Original article

Calandra lark habitat selection: Strong fragmentation effects in a grassland specialist

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ABSTRACT

Conserving grassland birds in farmed landscapes requires the maintenance of favourable agricultural land uses over a range of spatial and temporal scales. Here we examined the field and landscape-scale habitat requirements of the calandra lark (*Melanocorypha calandra*), an obligate grassland bird often associated with open Mediterranean farmland. Breeding and wintering lark densities were assessed in 42 fallow fields in southern Portugal, and related to three sets of variables reflecting field, landscape and neighbourhood effects. Variation partitioning was used to isolate the unique and shared contributions of sets of variables to explained variation in lark distribution and abundance models. At the field scale, the presence of trees and shrubs showed the strongest negative effects on calandra lark. At the landscape scale there were strong positive response of larks to the amount and patch size of open farmland habitats, and negative responses, albeit weaker, to drainage and road densities. Calandra lark distribution and abundance was also positively related to that of conspecifics in surrounding fields, particularly in spring. Results suggest that calandra larks are highly sensitive to habitat fragmentation, requiring fallow fields with no shrubs or trees, embedded in large expanses of open farmland. This supports the view that grassland bird conservation in Mediterranean agricultural landscapes may require a combination of land-use regulations and agri-environment schemes preventing ongoing shrub encroachment and afforestation of marginal farmland.

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1. Introduction

In many regions worldwide, grassland birds have shown pronounced declines due to the conversion of their habitats to agriculture, forest, and urban land uses (Jones and Bock, 2002; Brennan and Kuvlesky, 2005; Laiolo and Tella, 2006). Despite these pervasive trends, some species have survived within human-dominated landscapes, mainly occupying habitats resulting from agricultural and pastoral activities such as pastures, fallow land, and even arable or row crops (Best et al., 2001; Delgado and Moreira, 2000; Batáry et al., 2007). Over the past three decades, however, the progressive intensification of agricultural practices has resulted in overall declines of farmland birds, including many grassland species (Barnett et al., 2004; Brotons et al., 2004; Brennan and Kuvlesky, 2005; Donald et al.,

2006). At the same time, large-scale rural depopulation and abandonment of marginal farming land has resulted likewise in the loss of farmland habitats, due to shrub encroachment and afforestation (Preiss et al., 1997; Diáz et al., 1998; Santos, 2000; Van Doorn and Baker, 2007; Sirami et al., 2007). As a consequence, much effort has been made to understand the interaction between bird populations and agricultural practices, trying to develop management prescriptions that can favour their conservation within farmed landscapes (Kleijn et al., 2006; Barnett et al., 2004; Moreira et al., 2005a; Whittingham et al., 2005; Santos et al., 2006).

The conservation of grassland birds in farmed landscapes may be particularly challenging, due to their specialized habitat requirements over a range of spatial scales (Moreira et al., 2005a; Batáry et al., 2007). On the one hand, these birds may be strongly dependent on local field characteristics, such as sward structure and composition (Milsom et al., 1998; Moreira, 1999; Barnett et al., 2004), which are largely contingent on the management decisions of individual farmers. On the other hand, grassland birds are affected by the landscape context in which usable fields are located,

frequently selecting large and homogeneous patches of open grassland habitat (Helzer and Jelinski, 1999; Winter and Faarborg, 1999; Johnson and Igl, 2001; Hamer et al., 2006), thereby depending on planning policies driving land uses at large spatial scales. Although this dual role of landscape and field conditions affecting the conservation of farmland birds has been recognized previously (Milsom et al., 1998; Pärt and Söderström, 1999; Best et al., 2001), there is still limited understanding on the relative role of factors operating at different scales in determining bird–agriculture relationships (but see Moreira et al., 2005a; Batáry et al., 2007, and references therein). This is a complex task because habitat features may be strongly correlated across scales, making it difficult to disentangle the unique contribution of factors operating at any given scale (Borcard et al., 1992; Legendre and Legendre, 1998). Furthermore, bird usage of fields may vary in relation to the distribution of conspecifics in the surrounding landscape, which may interact with field and landscape characteristics to determine local bird abundances (Jensen and Cully, 2005). These interactions may vary over the year, due to seasonal shifts in social behaviour from winter gregariousness to spring territoriality (Tellería and Pérez-Tris, 2003), further complicating the identification of grassland bird habitat requirements in farmed landscapes.

