



## Effects of changed grazing regimes and habitat fragmentation on Mediterranean grassland birds

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### ARTICLE INFO

#### Article history:

Received 15 October 2009

Received in revised form 17 March 2010

Accepted 18 March 2010

Available online 18 April 2010

#### Keywords:

Agri-environment schemes

CAP reform

Cereal-steppe

Conservation

Decoupling

Farmland birds

### ABSTRACT

In Iberian cereal-steppes, decoupling of payments from current production levels through the Single Farm Payment raised concerns regarding the potential for land abandonment and replacement of sheep by cattle, with eventual negative consequences for declining grassland birds. This study addressed this issue by analysing the responses of five grassland bird species of conservation concern to spatial land use gradients, which are expected to reflect changes potentially associated with the CAP reform. Our results show that both habitat fragmentation and grazing regimes were major drivers of breeding bird densities, though responses to these factors were species-specific. Thekla larks were most abundant in landscapes with small grassland patches and high edge density, whereas calandra larks were abundant only in large expanses of continuous open farmland habitat. Little bustard and short-toed lark densities declined in highly fragmented landscapes, but they appeared to tolerate or even benefit from low to moderate levels of open habitat fragmentation. Corn buntings were little affected by landscape patterns. At the field scale, little bustard and corn bunting densities were highest in fields grazed by cattle, whereas short-toed larks were mostly associated with sheep pastures. Short-toed larks and Thekla larks were most abundant in old fallow fields where cattle was largely absent, whereas corn buntings showed the inverse pattern. These results confirm the view that the same agricultural policies may be favourable for some species of conservation concern but detrimental to others, and so they cannot be assumed to bring uniform conservation benefits.

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### 1. Introduction

The introduction of the Single Farm Payment, and the associated decoupling of payments from current production levels, is one aspect of CAP (Common Agricultural Policy) reform with the potential for determining major land use changes in marginal farming areas (Oñate et al., 2007; Tranter et al., 2007; Stoate et al., 2009). There is a risk that decoupling of crop payments may promote abandonment of low-income farming systems (Oñate et al., 2007; Tranter et al., 2007), particularly where the added costs of cross-compliance requirements cannot be met by production increases (de Graaff et al., 2010). This might contribute to further losses and

fragmentation of farmland habitats, thereby maintaining the tendencies encouraged by past financial incentives such as European regulation 2080/92, which supported the afforestation of marginal agricultural land (Robson, 1997). Decoupling may also spread idling into areas of extensive production systems that were formerly carried out in order to receive livestock payments (Tranter et al., 2007). Further land use changes are expected from the possibility given to Member States for maintaining variable levels of coupled support to suckler cow, goat and sheep, which is likely to favour particular herbivore species depending on the level of coupled support retained in each country, as well as promoting shifts from crop to livestock production (Röder et al., 2008).

Iberian cereal-steppes cover over 4.5 million ha and are among the European farmland landscapes with the highest value for biodiversity conservation, mainly due to their importance for grassland birds (EEA, 2004; Bota et al., 2005). These are extensively farmed, mixed rotational systems of winter cereals, fodder crops and grazed fallow land and pastures, which are under increasing pressure from

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abandonment and intensification (Bota et al., 2005; Oñate et al., 2007). Fears have been expressed that the CAP reform will exacerbate these trends, due to a potential reduction of gross profit margins under the new CAP mechanisms and a derived risk of activity cessation (Oñate et al., 2007; Tranter et al., 2007). It is also possible that changes in livestock headage payments will affect pastoral regimes, fostering the decline of traditional systems of extensive sheep grazing and their eventual replacement by more rewarding cattle production systems (Serrão and Coelho, 2005; Tranter et al., 2007). There is thus an urgent need for understanding in detail the responses of cereal-steppe birds to these land use changes, in order to prevent undesired effects of the CAP reform.

In this study we examined variation in grassland bird breeding densities in relation to grazing regimes and the fragmentation of open agricultural land, across a spatial gradient ranging from intensive dry cereal cultivation to land abandonment, in cereal-steppes of Southern Portugal. The study focused on fallow land habitats because they tend to occupy a large proportion of the traditional cereal-steppe landscape, they are highly vulnerable to changing farming practices, and they are particularly important for grassland bird conservation (Delgado and Moreira, 2000; Moreira et al., 2005). Results were used to discuss the likely impact of land use changes resulting from CAP reform and to formulate recommendations for agri-environment schemes targeted at Mediterranean grassland birds.

## 2. Methods

The study was conducted in Southern Portugal, mostly within the Special Protection Area (SPA) of Castro Verde (85,000 ha). Climate is Mediterranean, with hot summers (averaging 24.2 °C in July), mild winters (averaging 9.3 °C in January), and more than 75% of annual rainfall (500–600 mm) concentrated in October–March. The landscape is flat or gently undulating (100–300 m a.s.l.) and is dominated by an open agricultural mosaic of cereal, fallow and ploughed fields, created by rotational dry cereal cultivation. From north to south there is a gradient of intensification–abandonment, associated with spatial variation in soil productivity. The northern part is flatter and soils more productive, and so the proportion of land cultivated each year is high and fallow fields are short-term (<3 years). In the south there is a mosaic of shrubland interspersed with old fallow fields (up to 10 years), as a result of agricultural abandonment and shrub encroachment. Finally, in the central part of the study area the cultivation of cereals is associated with medium to long rotations (2–5 years), and so grazed fallow fields predominantly occupy the arable land. Throughout the region there are holm oak (*Quercus rotundifolia*) pastoral woodlands of variable tree cover (*montados*). Forest plantations are increasing due to afforestation of abandoned arable land with umbrella pine (*Pinus pinea*) and holm and cork oaks (*Q. suber*). In part of the area there is an agri-environment subsidy scheme, whereby farmers are compensated for maintaining agricultural practices favouring bird conservation. Details of the study area are provided elsewhere (Moreira et al., 2007).

