uses or other environmental variables where the species are present or absent. Both sorts of information are now available in Catalonia thanks to the Catalan Breeding Bird Atlas project (CBBA, 1999–2002), and to the development of large scale Geographical Information Systems (GIS) (Ninyerola et al. 2000; Viñas and Baulies 1995). Furthermore, since HSM establish direct links between probability of species occurrence and environmental features of locations within the studied area, these models allow the assessment of changes in species distribution under different scenarios of land use change. This may be done by developing HSM and using predicted habitat changes under such scenarios to predict future species distribution. This methodology enables the quantitative assessment of the effect of irrigation schemes on steppe bird species distribution, and thus offers a management tool to minimise such impact by identifying areas most likely to be affected by land use changes.

We apply HSM to the available environmental data sets, including land use and relief GIS layers, to model current steppe bird distribution in the cereal steppes of the Catalan Ebro basin (Lleida plain). We then employ HSM to assess the future impact of changes in land use on the potential distribution range of these species in the area under two scenarios of land transformation following irrigation of present extensive cereal steppes.

Methods

Study area

The study area is located in the northwestern Iberian Peninsula, within the Catalan Ebro basin. It covers the whole of the Lleida plain north of river Ebro and south of the Pre-Pyrenees and neighbouring areas (approximately 5200 km²) at an altitude ranging between 120 and 500 m (Figure 1). Forested areas are only found at the edges of the study area in the limits with the surrounding mountain chains (Figure 2). The Lleida plain is little but homogeneously inhabited. It is mainly covered by various croplands. Due to the relatively dry conditions prevailing in the area (low annual rainfall, from 325 to 500 mm, with very dry summers), extensive cereal crops occupied most of the plain until recently. However, starting after the mid-19th century and consolidating during the 20th century, different irrigation projects have progressively transformed agricultural practices in the lower parts of the Lleida plain, which at present is largely dominated by intensive agriculture

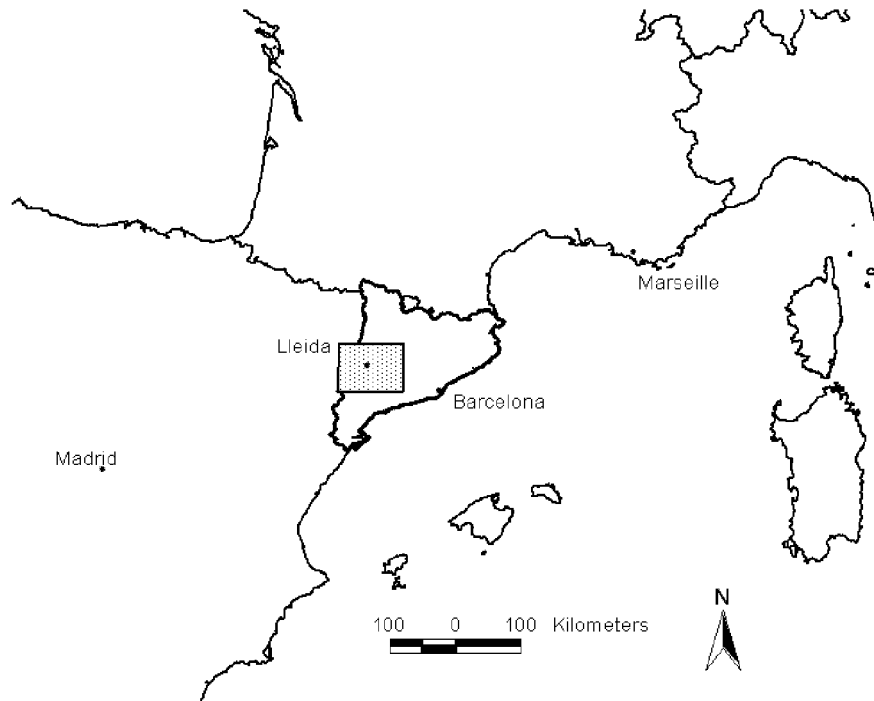


Figure 1. Location of the Lleida plain (dotted square) in the northwest of the Mediterranean basin.

(Figure 2). Irrigated lands grow a large variety of crops ranging from herbaceous crops (dominated by fodder crops) to corn and fruit trees. Non-irrigated agriculture is dominated by almond and olive trees in the south of the plain and extensive cereal crops and fallows in the east of the plain. Large patches of the latter are found also to the north and south of the irrigated areas (Table 1). Extensive cereal crops occupy at present about 37% of the Lleida plain.