The calandra lark is a suitable model species to analyze multi-scale factors affecting grassland bird conservation in agricultural landscapes (Suárez-Seoane et al., 2002; Osborne et al., 2007; Reino et al., 2009). In the Iberian Peninsula, calandra larks are particularly abundant within open farmland devoted to rotational dry cereal cultivation and livestock grazing, where they mainly use fallow fields (Delgado and Moreira, 2000; Suárez-Seoane et al., 2002; Moreira et al., 2005a). Fallow fields typically remain uncultivated for 2–5 years (or more) and occupy 30–80% of these farmed landscapes, providing particularly important feeding and breeding conditions for both migratory and resident grassland species of conservation concern (Suárez et al., 1997; Delgado and Moreira, 2000; Moreira et al., 2005a). Presently this farming system of low economic value is suffering the dual threats of intensification and abandonment, both of which contribute to the loss of valuable habitats for grassland birds. Under more intensive regimes the area occupied by fallow land is smaller, rotation cycles are shorter, and frequently there are increases in grazing pressure, the replacement of sheep by cattle, and the sowing of improved pastures (Suárez et al., 1997). Abandonment results in longer rotations, scrub encroachment and even afforestation (Suárez et al., 1997; Van Doorn and Bakker, 2007). These changing farming regimes are expected to cause severe declines in the range and numbers of calandra larks, along with that of many grassland bird species of conservation concern (Suárez et al., 1997; Brotons et al., 2004; Moreira et al., 2005a; Reino et al., 2009), thereby calling for a detailed understanding of their habitat requirements at multiple spatial and temporal scales. This is essential if we are to predict the consequences of ongoing landscape changes and to devise adequate management prescriptions that could benefit the species in this changing agricultural environment.

This study examined field and landscape-scale habitat requirements of calandra lark during the breeding and winter seasons, across a gradient of agricultural intensification-abandonment in southern Portugal. The study adopted a variation partitioning approach (*sensu* Borcard et al., 1992; Legendre and Legendre, 1998) to isolate the unique contributions of field and landscape sets of variables to the explanatory power of distribution and abundance models, thereby contributing to identify critical elements that should be considered for the conservation management of this species (Moreira et al., 2005a). Neighbourhood effects were also considered in variation partitioning, to account for eventual spatial autocorrelation in species distributions resulting from spatially structured habitat conditions or demographic effects (e.g., Magalhães et al., 2002; Reino et al., 2006). This information was then used to discuss agri-environment prescriptions favouring the persistence of calandra larks and other open grassland birds in Mediterranean farmland.

2. Methods

2.1. Study area

The study was conducted in the region of Castro Verde (southern Portugal), within a 20×30 km^2 rectangle encompassing a north-south gradient of agricultural intensification-abandonment. The climate is Mediterranean, with hot summers (averaging 24 °C [16–32 °C] in July), fairly cold winters (averaging 9 °C [5–14 °C] in January), and >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 dominated by an open farmland mosaic of cereal, fallow and ploughed fields, created by rotational dry cereal cultivation. Typically, fields are cultivated with cereals (generally, wheat *Triticum* spp. and barley *Hordeum* spp.) for two consecutive years, when they are sown in September–November and harvested in June–July. Cultivation is followed by a period with no agricultural management that may last from two to several years, and then land is ploughed to re-initiate the rotation cycle. Fallow fields are often grazed by sheep and, to a lesser extent, by cattle. The proportion of land cultivated each year and the period of fallowing depends on soil productivity, varying markedly across the study area. 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), many consisting of stubble fields. In the south there is a mosaic of shrubland interspersed with old fallow fields (up to 10 years old), as a result of agricultural abandonment and scrub 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* woodlands of variable tree cover, frequently grazed by livestock. Forested areas are increasing, due to afforestation of abandoned arable land with umbrella pines *Pinus pinea*, and holm and cork oak *Quercus suber*. Large patches of continuous shrubland (mostly *Cistus ladanifer*) can be found in the most rugged areas, especially along river valleys, and covering recently abandoned cropland. The study area was partly included in the Special Protection Area of Castro Verde, designated under the European Union Birds Directive (79/409/EEC) due to its importance for open grassland birds. In part of the area there is an agro-environment subsidy scheme, whereby farmers are compensated for maintaining agricultural practices favouring bird conservation. Details of the study area and its bird communities can be found in previous studies (Moreira, 1999; Delgado and Moreira, 2000; Moreira et al., 2005a; Reino et al., 2009).