The study focused on the most abundant grassland bird species breeding in fallow fields of Castro Verde SPA (Moreira et al., 2007), all of which are species of European conservation concern (BirdLife International, 2004): little bustard *Tetrax tetrax*, calandra lark *Melanocorypha calandra*, short-toed lark *Calandrella brachydactyla*, Thekla lark *Galerida theklae*, and corn bunting *Emberiza calandra*. The distribution and abundance of these species at Castro Verde were recently described by Moreira et al. (2007): corn bunting was the most abundant species (ca. 16,000 pairs), showing the highest breeding densities in cereal fields; little bustards (ca. 4200 displaying males) and calandra larks (ca. 6200 pairs) were

also abundant, and they were strongly associated with fallow fields; short-toed larks (ca. 1500 pairs) were common in ploughed land and, to a lesser extent, in fallow fields, whereas Thekla larks (ca. 3700 pairs) occurred most often in grasslands interspersed with shrubs and trees.

### 2.1. Sampling design

Sampling was carried out on fallow fields selected within a 20 km × 30 km rectangle following the stratified random procedure described by Moreira et al. (2005), in order to cover the north–south spatial gradient of agricultural intensification–abandonment. A total of 49 fallow fields of approximately 10 ha each (mean = 9.4 ha ± 1.6 S.D., range: 5.5–13.6) were selected in 2000, with the constraints of just one field per farm and a minimum distance of 500 m between fields, to reduce eventual non-independence due to similarities in farm management and spatial autocorrelation. Long-abandoned fields (>20% cover by shrubs) and open oak woodlands (>5% cover by trees) were dropped from selection because they tend to be less used by steppe birds of conservation concern than open fields (Delgado and Moreira, 2000; Moreira et al., 2005). Due to logistical constraints, 36 fields were sampled in spring 2000 and another 13 in spring 2001. Sampling was repeated in 2004, using the same set of fields selected in 2000/01. However, part of these (19) had been ploughed or sown with cereals due to the normal rotation cycle, and so a new fallow field that met the initial criteria was selected at <500 m of each transformed field. In nine cases there were no fields meeting the selection criteria, and so sampling in 2004 was reduced to 40 sites and the remaining nine sites were discarded from further analysis.

### 2.2. Bird sampling

Bird sampling was based on the territory mapping technique (Bibby et al., 2000). Each field was counted six times, at about 2-w. intervals, from mid-March to mid-June. In each visit, the entire field was walked so that the observer approached to within 50 m or less of every point. All individuals were identified and recorded on detailed field maps (1:2000), where the position of marking poles and noteworthy topographical features (e.g., dirt tracks, stone piles and shrub patches) was depicted. Counts were always carried out within 4 h after sunrise and 2 h before sunset, with none in rainy or windy conditions. The number of breeding territories was estimated by compiling the information obtained in the six counts. Little bustard estimates refer to territorial males, because this species has a polygynous mating system (Traba et al., 2008). Sampling was carried out by five experienced ornithologists (AD, FM, LG, LR, RM) in 2000/01 and by a single one (LR) in 2004, but the estimate of breeding territories from field sketches of bird observations was always carried out by the same person (RM). This was considered adequate to enhance comparability across sites and over time, because the territory mapping technique is rather robust to variation in observer efficiency (Bibby et al., 2000), and because only five easily identified species were studied in an open landscape with unobstructed views.

### 2.3. Explanatory variables

Factors influencing bird densities were analyzed using two sets of explanatory variables, reflecting field management and landscape context. Variables were selected based on consideration of the existing literature on habitat associations of Mediterranean grassland birds (e.g., Bota et al., 2005; Serrano and Astrain, 2005; Reino et al., 2009; Morgado et al., 2010). Fields were characterized from six variables expressing the age and height of the herbaceous sward, the type and intensity of use by livestock, and the presence

**Table 1**

Description and summary statistics (mean  $\pm$  S.D.) of variables used to characterize fallow fields in Southern Portugal. Changes between sampling periods were evaluated using paired *t*-tests; ns –  $P > 0.05$ .