Study species

We selected for this study a set of 13 steppe birds (Table 1), including species associated with or more abundant in areas with steppe-like vegetation and/or dominated by extensive cereal agricultural practices in Catalonia (Estrada et al. 1996). Among these, four species were not used in the large scale habitat suitability analyses due to their rarity and subsequent low sample size (Table 1). From the remaining nine species we selected, as the most convenient indicators of suitable steppe-like habitat in the study region, five species with their current distributional range in Catalonia concentrated within the Lleida plain (more than 80% of the total Catalan population): the Montagu's harrier (*Circus pygargus*), the Little bustard (*Tetrax tetrax*), the Stone curlew (*Burhinus oedipus*), the Roller (*Coracias garrulus*) and the Calandra lark (*Melanocorypha calandra*). These species have been considered

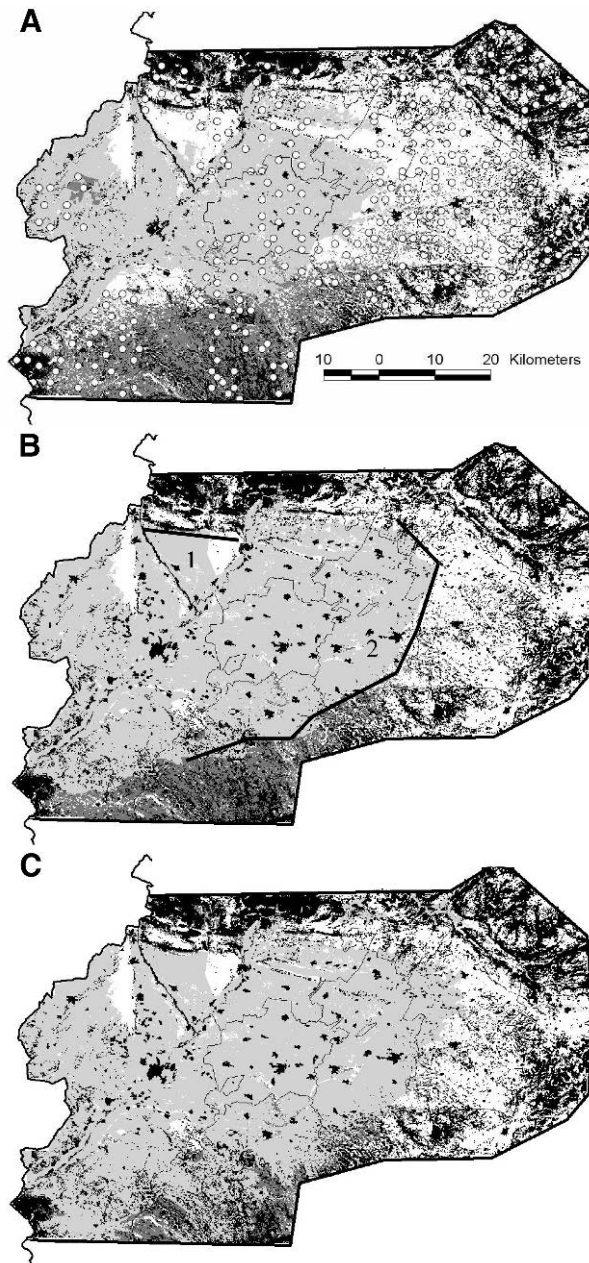


Figure 2. Present (year 1997) main land uses within the Lleida plain (A) and predicted in two scenarios of increasing extent of irrigation practices (B and C). White areas represent dry herbaceous crops, mainly cereals. Dark grey represents dry arboreal crops dominated by olive trees and almonds. Light grey represents irrigated areas both of herbaceous and arboreal nature. Black areas represent forests, shrublands and urban areas all completely unsuitable to steppe birds. In (A) empty circles represent locations of 1×1 km squares in which bird occurrence was assessed. In (B) thick black lines show approximate locations of planned irrigation channels, Algerri-Balaguer (1) and Segarra-Garrigues (2).

in previous studies (Estrada et al. 1996) as representative of steppe-like habitat due to their habitat needs closely associated with high-quality cereal steppe (Mañosa et al. 1996). Furthermore, these species are of conservation concern in Catalonia and their present populations are abundant and widespread enough to allow critical assessment of future changes (Estrada et al. 1996).

Bird data

Data on species occurrence was obtained from the Catalan Breeding Bird Atlas (CBBA, 1999–2002, in preparation). The CBBA is a large-scale survey that covers the entire Catalan region (31 000 km²), and maps the distribution of breeding birds in Catalonia. Within our study area (Figure 2), 313 squares of 1×1 km had available data (equivalent to about 6% of the study area) obtained from standardised surveys of species presence during the breeding seasons 1999–2001. Squares were selected by volunteers in a stratified manner, given the premise that they should representatively cover the main habitat types present in the 10×10 km Universal Transverse Mercator grid square in which they were located. On each selected square, two 1-h visits were conducted and except for those individuals flying over the square at high altitudes, the presence of any species detected either visually or by sound was noted. The non-detection of the species was considered as an indicator of absence or very low density of the species in the sampled square. The first visit was made in March–April and the second during May–June to better cover the breeding phenology span of different species.

Environmental data

Environmental variables (ENV) were generated from environmental information available as GIS layers. Habitat composition and distribution were analysed from land-use rasters generated by the Cartographic Institute of Catalonia (ICC; Table 2). The land use raster of ICC was based on spectral TM images obtained by satellite Landsat 5 during 1997 (Viñas and Baulies 1995). After successive processes of simplification and classification, the definitive raster maps were resampled to 50 m pixels and converted to several Boolean maps according to the different habitat categories used (Table 2). Then we calculated the number of pixels within each square as the value describing the amount of a given habitat present. We also calculated distance of pixels to selected landscape features (cities > 10 000 people, cities < 10 000 people, roads, and forests) and calculated the mean value for all pixels in each square. We also described habitat heterogeneity within each square by using the Shannon diversity index for land use cover categories (Table 2). Before calculation of this index, all urban categories (industrial, roads and urban) were re-assigned to the same category.