2.2. Bird sampling

Calandra larks were counted in 42 fallow fields of approximately 10 ha each (mean = 9.4 ha, 5.5–13.6 ha), 30 of which were sampled in winter 1999/2000 and spring 2000, and 12 in winter 2000/2001 and spring 2001. Fields were selected as part of a larger study assessing habitat requirements of open farmland birds, following the stratified random procedure described by Moreira et al. (2005a). Briefly, fields were selected to cover homogeneously the spatial intensification-abandonment gradient, with the additional constraints of just one field per farm and a minimum distance of 500 m between fields, to reduce spatial autocorrelation due to similarities in farm management. Fields were selected within the open farmland mosaic that is

the most important for steppe birds of conservation concern (Moreira, 1999; Delgado and Moreira, 2000; Moreira et al., 2005a), thereby avoiding long-abandoned fields (>20% cover by shrubs) and open oak parklands (>5% cover by trees).

In winter, bird counts were carried out in each field, at about two-week intervals between December and mid-February (Moreira et al., 2005a). On each visit, the entire field was walked so that the observer approached to within 50 m or less of every point. All individuals and flocks were identified and recorded on previously prepared 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. In spring, the number of breeding territories was estimated using the territory mapping technique (Bibby et al., 2000), by compiling the information obtained in seven counts made from mid March to mid June, at about two-week intervals. Counts were carried out within 4 h after sunrise and within 2 h before sunset, with none in heavy or persistent rain, or in strong wind conditions.

2.3. Explanatory variables

Factors influencing calandra lark were analyzed using three sets of explanatory variables, reflecting field management, landscape context, and neighbourhood effects (Table 1). Variables were selected based on consideration of the existing literature on habitat associations of the calandra lark (Delgado and Moreira, 2000; Moreira, 1999; Suárez-Seoane et al., 2002; Moreira et al., 2005a) and other open grassland birds (e.g., Wilson et al., 1997; Milsom et al., 1998; Best et al., 2001; Coppedge et al., 2001; Johnson and Igl, 2001; Ribic and Sample, 2001; Barnett et al., 2004). Fields were described from seven variables characterizing grazing intensity, fallow field age and vegetation structure. For each season, an index of grazing intensity was obtained from the proportion of bird counting visits where livestock (mostly sheep) were observed. 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. The occurrence of stubbles was quantified using a binary variable. Mean vegetation height was estimated in January and May from 60 evenly spaced measurements taken along a transect crossing the longest axis of each field

(Moreira, 1999). Cover by bare ground was estimated likewise as the proportion of the 60 measurements with no vegetation. The presence of shrubs and trees were coded as binary variables.

Landscape context was described using six variables reflecting the amount and fragmentation of calandra lark habitats. These were quantified in 1-km-radius circles centred on sampling fields, from land-use maps prepared using aerial photography and field surveys, within a geographical information system (GIS). This radius was set large enough to encompass different land uses despite the relative homogeneity of the landscape, while remaining within the range of scales used to assess landscape influences on farmland birds (Söderström and Pärt, 2000; Best et al., 2001; Moreira et al., 2005a). The quantity of potential habitat was estimated from the proportion of open farmland, defined as continuous expanses of fallow, cereal and ploughed fields, with virtually no trees, shrubs or hedgerows, based on previous information about the ecological requirements of calandra lark in southern Portugal (Moreira, 1999; Delgado and Moreira, 2000). Patches of open farmland were bordered by unsuitable shrubland and forest habitats, and so fragmentation was estimated from the size (ha) of the continuous patch of open farmland where each sampled fallow field was inserted and by the mean size (ha) of open farmland patches in the surrounding landscape. The extent to which patch shapes deviated from circularity was estimated from the Area Weighted Mean Shape Index (AWMSI), because increases in edge-affected habitats with increasing patch complexity may influence grassland bird distributions (Helzer and Jelinski, 1999). Landscape metrics were computed using the Patch Analyst extension (version 3.1) of Arc View® GIS (Rempel and Carr, 2003). Stream and road densities were estimated from digitized 1:25,000 topographic maps, and used also to reflect open farmland fragmentation.