Variable (unit)	Description (transformation)	2000/01	2004	P
<b>Field variables</b>				
Age (years)	Time since last cultivation or ploughing ( $\text{Log}_{10}[X]$ )	1.9 $\pm$ 2.6	3.0 $\pm$ 2.2	ns
Sheep (animals/10 ha)	Average sheep density recorded across sampling visits ( $\text{Log}_{10}[X]$ )	49.2 $\pm$ 79.9	20.0 $\pm$ 3.31	<0.05
Cows (animals/10 ha)	Average cattle density recorded across sampling visits ( $\text{Log}_{10}[X]$ )	4.8 $\pm$ 16.7	2.5 $\pm$ 7.8	ns
Vegetation height (cm)	Mean height of herbaceous vegetation ( $\text{Log}_{10}[X]$ )	22.0 $\pm$ 9.4	16.5 $\pm$ 7.4	<0.001
Shrubs	Presence of shrubs	0.4 $\pm$ 0.5	0.5 $\pm$ 0.5	ns
Trees	Presence of trees	0.5 $\pm$ 0.5	0.5 $\pm$ 0.5	ns
<b>Landscape variables</b>				
Open farmland (%)	Percentage of area within 1-km radius with fallow and ploughed fields, pastures, cereal and other dry crops ( $\text{Asin}[\sqrt{p}]$ )	70.5 $\pm$ 23.8	70.5 $\pm$ 24.4	ns
Pastoral woodland (%)	Percentage area within 1-km radius with grazed open oak woodlands ( $\text{Asin}[\sqrt{p}]$ )	11.7 $\pm$ 21.4	10.3 $\pm$ 20.3	ns
Eucalyptus plantations (%)	Percentage of area within 1-km radius with eucalyptus plantations ( $\text{Asin}[\sqrt{p}]$ )	0.2 $\pm$ 1.1	0.3 $\pm$ 2.8	ns
Pine plantations (%)	Percentage of area within 1-km radius with pine plantations ( $\text{Asin}[\sqrt{p}]$ )	6.5 $\pm$ 10.8	6.5 $\pm$ 9.6	ns
Oak plantations (%)	Percentage of area within 1-km radius with oak plantations ( $\text{Asin}[\sqrt{p}]$ )	1.7 $\pm$ 5.2	3.2 $\pm$ 6.6	<0.05
Total forest plantations (%)	Percentage of area within 1-km radius with forest plantations ( $\text{Asin}[\sqrt{p}]$ )	8.9 $\pm$ 11.3	10.7 $\pm$ 12.7	<0.05
Shrubland (%)	Percentage of area within 1-km radius with shrubland ( $\text{Asin}[\sqrt{p}]$ )	7.3 $\pm$ 10.3	7.0 $\pm$ 10.0	ns
Permanent crops (%)	Percentage of area within 1-km radius with orchards, olive groves, and vineyards ( $\text{Asin}[\sqrt{p}]$ )	0.9 $\pm$ 1.1	0.9 $\pm$ 1.1	ns
Built-up areas (%)	Percentage of area within 1-km radius with urban areas, isolated farmhouses and infrastructures ( $\text{Asin}[\sqrt{p}]$ )	0.5 $\pm$ 0.6	0.5 $\pm$ 0.6	ns
Mean patch size (ha)	Mean size of open farmland patches ( $\text{Log}_{10}[X]$ )	179.5 $\pm$ 106.0	191.3 $\pm$ 108.1	ns
Edge density (km/km <sup>2</sup> )	Edge density of open farmland patches ( $\text{Log}_{10}[X]$ )	5.8 $\pm$ 2.9	5.6 $\pm$ 3.1	ns
AWMSI	Area weighted mean shape index of open farmland patches	3.3 $\pm$ 1.6	3.1 $\pm$ 1.6	<0.05
Road density (km/km <sup>2</sup> )	Density of roads within 1-km radius	2.3 $\pm$ 1.0	2.4 $\pm$ 0.9	ns

of trees and shrub patches (Table 1). Fallow age was assessed from inquiries to landowners and defined as the time in years since last cultivation, assigning an age of zero to fields harvested in the previous summer. Mean vegetation height was estimated in May of each sampling year from 60 evenly spaced measurements taken along a transect crossing the longest axis of each field. Use by livestock was quantified as the densities of sheep and cattle (animals per 10 ha) recorded at fallow fields during the six bird sampling visits. Presence of trees and shrub patches were quantified as binary variables.

Landscape context was characterized from 13 variables quantified in 1-km radius circles centred on each field (Table 1). This radius was adopted because previous research in the study area showed its adequacy to estimate bird-habitat relationships at the landscape scale (Moreira et al., 2005). Landscape composition was quantified considering the proportional cover by nine dominant land use categories, determined in a geographic information system from land-use maps prepared using aerial photography and field surveys: (i) open farmland (cereal crops, pastures, fallow and ploughed fields, with only scattered trees or very small shrub patches); (ii) pastoral woodlands (open oak woodlands grazed by livestock); (iii) forest plantations; (iv) shrublands; (v) permanent crops (orchards, olive groves and vineyards); and (vi) built-up areas (villages, isolated farmhouses and infrastructures). Forest plantations were further discriminated according to the dominant tree (eucalyptus, pine or oak), because grassland bird responses may vary according to plantation structure and composition (Reino et al., 2009). Habitat fragmentation was estimated from the mean size, edge density and shape complexity (AWMSI) of open farmland patches, computed using the Patch Analyst extension for ArcView (Rempel and Carr, 2003). The density of road networks estimated

from aerial cartography was used to indicate the fragmentation of open habitats by human infrastructures.

#### 2.4. Data analysis

Prior to statistical analysis, skewed variables were transformed to approach normality and to reduce the influence of a few large values, using the angular transformation for proportional data and the logarithmic transformation for continuous variables (Table 1). Because explanatory variables were strongly intercorrelated, Principal Component Analyses (PCA) of both field and landscape scale sets of variables was used to investigate multicollinearity and to describe dominant ecological gradients (Legendre and Legendre, 1998). For each PCA, a varimax normalized rotation was applied to the set of principal components with eigenvalues  $>1.0$ , to obtain simpler and more interpretable gradients (Legendre and Legendre, 1998).