Climatic variables (temperature, precipitation and solar radiation) were obtained from the Catalan Digital Atlas (CDA; Ninyerola et al. 2000). Climatic layers were generated by a climatic model using a network of weather stations in Catalonia (257 stations for precipitation and 160 for temperatures). To obtain a value for each

Table 2. Environmental variables (ENV) used to generate habitat suitability models of bird species. Unless otherwise mentioned, variables referring to 1x1 km squares correspond to means obtained from averaging individual values from pixels contained in each 1x1 km square (see Methods for further details). Cartographic sources are indicated when necessary.

Descriptor type	Environmental variables	Source	Variable description	Range of values (n=313)
Land use	Dfor	Land use map (ICC) ^a	Distance to nearest forest patch (m) $\log(x+1)$ transformed	0–10
	Dyrcrop	Land use map (ICC)	Number of dry herbaceous cropland pixels (cereals) in 1x1 km squares	0–400
	Irricrop	Land use map (ICC)	Number of irrigated herbaceous cropland pixels (corn) in 1x1 km squares	0–400
	Dyarb	Land use map (ICC)	Number of dry arboreal cropland (olive tree, almond) pixels in 1x1 km squares	0–400
	Irriarb	Land use map (ICC)	Number of irrigated arboreal cropland (fruit trees) pixels in 1x1 km squares	0–390
	Scrub	Land use map (ICC)	Number of scrub pixels in 1x1 km squares	0–400
Landscape	Divland	Land use map (ICC)	Shannon diversity index of land uses in 1x1 km squares (based on land use cover 1997, urban and industrial categories clumped)	0–1.90
	Dcity	Urbanised areas map (DMA) ^b	Distance to cities >10,000 h (m) $\log(x+1)$ transformed	0–11
Human impact	Infrast	Land use map (ICC)	Number of infrastructure (transport network and urban areas) pixels in 1x1 km squares	0–390
	Droad1 Droad2	Primary road network map (ICC) Secondary road network map (ICC)	Distance to main roads of the primary road network (m) $\log(x+1)$ transformed Distance to roads of the secondary road network (m) $\log(x+1)$ transformed	0–10 0–10
Climate	Insol	Digital climatic atlas (CREAF) ^c	Mean solar radiation ($10 \text{ kJ}^{-1} \cdot \text{m}^{-2} \cdot \text{day}^{-1} \cdot \mu\text{m}^{-1}$)	120–810
	SummP	Digital climatic atlas (CREAF)	Mean accumulated summer precipitation (June–September) (l/m^2)	50–500
	WinP ^d	Digital climatic atlas (CREAF)	Mean accumulated annual precipitation (l/m^2)	350–1562
	AnuT ^d	Digital climatic atlas (CREAF)	Mean accumulation of mean annual temperatures (degrees)	1–170
	WinT	Digital climatic atlas (CREAF)	Mean accumulation of mean winter temperatures (December–March) (degrees)	–50–105
	SummT ^d	Digital climatic atlas (CREAF)	Mean accumulation of mean summer temperatures (June–September) (degrees)	70–250
Relief	Mde	Digital elevation model (ICC)	Mean altitude (m)	25–540
	Slope	Digital elevation model (ICC)	Mean slope	0–39

^aInstitut Cartogràfic de Catalunya. ^bDepartament de Medi Ambient de la Generalitat de Catalunya. ^cCentre de Recerca Ecològica i Aplicacions Forestals. ^dVariables not included in HSM models due to high correlations with other variables (>0.70).

square we calculated the mean value for all pixels (200 m side) in that square (Table 2). Data on relief of the study area were obtained from a Digital Elevation Model (DEM) generated by the ICC from topographic 1:50 000 maps. The DEM was used to calculate the mean altitude of each square and its mean slope value (Table 2).

Correlation analysis between all environmental variables allowed selecting the best set of predictors. To reduce collinearity between predictors and to make model interpretation easier, we identified variables which were highly correlated ($r > 0.7$) and eliminated those with an *a priori* more indirect relationship with species ecology. Elimination of correlated variables was also directed at minimising the number of ENV in the initial HSM (Table 2). The final number of environmental variables included in model selection was 16.

Land use change scenarios

The most important landscape change predicted to impact the Lleida plain in the near future is the extension of irrigated agriculture at the expense of extensive cereal areas (DARP 1999). In particular, new irrigation channels (i.e. Segarra-Garrigues channel, Algerri-Balaguer channel, Figure 2) aim at converting extensive cereal crops adjacent to the plain centre (already irrigated) into intensive agriculture. Given that the location of these channels and their future areas of influence are known, it is possible to model possible impacts of predicted landscape transformation in the Lleida plain with high spatial accuracy. Water from irrigation channels is optimally used downslope (optimal irrigation areas), whereas upslope water can only be used as support irrigation. The latter areas do not have priority in the irrigation plans. We therefore developed two different scenarios of landscape change in the study area in relation to irrigation plans. Scenario 1 assumed that only optimal areas downslope of the irrigation channels are irrigated. In this scenario, we reclassified all pixels corresponding to dry herbaceous crops and arboreal dry crops within the area of predicted change to irrigated herbaceous crops and irrigated arboreal crops, respectively, thus simulating current changes in land use associated with irrigation (Figure 2). Our scenario 2 assumed that all area potentially irrigated by future channels (either partially or completely, both up- and downslope) undergoes landscape transformation of dry, arboreal and herbaceous crops (Figure 2). All currently protected areas within the region affected by future irrigation plans or expected to be so in the near future were considered not to change in any of the two scenarios.

Whereas irrigated herbaceous crops often substitute dry herbaceous crops once water is available, other types of crops involving stronger changes in vegetation structure may also occur (i.e. irrigated fruit trees). Given that an increase in vegetation development is negatively associated with habitat quality for steppe birds, in the absence of a more detailed description of final crop distribution in the irrigation areas, our models of landscape change represent conservative scenarios of land use changes. Both scenarios of land use transformation assume that all dry herbaceous and arboreal crops within the irrigable areas are indeed converted to

irrigation. We think that this is a justified assumption of our landscape models, because the present landscape structure (year 1997) within the centre of the Lleida plain clearly suggests that all potential irrigation areas are effectively transformed to intensive agriculture (see Figure 2).

Statistical models

We developed models for all species from which we obtained presence in at least 10 of the 1×1 km squares available for analysis. To analyse binary data such as the presence/absence of species within each square, we applied linear regression techniques with binomial error distribution (Generalized linear models, GLM; Crawley 1993). We included in initial models all linear and second order terms for all the predictor variables utilised. To select the most parsimonious model, we used an automatic stepwise model selection procedure. The 'step.glm' function in S-Plus builds models by adding new terms and investigating how much they improve the fit, and by dropping terms that do not degrade the fit by a significant amount (Anonymous 1999). The statistic used to improve the fit was the Akaike Criteria Information (AIC) selection criterion (Chamber and Hastie 1997).

Results of GLM models were assessed across the full range of possible cut-off points using receiver operating characteristic (ROC) plots (Fielding and Bell 1997). A ROC plot depicts on the y-axis sensitivity (percentage of true presences correctly predicted) against 1-specificity (1-percentage of true absences correctly predicted). The area under the ROC curve (AUC) is a convenient measure of overall fit and varies between 0.5 (for chance performance) and 1 (perfect fit). We obtained AUC and its standard error using S-Plus software.

To represent current potential species distribution, false negatives (absences wrongly predicted as presences) and false positives (presences wrongly predicted as absences) are both important. Therefore, we chose the cut-off point to separate suitable from unsuitable habitat that minimises these two proportions (Fielding and Bell 1997). While this objective method is preferred over more arbitrary threshold choices (i.e. 0.5), the threshold values optimised by ROC tend to overestimate true occurrences among scarcer organisms (Manel et al. 2001). For conservation studies in which the goal is to delimit the range of threatened species, a liberal modelling threshold is necessary to minimize the percentage of false negative errors. In order to include the maximal amount of the potential range of the species studied, but control for overestimates in the total amount of suitable habitat, we calculated the effective surface of suitable habitat for each species by summing up the areas of all squares with values above the ROC threshold and using the estimated probability of occurrence for each square as a correction factor. Thus, squares within the estimated range but with low probabilities of occurrence contributed less to the total amount of suitable habitat for a given species. We calculated combined species maps by summing up predicted presences for each species using the specific cut-offs based on the ROC (see Suárez-Seoane et al. (2002) for a similar approach).

The amount of habitat suitable for each species under different scenarios of landscape transformation was generated by using the obtained GLM models and

applying them to the modified predictors (dry crops and irrigated crops variables) as calculated from the corresponding land use GIS layers in each of the two scenarios.

Results

We were able to perform GLM models on nine of the species included in the study (Table 1). From all the modelled species, GLM performed consistently better than random (AUC significantly higher than 0.5 in all cases; Table 3). Model accuracy ranged from good (AUC between 0.75–0.9; Partridge, Quail, Stone curlew, Short-toed lark, Montagu's harrier and Thekla lark) to excellent (AUC between 0.9–1; Calandra lark, Roller and Little bustard).

Role of environmental variables

Presence of dry herbaceous crops (Drycrop) was the most important environmental predictor for the presence of the species studied. All species, except the Stone curlew, the Thekla lark and the Short-toed lark, were positively associated with the presence of extensive dry crops in the squares (Table 3). Among the species for which the best models did not include Drycrop, Thekla lark presence was negatively associated with the amount of irrigated herbaceous crops, whereas the Stone curlew and the Short-toed lark were not associated with the amount of any herbaceous crop category. Only the presence of the Quail was to some extent positively associated with the presence of irrigated herbaceous crops (Table 3).

From the other land use variables included as possible predictors of bird distribution, forest distribution tended to negatively influence occurrence in the studied species. Four species (Stone curlew, Short-toed lark, Thekla lark and Partridge) decreased their occurrence near forested areas (Table 3). Other habitat variables were not strong predictors of species occurrence and only the amount of scrub was positively associated with the presence of the Thekla lark and the Little bustard; dry arboreal crops were negatively associated with the presence of the Stone Curlew and the Quail; and land diversity was negatively related with presence of Thekla and Short-toed lark (Table 3).