Relations between bird densities (territories per 10 ha) and ecological gradients extracted from PCA were investigated with Generalized Linear Models (GLM) of the Gaussian family (McCullagh and Nelder, 1989). Analyses were carried out separately for data collected in 2000/01 and 2004, to check for consistency in bird-habitat relationships across two time periods. Inter-annual variation between 2000 and 2001 was controlled by forcing a variable coding the sampling year into the analysis (see also Moreira et al., 2005). Modelling involved a two-stage procedure based on the Information Theoretic Approach (ITA) of Burnham and Anderson (2002), which looks for simplicity and parsimony of several working hypothesis and is based on the strength of evidence of each candidate predictive model. The Akaike Information Criteria adjusted for small samples (AICc) was used as a measure

of information loss of each candidate model, with the best fitting model having the lowest AICc and the highest Akaike weight ( $w_i$ ), which measures the posterior probability that a given model is true, given the data and the set of competing candidate models (Burnham and Anderson, 2002). Model selection started by evaluating alternative response curves of grassland birds to each field and landscape gradient. Only linear ( $y = a + bx$ ), square-power ( $y = a + cx^2$ ) and quadratic ( $y = a + bx + cx^2$ ) functions were evaluated, to avoid developing overly complex models given the relatively limited dataset (Legendre and Legendre, 1998). For each response variable and principal component, the best non-null response curve was carried forward to subsequent analysis, using  $w_i$  as model selection criteria (Burnham and Anderson, 2002). Non-null responses were always selected for further analysis even when the largest  $w_i$  corresponded to the null model (model fitted to the intercept only [2004] or to the intercept and sampling year [2000/01]), because support to the effect of some variables may only be perceptible after accounting for the effects of other variables in a multivariate modelling context. In every case, scatterplots and regression diagnostics were used to inspect the shape of the fitted curves and to check for eventual problems resulting from outliers and influential points (Legendre and Legendre, 1998).

A second set of analyses involved the development of multivariate models based on the polynomial terms ( $x$ ,  $x^2$ , or  $x + x^2$ ) selected in univariate analysis for each field and landscape gradient. Field and landscape multivariate models were built separately to assess factors operating at different scales. In each case, candidate models were developed from all possible combinations of principal components, and  $w_i$  were used as a measure of model plausibility. The probability that a variable is included in the best approximating models, given the set of variables considered, was estimated by summing the  $w_i$  of all candidate models where the variable was included (Burnham and Anderson, 2002). Additionally, we used Multimodel Inference (MI) to assess the shape and magnitude of the effects of predictors on the response variables, which is based on an estimated weighted average across all models based on the model weights (Burnham and Anderson, 2002). Unconditional standard errors of estimates were used to evaluate the precision of model average estimates using a 95% confidence interval. Estimates whose confidence limits included zero were viewed as having equivocal meaning (Burnham and Anderson, 2002). Although testing all possible models is not the best strategy in model selection, this approach is often used when there is not enough *a priori* information to build a more reduced set of plausible candidate models (e.g., Whittingham et al., 2005). The possibility of finding spurious relations was reduced, however, by analysing a small number of environmental gradients extracted from PCA, which were based on habitat variables that were previously suggested to strongly influence grassland birds.

The most plausible field and landscape models, as judged from the corresponding  $w_i$ , were used in variation partitioning to isolate the contributions of factors operating at different scales to the explanatory power of abundance models (Borcard et al., 1992; Legendre and Legendre, 1998). This approach isolated three components of explained variation: (i) pure field effects; (ii) pure landscape effects; and (iii) shared field and landscape effects.

### 3. Results

The PCA of field variables extracted three axes with eigenvalues > 1.0, together accounting for 64.6% of variance in the original data (Table 2). The varimax rotation revealed a major gradient (FPC1) contrasting fields stocked with increasing numbers of either sheep or cattle, the later tending to be associated with taller swards. The second gradient (FPC2) largely reflected the age of fallows,

**Table 2**

Loadings of field variables on the first three axes extracted by a PCA, after a varimax normalized rotation, and the proportion of variance accounted for by each axis. Values underlined indicate  $|\text{factor loadings}| > 0.50$ .

Field variables	FPC1	FPC2	FPC3
Age	0.17	<u>0.89</u>	0.05
Sheep	<u>-0.79</u>	-0.23	0.08
Cows	<u>0.68</u>	-0.50	0.01
Vegetation height	<u>0.59</u>	0.07	-0.15
Shrubs	-0.17	0.02	<u>0.74</u>
Trees	-0.03	0.03	<u>0.82</u>
% Variance	25.0	18.6	20.9

with a tendency for higher cattle stocking densities in recent fallow fields. The third gradient (FPC3) was mostly related to the presence of trees and small shrub patches. The PCA of landscape variables extracted four axes with eigenvalues > 1.0, together accounting for 78.3% of variance in the original data (Table 3). The primary gradient (LPC1) largely reflected the fragmentation of open farmland through shrub encroachment, as suggested by the concurrent increase in edge density, patch complexity (AWMSI) and shrubland cover. The second gradient (LPC2) was also related to habitat fragmentation, contrasting landscapes with high cover and large size of open farmland patches, with that with high cover by pastoral woodlands. The third axis (LPC3) was associated with increasing human occupation, as indicated by the increasing cover by permanent crops and built-up areas, and by increasing road density. The fourth axis (LPC4) was associated with farmland afforestation, as indicated by the concurrent increase in cover by all forest plantation types.