Relief variables were also important predictors, with elevation and slope being included in the final best models of five and three species, respectively. Elevation tended to negatively influence species occurrence (Partridge, Little bustard and Roller), suggesting lower relative suitability values for higher elevation (Table 3). Slope showed a consistent pattern for all species, including four of the five indicator steppe species (Montagu's harrier, Little bustard, Stone curlew and Calandra lark), their occurrence being more likely in flat areas (Table 3).

Variables related to human activity only appeared in four of the final models and tended to have a negative influence on the species distribution. Occurrence probability increased far from main cities for the Short-toed lark or in areas with low

Table 3. Results of best GLMs explaining species occurrence in the Lleida plain. Only the five more significant variables as judged by changes in deviance and the signs of their coefficients are shown for each species. Variables were selected using a stepwise method (see Methods for procedures on variable selection). Significant second order polynomials are identified by the term 'pol' followed by the sign of the overall effect. # indicates a strong bell-shaped response without a clear linear effect. See Table 1 for details on environmental variables.

	Null model χ^2 , df	Final model χ^2 , df	Variables in final model Total number	Main variables	Model accuracy AUC \pm S.E.
Red-legged partridge (<i>Alectoris rufa</i>)	433.83, 312	346.21, 303	6	Drycrop (+), pol(Mde-), pol(SummP+), pol(Dfore+), pol(Infras-)	0.79 \pm 0.025
Quail (<i>Coturnix coturnix</i>)	419.46, 312	319.67, 303	6	pol(Drycrop+), pol(Irricrop+), SummP(+), Slope(-), Dryarb(-)	0.81 \pm 0.024
Short-toed lark (<i>Catalandrella brachydaetyla</i>)	108.17, 312	89.63, 308	3	pol(Dfor) (+), Divland(-), Dcity(+)	0.81 \pm 0.050
Thekla lark (<i>Galerida theklae</i>)	327.65, 312	261.79, 306	5	pol(Dfore+), Irricrop(-), SummP(-), Scrub(+), Divland(-)	0.80 \pm 0.027
Montagu's harrier (<i>Circus pygargus</i>)	101.81, 312	74.26, 307	3	pol(Drycrop+), pol(Slope-), WinT(-)	0.88 \pm 0.041
Little bustard (<i>Tetrax tetrax</i>)	235.37, 312	101.44, 308	5	pol(Drycrop+), pol(Slope-), pol(Dcity#), pol(Scrub+), pol(SummP#)	0.96 \pm 0.012
Stone curlew (<i>Burhinus oedipus</i>)	325.07, 312	247.86, 304	7	pol(Slope-), Mde(-), Infras(-), Dryarb(-), Dfore(+)	0.83 \pm 0.025
Roller (<i>Coracias garrulus</i>)	120.41, 312	84.57, 308	3	pol(Mde-), Drycrop(+), WinT(+)	0.92 \pm 0.041
Calandra lark (<i>Melanocorypha calandra</i>)	159.24, 312	101.44, 308	2	pol(Drycrop+), pol(Slope-)	0.91 \pm 0.028

human settlement for the Red-legged partridge, the Little bustard and the Stone curlew (Table 3). Climate variables were selected in seven of the final models in a species idiosyncratic manner and never among the two most important variables, suggesting a secondary, smoothing role in predicting steppe species distribution once habitat and relief variables are already included in the models (Table 3).

Species distribution in the Lleida plain

As indicated by GLM models, distribution of steppe birds was strongly associated with extensive cereal crops in flat areas and greatly overlapped with the areas of the Lleida plain with this type of agriculture within the external limits of the main central basin (Figures 2A and 3A). Lower suitability areas, potentially hosting fewer indicator species, concentrated in irrigated areas in the centre of the plain and in the boundaries of the area (Figures 2A and 3A). High-quality areas (those with a probability of hosting two or more of the indicator steppe species) were limited to 14.5% of the total surface of the Lleida plain (Table 5), whereas core areas (areas with a probability of hosting more than three out of the five indicator steppe species) occupied only about 9.6%. High-quality areas for steppe birds were clearly different in terms of land use and environmental variables from other areas within the rest of the plain (Table 4). In particular, these areas had more dry extensive herbaceous crops than surrounding areas, and were scarcely occupied by other land uses such as irrigated crops or dry arboreal crops (Table 4). Urban density and land diversity within optimal areas was lower than in other areas of the Lleida plain. High-quality areas were also less abrupt (smaller slopes) than the surroundings (Table 4).

Landscape change scenarios and steppe bird distribution

Amount of dry herbaceous crops within the Lleida plain decreased from 193 000 ha (37% of the total area) in the present to estimated figures of 140 000 ha in scenario 1 (a 28% decrease) and 123 000 ha in scenario 2 (a 36% decrease). This decrease is concentrated in the central areas of the basin adjacent to current irrigated areas (Figure 2B). Concomitant increases in irrigated herbaceous crops will bring the total surface occupied by this type of crop from 108 000 ha (20.1% of the total surface of the basin) to estimates of 161 000 ha in scenario 1 and 178 000 ha in scenario 2 (respectively, 49 and 65% increase in the total surface of irrigated crops in relation to the present; Figure 2B and C).

Overall, predicted suitable areas for the nine steppe species modelled strongly decreased in the irrigation scenarios compared to the present distribution (Repeated measures ANOVA, $F_{1,8}=18.22$, $p < 0.01$, Table 5). A more detailed analysis of changes in the predicted range occurring within the nine species studied showed that whereas the decrease in species range occurring between the present distribution and scenario 1 was significant (*post hoc* Tukey test, $p < 0.01$), further decreases in suitable habitat between scenario 1 and scenario 2 were not significant (*post hoc* Tukey test, $p = 0.82$). High-quality areas for steppe birds within the Lleida plain

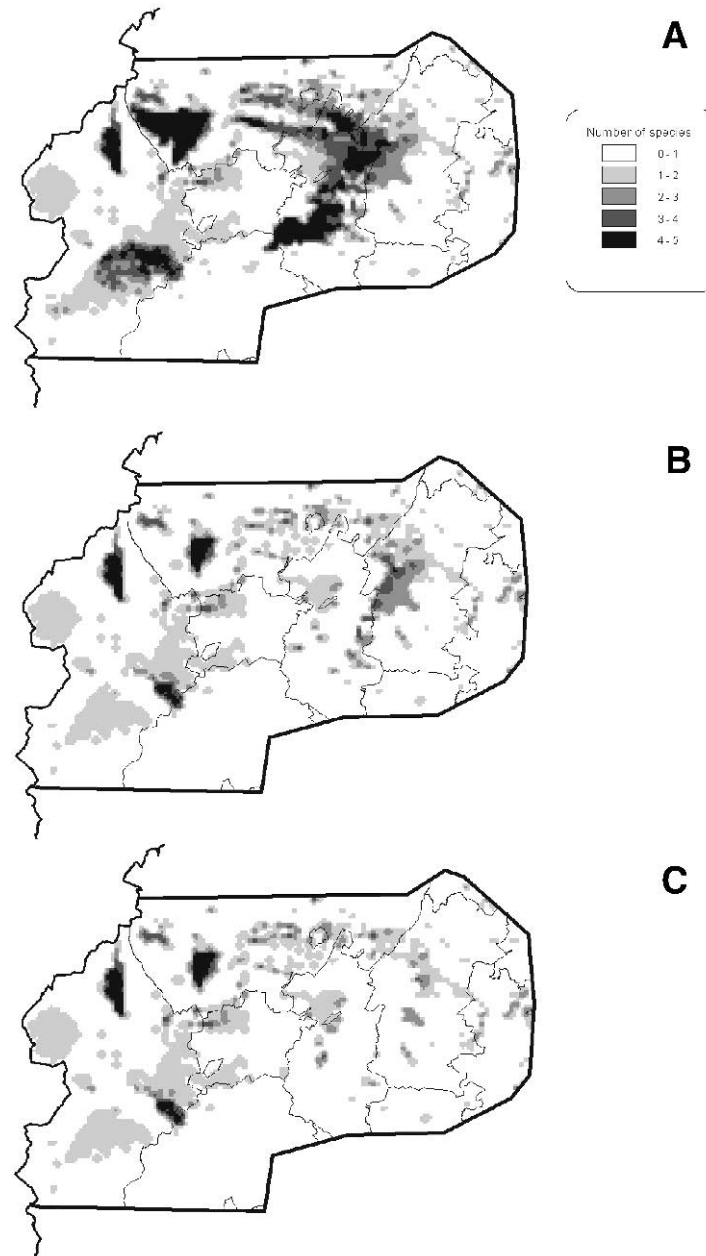


Figure 3. Spatial representation of the distribution of indicator steppe bird species in the Lleida plain (five species endangered in Catalonia: Montagu's harrier, Stone curlew, Little bustard, Roller and Callandra lark). Maps were calculated from the sum of predicted species occurrence as obtained from specific cut-off points on modelled probabilities of presence (see Methods). Maps were smoothed to the nearest neighbour for clarity of representation. We represent the present combined potential distribution of the five species (A) and the predicted distribution under two future landscape change scenarios (B and C; see Figure 2).

Table 4. Comparison of land use and relief variables (mean \pm S.E.) of core areas for steppe birds (those predicted to host more than three indicator species out of a total of five; Figure 2A) and the remainder of the study region. Core areas cover approximately 50 000 ha, approximately 11% of the region. Only variables selected among the three best predictors in GLM models are summarised. All comparisons are statistically significant at $p < 0.0001$.

	Core areas (n=542)	Other areas (n=4850)
Drycrop	333.62 \pm 79.13	120.22 \pm 126.42
Irricrop	19.75 \pm 56.46	86.11 \pm 135.21
Dryarb	17.88 \pm 33.01	53.93 \pm 98.50
Dfor	7.33 \pm 0.83	6.09 \pm 1.82
Divland	34.63 \pm 35.22	81.31 \pm 37.56
Dcity	9.16 \pm 0.54	9.53 \pm 0.69
Infras	2.52 \pm 13.23	8.87 \pm 30.12
Mde	168.12 \pm 44.95	197.78 \pm 98.14
Slope	2.04 \pm 0.97	4.57 \pm 3.30

Table 5. Effects of irrigation scenarios on the amount of potential suitable habitat of steppe and open habitat species (see Methods for details on calculations). Present: land use patterns in 1997. Scenario 1: land transformation occurs in optimal irrigation areas (areas located downslope of the irrigation channels). Scenario 2: irrigation areas reach their maximum (downslope + upslope of channel). For each species and land use scenario, we show the total estimated surface (ha) of suitable habitat and the percentage (%) of suitable habitat remaining in comparison to present estimates. Total area of the study region is 520 000 ha.