Field conditions showed some changes between sampling periods, with a significant tendency towards fewer sheep and shorter herbaceous vegetation in 2004 relative to 2000/01 (Table 1). At the landscape scale, cover by oak plantations nearly doubled, determining a significant increase in total cover by forest plantations, whereas the complexity of open farmland patches slightly declined (Table 1). Despite these temporal changes detected for some individual variables, there were no significant differences between sampling periods on the gradients defined by the field and landscape PCAs.

#### 3.1. Bird densities

A total of 327 and 189 territories of the five study species were recorded in 2000/01 and 2004, respectively, reflecting an overall significant decline in grassland bird densities (Table 4). Corn buntings were by far the most abundant species in both sampling occasions (90 and 55 territories), whereas short-toed larks were

**Table 3**

Loadings of landscape variables on the first four axes extracted by a PCA, after a varimax normalized rotation, and the proportion of variance accounted for by each axis. Values underlined indicate  $|\text{factor loadings}| > 0.50$ .

Landscape variables	LPC1	LPC2	LPC3	LPC4
Open farmland	-0.03	<u>0.88</u>	-0.02	-0.39
Pastoral woodland	-0.49	<u>-0.78</u>	-0.12	-0.08
Eucalyptus plantations	-0.43	<u>0.37</u>	-0.19	<u>0.52</u>
Pine plantations	-0.01	-0.23	0.31	<u>0.75</u>
Oak plantations	0.16	-0.14	-0.19	<u>0.55</u>
Total forest plantations	0.15	-0.25	0.09	<u>0.91</u>
Scrubland	<u>0.88</u>	-0.14	-0.03	0.10
Permanent crops	0.20	-0.09	<u>0.86</u>	0.06
Built-up areas	0.17	0.05	<u>0.82</u>	-0.09
Mean patch size	-0.07	<u>0.88</u>	0.00	-0.31
Edge density	<u>0.90</u>	0.28	0.15	0.07
AWMSI	<u>0.93</u>	0.07	0.10	0.10
Road density	-0.45	0.15	<u>0.64</u>	0.14
% Variance	25.0%	19.7%	16.0%	17.6%

**Table 4**

Conservation status (SPEC), frequency of occurrence (F.O.) and density (territories per 10 ha), of breeding grassland birds in Southern Portugal. Changes between periods were evaluated using paired *t*-tests; ns –  $P > 0.05$ .

Species	SPEC <sup>a</sup>	F.O. (n = 40)		Mean density ± S.D.		P
		2000/01	2004	2000/01	2004	
<i>Tetrax tetrax</i> <sup>b</sup>	1	59.0%	51.3%	1.47 ± 1.80	0.86 ± 1.01	<0.05
<i>Galerida theklae</i>	3	77.0%	56.4%	2.16 ± 1.93	0.91 ± 0.97	<0.001
<i>Calandrella brachydactyla</i>	3	59.0%	41.0%	0.98 ± 1.02	0.60 ± 0.84	<0.01
<i>Melanocorypha calandra</i>	3	46.2%	48.7%	1.76 ± 2.51	1.32 ± 1.71	<ns
<i>Emberiza calandra</i>	2	82.1%	69.2%	2.49 ± 1.92	1.54 ± 1.42	<0.01

<sup>a</sup> SPEC: Species of European Conservation Concern. 1: Globally threatened species; 2: European species with unfavourable conservation status; 3: Global species with unfavourable conservation status in Europe (BirdLife International, 2004).

<sup>b</sup> Densities refer to territorial males.

always the least abundant (35 and 21 territories). Calandra larks were present in less than half the sampled fields, but they were always abundant where they occurred (65 and 51 territories). There were marked declines in the abundance of Thekla lark (81 and 30 territories) and little bustards (56 and 32 territorial males).

### 3.2. Bird responses to field management

Preliminary univariate screening of alternative response curves provided strong support for field patterns influencing grassland bird densities (Supplementary Table S1), though the type and strength of such relationships varied greatly among species (Supplementary Figure S1). Bird responses tended to be linear, with only weak support for unimodal response curves reflecting the presence of peaks abundances at intermediate values of the field gradients identified. In a few cases, there was support for U-shaped curves, reflecting maximal abundances at both extremes of a field gradient. In multivariate modelling there was a large set of plausible models (i.e., 95% confidence set of models) for each response variable (4–8 out of 8 possible models), with relatively low to moderate plausibility for the best ranking models in terms of AICc ( $0.19 \leq w_i \leq 0.60$ ) (Table 5). Nevertheless, some field gradients showed high selection probabilities (Table 5) and consistent estimates of regression coefficients (Supplementary Table S3), indicating strong effects on bird densities.

The gradient reflecting the presence of shrubs and trees in grassland fields (FPC3) showed some of the highest selection probabilities, providing moderate to strong support (0.60–1.00) for negative responses by little bustards (only in 2000/01), short-toed larks (only in 2004), and calandra larks, whereas Thekla larks showed the opposite trend (Table 5). There was also some support for bird responses to the gradient contrasting fields grazed by

either sheep or cattle (FPC1), with a tendency for little bustard and corn buntings increasing in fields grazed by cattle, whereas short-toed lark densities in 2004 tended to increase with sheep grazing (Table 5). Short-toed lark and extent Thekla lark densities tended to increase with fallow age (FPC2), though the later effect was less supported (Table 5). In 2004, there was strong support for a U-shaped response by corn buntings to this gradient (Table 5).

### 3.3. Bird responses to landscape context

Preliminary univariate analysis also provided strong support for landscape context influencing the local breeding densities of grassland birds (Supplementary Table S2), showing the presence of both linear and unimodal response curves (Supplementary Figure S2). In multivariate modelling there was a large set of plausible models for each response variable (5–13 out of 16 possible models), with low to moderate plausibility for the best ranking models in terms of AICc ( $0.20 \leq w_i \leq 0.60$ ) (Table 6). Nevertheless, some landscape gradients showed high selection probabilities (Table 5) and consistent estimates of regression coefficients (Supplementary Table S4), indicating strong effects on bird densities.

The gradient reflecting increasing edge density and patch complexity through shrub encroachment (LPC1) had marked effects on little bustards, Thekla larks, calandra larks and short-toed larks (only in 2000/01), showing moderate to very high selection probabilities (0.66–1.00) (Table 6). Little bustard (in 2000/01) and calandra lark densities steadily declined in more fragmented landscapes, whereas Thekla and short-toed larks showed the opposite pattern (Table 6). In 2004, little bustards and, to a lesser extent, corn buntings showed a tendency for maximum densities in landscapes with intermediate levels of open habitat fragmentation, declining where edge density was either too high or too low

**Table 5**

Summary results of model selection for the relationships between grassland birds and field habitat gradients (FPCn), including the number of models in the 95% confidence sets (%95), the Akaike weights ( $w_i$ ) and percentages of explained variance ( $R^2$ ) of the best approximating models, and the selection probabilities and directions of association with explanatory variables: (+) positive, (–) negative, (∩) unimodal, and (∪) U-shaped. Variables included in the best approximating models are underlined.

Species	Years	%95	$R^2$	$w_i$	FPC1	FPC2	FPC3
<i>Tetrax tetrax</i>	2000/01	4	44.4	0.60	<u>0.83</u> (+) <sup>a</sup>	0.26 (–)	<u>0.96</u> (–) <sup>a</sup>
	2004	8	6.4	0.19	<u>0.56</u> (+)	0.39 (–)	0.40 (–)
<i>Galerida theklae</i>	2000/01	4	26.6	0.40	0.26 (∩)	<u>0.57</u> (+)	<u>0.96</u> (+) <sup>a</sup>
	2004	8	16.4	0.27	0.35 (∩)	<u>0.57</u> (+)	<u>0.66</u> (+)
<i>Melanocorypha calandra</i>	2000/01	4	46.2	0.40	0.46 (+)	0.23 (∪)	<u>1.00</u> (–) <sup>a</sup>
	2004	4	28.8	0.46	0.24 (+)	0.39 (∩)	<u>1.00</u> (–) <sup>a</sup>
<i>Calandrella brachydactyla</i>	2000/01	6	16.7	0.43	0.25 (∩)	<u>0.88</u> (+) <sup>a</sup>	0.36 (+)
	2004	7	26.4	0.34	<u>0.81</u> (–) <sup>a</sup>	<u>0.68</u> (+)	<u>0.60</u> (–)
<i>Emberiza calandra</i>	2000/01	7	12.1	0.28	<u>0.56</u> (+)	0.50 (–)	0.23 (–)
	2004	6	30.1	0.34	<u>0.69</u> (+) <sup>a</sup>	<u>0.79</u> (∪) <sup>a</sup>	0.34 (+)

<sup>a</sup> 95% confidence intervals of regression coefficients do not intersect zero.

**Table 6**  
Summary results of model selection for the relationships between grassland birds and landscape gradients (LPCn), including the number of models in the 95% confidence sets (%95), the Akaike weights ( $w_i$ ) and percentages of explained variance ( $R^2$ ) of the best approximating models, and the selection probabilities and directions of association with explanatory variables: (+) positive, (–) negative, (n) unimodal, and (U) U-shaped. Variables included in the best approximating models are underlined.