	Present	Scenario 1	Scenario 2
Red-legged partridge (<i>Alectoris rufa</i>)	193 000 ha	138 900 ha (72%)	131 240 ha (68%)
Quail (<i>Coturnix coturnix</i>)	154 000 ha	150 900 ha (98%)	149 400 ha (96%)
Short-toed lark (<i>Calandrella brachydactyla</i>)	34 300 ha	No change in area	No change in area
Thekla lark (<i>Galerida theklae</i>)	85 800 ha	71 200 ha (83%)	63 500 ha (74%)
Montagu's harrier (<i>Circus pygargus</i>)	26 450 ha	12 100 ha (46%)	10 250 ha (39%)
Little bustard (<i>Tetrax tetrax</i>)	51 200 ha	20 100 ha (39%)	15 500 ha (30%)
Stone curlew (<i>Burhinus oedicmus</i>)	129 900 ha	No change in area	No change in area
Roller (<i>Coracias garrulus</i>)	22 900 ha	9300 ha (41%)	8250 ha (36%)
Calandra lark (<i>Melanocorypha calandra</i>)	33 100 ha	14 950 ha (45%)	11 600 ha (35%)
High-quality areas ^a	75 800 ha	28 675 ha (38%)	21 275 ha (28%)
Core areas ^b	50 000 ha	12 250 ha (24%)	9750 ha (19%)

^aMore than two species predicted out of the five indicator steppe species. ^bMore than three species predicted out of the five indicator steppe species.

dropped by more than 60% from the present situation to scenario 1 (Figure 3B), whereas a further 10% decrease was detected from scenario 1 to scenario 2 (Figure 3B and C; Table 5). The reduction of core area extent for steppe species was even larger, about 76% in scenario 1 and about 81% in scenario 2 (Figure 3B and C).

The species whose potential distributions were predicted to experience smaller changes were the Quail, Short-toed lark and Stone curlew (Table 5). On the other side of predicted effect, Montagu's harrier, Little bustard, Roller and Calandra's lark

showed decreases in their potential distribution ranging from 54–61% of the initial suitable areas in scenario 1, to 61–70% in scenario 2 (Table 5). Moderate effects of irrigation were detected for Partridge and Thekla lark, which showed decreases in their suitable area of about 17–32% compared to present land use patterns (Table 5).

Discussion

Extensive agriculture and steppe birds

We have shown that environmental habitat modelling is a useful tool to map suitable habitat for steppe bird species and that projection of future habitat availability estimated under different scenarios of landscape transformation may provide critical quantitative information of predicted changes in species distribution (Guisan and Zimmerman 2000). In particular, the analyses conducted in the Lleida plain have confirmed the close associations between steppe bird distribution and the current extent of extensive cereal agriculture previously found by Mañosa et al. (1996). Considering the five indicator species, current suitable habitats extend over 4–10% of the total surface of the Lleida plain (with the exception of the Stone Curlew, which extends over 24% of the region). However, not all dry cereal areas appeared equally suitable for steppe birds in the Lleida plain. Our results indicate a concentration of high-quality habitats for these species in the remaining flat, extensive cereal areas located in the centre of the plain, whereas at the edges, where relief is more abrupt and forest cover more important, species occurrences were scarcer (Figure 3). The habitat models show that the current distribution of species such as the Little bustard, the Montagu's harrier or the Calandra lark is highly restricted to cereal crops in the flattest area, suggesting that the same habitat in more sloping areas should be considered as low-quality habitat for many steppe birds. Possible reasons are an increase in perceived predation risk in areas with reduced visibility resulting from the undulating relief (Ferns and Hinsley 1995). Overall, a more abrupt relief is also associated with an increase in the occurrence of habitats such as forest patches or shrubs, which are avoided by steppe birds. While a mosaic of different herbaceous habitats has been shown to benefit several steppe species (Salamolard et al. 1996; Wolff et al. 2001), a mosaic of suitable and unsuitable habitats at small spatial scales may be a landscape of poor value for steppe birds.

Although it is expected that most species closely associated with extensive dry cereal crops suffer most from intensification of agriculture practices (Tella et al. 1998), an expectation confirmed by our analysis, a few species such as the Stone curlew and, to a large extent, the Quail were predicted to occupy areas currently devoted to irrigated crops as well as those with extensive cereal areas. The Stone curlew is known to occupy irrigated agriculture areas provided that small patches of stubble or uncultivated land are maintained (Salamolard et al. 1996), whereas the Quail is present at lower densities in intensive agriculture compared to dry areas, provided that cereal crops are available (Mañosa et al. 1996).