Species	Years	%95	$w_i$	$R^2$	LPC1	LPC2	LPC3	LPC4
<i>Tetrax tetrax</i>	2000/01	11	0.31	30.5	<u>0.83</u> (–) <sup>a</sup>	<u>0.28</u> (+)	0.30(–)	0.25(U)
	2004	5	0.49	30.5	<u>0.97</u> (n) <sup>a</sup>	0.25(U)	<u>0.97</u> (–) <sup>a</sup>	0.30(+)
<i>Galerida theklae</i>	2000/01	7	0.36	33.6	<u>0.99</u> (+) <sup>a</sup>	<u>0.64</u> (–)	0.25(+)	0.24(n)
	2004	5	0.60	50.5	<u>1.00</u> (+) <sup>a</sup>	<u>0.89</u> (–) <sup>a</sup>	0.24(U)	0.11(n)
<i>Melanocorypha calandra</i>	2000/01	11	0.25	24.3	<u>0.83</u> (–) <sup>a</sup>	<u>0.86</u> (+) <sup>a</sup>	0.30(–)	0.44(n)
	2004	11	0.22	22.7	<u>0.74</u> (–) <sup>a</sup>	<u>0.90</u> (+) <sup>a</sup>	0.37(–)	0.42(–)
<i>Calandrella brachydactyla</i>	2000/01	12	0.20	28.4	<u>0.66</u> (+)	<u>0.62</u> (n) <sup>a</sup>	0.21(U)	0.25(n)
	2004	13	0.20	11.3	0.30(+)	<u>0.33</u> (n)	<u>0.75</u> (+) <sup>a</sup>	0.37(n)
<i>Emberiza calandra</i>	2000/01	13	0.20	8.4	0.24(U)	0.26(n)	0.33(U)	<u>0.50</u> (+)
	2004	13	0.23	7.7	<u>0.54</u> (n)	0.27(n)	0.29(n)	0.24(–)

<sup>a</sup> 95% confidence intervals of regression coefficients do not intersect zero.

**Table 7**  
Variation partitioning in grassland bird densities in Southern Portugal explained by habitat models incorporating field and landscape effects.

Species	Years	Pure components		Shared component	Unexplained variation
		Field	Landscape	Field/landscape	
<i>Tetrax tetrax</i>	2000/01	17.2	3.3	27.2	52.3
	2004	5.1	22.2	8.3	64.4
<i>Galerida theklae</i>	2000/01	6.8	13.8	19.8	59.6
	2004	0.5	38.1	12.4	49.0
<i>Melanocorypha calandra</i>	2000/01	29.5	7.6	16.7	46.2
	2004	13.3	8.1	14.6	63.7
<i>Calandrella brachydactyla</i>	2000/01	5.9	17.6	10.8	65.7
	2004	11.2	3.6	7.9	77.3
<i>Emberiza calandra</i>	2000/01	7.1	3.4	5.0	84.5
	2004	18.5	2.7	5.0	73.8

(Table 6). The second gradient reflecting habitat fragmentation (LPC2) showed relatively high selection probabilities (0.69–0.90) for calandra and Thekla larks, highlighting the strong tendency for the first species to increase along with the amount and patch size of open farmland habitats, and for the second species to show the opposite pattern (Table 6). In 2000/01, short-toed larks had a moderately supported unimodal response to this landscape gradient (Table 6). Responses to landscape occupation by roads, houses and permanent crops (LPC3) were generally weak, though in 2004 there was strong support for little bustard densities declining in more humanized landscapes, and for short-toed larks showing the opposite trend (Table 6). The relationships between grassland birds and the gradient reflecting farmland afforestation were always weak, with only some support for corn buntings increasing along with cover by forest plantations in 2000/01 (Table 6).

#### 3.4. Relative importance of field and landscape patterns

Partitioning of explained variation between field and landscape sets of variables showed marked differences among species and between sampling periods (Table 7). Field effects were particularly important for little bustards in 2000/01, whereas landscape effects were most important in 2004. The inverse was observed for the short-toed lark, for which explained variation in density was mostly accounted for by landscape effects in 2000/01, and by field effects in 2004. The importance of landscape variables was always superior to that of field variables for the Thekla lark, whereas field variables were always most important for the calandra lark and the corn bunting. For both Thekla and calandra larks, however, a relatively large proportion of explained variation was

shared between field and landscape sets of variables, underlining a strong correlation between influential factors operating at the two scales.

## 4. Discussion

### 4.1. Grazing regimes

Grassland bird species tended to be associated with either sheep or cattle, which may reflect the widely different characteristics of herbaceous vegetation in pastures stocked with each of these herbivores (Vickery et al., 2001; McCracken and Tallwin, 2004; Buckingham and Peach, 2005). Intensive grazing by sheep reduces sward structural complexity and promotes short and uniform pastures, whereas moderate grazing, especially by cattle, increases structural heterogeneity and leads to patchy swards with areas of long and short cover (Devereaux et al., 2004). This pattern probably occurred within the study area, as suggested by the lower vegetation height in sheep than in cattle pastures. Sheep pastures thus favoured species normally associated with homogeneous short swards such as the short-toed lark (Suárez et al., 2002; Serrano and Astrain, 2005). Conversely, corn buntings were more associated with cattle pastures, probably because they prefer taller and more heterogeneous sward heights to feed on seeds and foliar invertebrates during the chick rearing period (Brickle et al., 2000). The positive association of male little bustards with cattle pastures may also be related to the availability of important food resources such as large beetles and other invertebrates, as this is a critical factor affecting the distribution of territories of this species (Traba et al., 2008), and cattle are known to favour invertebrate abundance by their grazing and dunging patterns (Buckingham et al., 2006).