Future effects of irrigation schemes on steppe birds

Our results show that the transformation of extensive cereal agricultural areas to irrigation will have a critical impact on steppe birds by reducing the amount of suitable habitat available. While keeping in mind that estimates of habitat availability derived from HSM are merely probabilistic (Guisan and Zimmerman 2000), high-quality and core areas for steppe birds are expected to decrease by 62 to 76% in the most conservative scenario and reach up to 81% in the more liberal one. Such large decreases in suitable steppe habitat are associated with more limited reductions in the surface of extensive cereal areas, ranging from 28% to 36% depending on the scenario considered. While our results on the impact of future irrigation scenarios showed that the critical impact on steppe habitat for birds will occur if priority areas for irrigation are transformed (scenario 1), a further increase in transformed land (scenario 2) is predicted to induce further habitat losses proportional to the dry cereal areas transformed. This would strengthen the conflict of interests between optimal irrigation areas and high-quality habitat areas for steppe bird conservation. Thus, the predicted overlap between future irrigation plans and current distribution of high-quality habitats for steppe birds in Catalonia poses a critical conservation threat to this group in terms of habitat loss, reaching up to 81% of current core areas. These results are in line with previous data suggesting that the progressive decrease in the populations of many steppe land species is strongly associated with the intensification of agriculture practices, in particular transformation of extensive cereal steppes to irrigated crops (Salamolard et al. 1996; Tucker 1997). The predicted impact may be even stronger, as some affected areas appear to be key habitats for some species in terms of individual abundance or because of particular ecological needs of the species. Although probability of occurrence and abundance are often correlated (Osborne et al. 2001), our HSM models based on presence-absence data are not adequate to unambiguously identify areas of very high individual density (i.e. key habitat types for species survival). However, the detailed specific local scale studies conducted within the study area found very high densities of species such as Little bustard, Montagu's harrier or Calandra Lark (Estrada et al. 1996) in the areas where our models predict the highest probability of occurrence. This suggests that in our study both variables might be closely associated. However, local abundance is not always an appropriate absolute indicator of habitat suitability. This might be the case, for instance, if large asymmetries in the reproductive value of individuals occur. In the case of lekking-like species such as the Little bustard, female density is a key factor driving population dynamics (Jiguet et al. 2002) and thus, local scale demographic studies are essential to finally identify most convenient areas for conservation.

In addition to the loss of suitable habitat predicted by the irrigation scenarios, fragmentation of remaining extensive cereal steppe will significantly increase. Compared to the present situation, this habitat within the Lleida plain will be reduced to highly isolated patches at larger distances from each other in future land use scenarios (Figure 2). Fragmentation may decrease the suitability of remaining habitat patches independently of pure habitat loss (Fahrig 2001). Among the indi-

rect ecological processes associated with habitat fragmentation and known to affect populations of steppe birds, we can mention the increased importance of negative edge effects, which may lead to increased nest predation rates due to predators inhabiting surrounding habitats (Suárez et al. 1993) and the increased difficulties in the exchange of individuals between populations, which can lead to higher probabilities of local extinction (Lane et al. 2001).

The Catalan population sizes of some of the steppe species analysed are comparable to those found in countries like France or Italy, where the species are under strict active management measures (Estrada et al. 1996). Furthermore, in some cases, the Catalan populations function as a link between the main population strongholds in the Iberian Peninsula and the French populations, where some of these species are suffering a marked decline in recent years (Jolivet 1996). Therefore, a large scale loss in potential habitat predicted for these species (i.e. Little bustard, Calandra's lark) in Catalonia could represent a significant threat to the species population from a European perspective (Tucker and Heath 1994). Furthermore, current populations of steppe species which we could not model due to inadequate sample size fall well within the areas identified as high-quality areas for steppe birds (Black-bellied sandgrouse (*Pterocles orientalis*), Pin-tailed sandgrouse (*Pterocles alchata*), Dupont's lark (*Chersophilus duponti*), Lesser Kestrel (*Falco naumanni*); Estrada et al. 1996). This further increases the conservation value of these areas and the threat posed by future irrigation schemes to steppe-like habitats in the Lleida plain.

Management of steppe birds and agricultural policy

In spite of the fact that steppe-like habitats are among those with higher conservation concern in Catalonia, only 5994 ha of the 76 000 (8%) steppe-like suitable areas (Table 5) are given some kind of protection, which is far from the 20.1% of overall protected land in Catalonia. Only 1.1% of all protected land in Catalonia involves steppe-like habitats (DMA 1996). This is because the establishment of protected areas in agricultural land does not generate social interest, and economic conflicts arise between the agricultural sector and the maintenance of large tracts of protected areas (Suárez et al. 1997; Beaufoy 1998). However, the large overlap between future irrigation areas and current steppe bird distribution, in combination with the predicted strong negative impact of irrigation schemes on this distribution, suggests that if one is to preserve viable populations for the species considered, conservation measures will have to set aside from irrigation the areas of extensive cereal steppe identified as core habitats. This can be achieved by devising a network of protected areas where agri-environmental measures are implemented to prevent habitat alteration and to encourage sensitive habitat conservation and farming management, which maintain extensive agriculture practices (Bignal and McCracken 1996; Tella et al. 1998). This can be achieved with the help, for example, of the agri-environmental measures designed by The Common Agricultural Policy (CAP) promoting the incorporation of economic incentives aimed at enhancing biological diversity in farmland systems (EU regulation 2078/92). Projected

changes in the CAP will further stress the biodiversity values and limit direct subsidies to crop production, thus reducing economic advantages of intensive agriculture. These changes in the CAP may be among the last opportunities for many extensive agriculture systems in Europe, such as the steppe habitats of Catalonia, to survive the current tendencies in agriculture intensification.

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