#### 4.2. Habitat fragmentation

There were strong responses to the presence of shrubs and trees at the field scale, and to the amount and spatial configuration of open farmland habitats in the surrounding landscape, thus confirming the importance of habitat fragmentation for Mediterranean grassland birds (Reino et al., 2009; Morgado et al., 2010). Thekla larks tended to reach high densities close to edges and apparently benefitted from increasing landscape fragmentation, whereas edge avoiders such as calandra lark only reached high densities over large open farmland (Reino et al., 2009). Although corn buntings were positively influenced by wooded edges (Reino et al., 2009), they were the least affected by landscape patterns, probably because they can occur over a wide range of habitat conditions. Patterns for the short-toed lark were more complex, because they were edge avoiders (Reino et al., 2009) but seemed to reach the highest densities in landscapes with high edge density. Results for little bustards were inconsistent, with negative responses to landscape fragmentation in 2000/01, whereas in 2004 the highest abundances were in landscapes with intermediate edge density. These results suggest that little bustards tend to decline steadily in open landscapes highly fragmented by shrublands and forest plantations, though they may be able to tolerate moderate levels of habitat fragmentation. Inter-annual variation in responses to edge density at low levels of habitat fragmentation may reflect temporal changes in species distribution irrespective of landscape context (Morales et al., 2005), as previous studies reported that the species is largely indifferent to wooded edges (Reino et al., 2009).

#### 4.3. Scale dependencies

The joint influence of field and landscape factors on grassland bird densities observed in Southern Portugal is in line with previous research underlining the value of investigating factors operating over a range of spatial scales to understand bird-agriculture relationships (Moreira et al., 2005; Batáry et al., 2007a). Strong covariation between scales was particularly evident for calandra larks, probably because they showed strong negative responses to both landscape fragmentation and local presence of shrubs or trees, while fields with shrubs and trees were most common in the most fragmented landscapes. Nevertheless, there was still a strong unique contribution of field variables to explain variation in calandra lark densities, thus suggesting a negative effect of local shrubs and trees irrespective of landscape fragmentation. The same reasoning may apply to the Thekla lark, which was positively influenced by both landscape fragmentation and local presence of shrubs and trees. In this case, however, the strongest unique contribution to explained variation was that of landscape variables, thus suggesting a positive effect of habitat fragmentation irrespective of the local presence of shrubs and trees.

There were also some marked differences between sampling periods in the relative importance of factors operating at the landscape and field scales, particularly for little bustards and short-toed larks. This supports previous research showing pervasive temporal variation in bird-landscape relations, though reasons for this are often unclear (Riffell and Gutzwiller, 2009). One possibility is that species may be responsive to landscape context in 1 year, but not as much in the other, due to fluctuations in the extent to which their life-history needs are met at the local scale (Riffell et al., 2003). The largest change in our study area was the reduction in sheep density, which more than halved between the two sampling periods and may have caused variation in the strength of bird responses at the field scale. In fact, little bustards showed the strongest negative responses to sheep grazing when sheep densities were highest in 2000/01, whereas the strongest positive responses of short-toed larks to sheep grazing were found in 2004 when sheep densi-

ties were lowest. Accordingly, little bustards and short-toed larks showed weak landscape responses in 2000/01 and 2004, respectively, probably underlining a tendency for landscape effects to be strongest when local conditions were globally most favourable.

#### 4.4. Conservation implications

Positive effects of land use transformations may be expected on the Thekla lark, due to their strong association with patchworks of woody and grassy habitats, and on the corn bunting, because it was largely indifferent to habitat fragmentation and appeared to prefer cattle over sheep pastures. Considering that these are species of European conservation concern (Table 4), it might be argued that ongoing agricultural change in Iberian cereal-steppes will bring conservation benefits. In contrast, these changes could be regarded as largely detrimental when considering the little bustard, the short-toed lark and the calandra lark (Table 4), which were associated with much less fragmented landscapes. Calandra larks are expected to decline steadily even with small levels of habitat fragmentation (Morgado et al., 2010; this study), whereas little bustards and short-toed larks may tolerate or even favour the initial fragmentation stages, but then decline once a given threshold is reached (Reino et al., 2009; this study). Likewise, short-toed larks will probably be negatively affected by the replacement of sheep by cattle, whereas little bustards may be favoured by this process.

Taken together, these results confirm the view that the same agricultural policies may be favourable for some species of conservation concern but detrimental to others, and so they cannot be assumed to bring uniform conservation benefits (Suárez-Seoane et al., 2002; Báldi et al., 2005). Efforts are thus needed for preventing undesired consequences of agricultural policies designed at the European scale, eventually through the implementation of regional or local agri-environment schemes (Stoate et al., 2009). This has already been recognised in the case of Iberian cereal-steppes, for which agri-environment schemes have been targeted at the protection of their valuable grassland bird communities against the dual threats of land abandonment and intensification (e.g., Bota et al., 2005; Oñate et al., 2007). Most of these schemes, however, assume often implicitly that all grassland birds have rather similar or at least compatible habitat requirements, disregarding the fact that the same management guidelines may elicit contrasting responses by different species. Solving this problem requires that agri-environment schemes for grassland bird species are tailored to meet clearly defined conservation objectives based on international and national criteria (e.g., Batáry et al., 2007b), which may need to be adjusted at the local scale to account for spatial variation in socio-economic and ecological conditions.

#### Acknowledgements

This study was funded by the Portuguese Science and Technology Foundation through grants SFRH/BD/14085/2003 and SFRH/BPD/62865/2009 to LR, SFRH/BD/28974/2006 to MP, SFRH/BD/64645/2009 to LG, and PRAXIS XXI/C/AGR/11063/98 to the project, and by the European Commission through research grant LACOPE\_EVK2-2001-00259. Thanks are due to “Liga para a Protecção da Natureza” for logistic support during fieldwork.

#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.03.013.

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