Variables reflecting neighbourhood effects were also used as explanatory variables to account for unmeasured spatially structured factors (e.g., Magalhães et al., 2002; Reino et al., 2006). Neighbourhood effects on local occurrences were estimated using a variable expressing the frequency of occurrence of calandra larks in surrounding fields (e.g., Reino et al., 2006). For each sampling field, this variable was computed as a distance-weighed mean of lark's occurrence in the other fields sampled during this study, coding the occurrence of larks as a binary variable and using inverse-square-distance weighing

Table 1
Summary statistics (mean ± standard deviation) of field, landscape and neighbourhood sets of variables used to characterize fallow fields with and without calandra lark, in the winter and spring seasons. Values for transformed variables are presented in the original scale.

Variable (abbreviation; unit)	Description (transformation)	Winter (Mean ± sd)		Spring (Mean ± sd)	
		Presences	Absences	Presences	Absences
Field variables					
Livestock (LVSTOCK; %)	Frequency of occurrence of livestock across sampling visits (Log_{10})	22.9 ± 30.2	17.1 ± 21.6	26.4 ± 27.4	24.1 ± 20.0
Fallow age (AGE; years)	Time since last cultivation or ploughing (Log_{10})	2.1 ± 3.0	1.6 ± 2.3	2.4 ± 3.2	1.4 ± 1.7
Stubbles (STUB)	Presence of stubbles	0.3 ± 0.5	0.3 ± 0.5	0.3 ± 0.5	0.3 ± 0.5
Vegetation height (VEGH; cm)	Mean height of herbaceous vegetation (Log_{10})	5.1 ± 3.6	5.1 ± 2.3	20.0 ± 7.4	22.4 ± 10.8
Bare ground (BARE; %)	Percentage cover by bare ground ($Asin[\sqrt{p}]$)	5.7 ± 6.2	8.4 ± 7.8	5.2 ± 5.7	4.8 ± 5.6
Shrubs (SHRUB)	Presence of shrubs	0.2 ± 0.4	0.5 ± 0.5	0.2 ± 0.4	0.6 ± 0.5
Trees (TREE)	Presence of trees	0.2 ± 0.4	0.6 ± 0.5	0.3 ± 0.4	0.7 ± 0.5
Landscape variables					
Open farmland cover (FARM; %)	Percentage of area with arable fields and pastureland ($Asin[\sqrt{p}]$)	62.3 ± 27.0	36.4 ± 24.9	60.0 ± 25.1	32.7 ± 24.7
Farmland patch (PATCH; ha)	Size of the open farmland patch where the sampled field was inserted (Log_{10})	168.9 ± 84.5	85.0 ± 78.8	155.1 ± 80.0	78.2 ± 82.3
Mean patch size (MPS; ha)	Mean size of open farmland patches (Log_{10})	137.3 ± 86.7	63.2 ± 70.7	119.6 ± 83.6	61.7 ± 75.0
Patch shape index (AWMSI)	Area weighted mean shape index of open farmland patches	1.6 ± 0.3	1.7 ± 0.33	1.6 ± 0.3	1.7 ± 0.4
Drainage density (RIVER; km/km²)	Density of stream network (Log_{10})	3.6 ± 0.4	4.1 ± 0.77	3.6 ± 0.4	4.1 ± 0.8
Road density (ROAD; km/km²)	Density of road network (Log_{10})	2.1 ± 0.61	2.3 ± 0.90	2.1 ± 0.6	2.3 ± 0.9
Neighbourhood variables					
Mean occurrence (NEIGH-OCCUR)	Distance-weighed mean prevalence of conspecifics in surrounding fields	0.5 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.2
Mean abundance (NEIGH-ABND)	Distance-weighed mean density of conspecifics in surrounding fields (Log_{10})	1.8 ± 4.0	0.7 ± 0.6	1.6 ± 1.2	0.8 ± 0.5

(Legendre and Legendre, 1998). Neighbourhood effects on local abundances were estimated likewise, by computing a weighted mean of lark densities at surrounding fields (e.g., Magalhães et al., 2002).

2.4. Statistical analysis

Analyses were designed to estimate factors influencing the local occurrence and density of calandra lark in both winter and spring. In winter, species presence in a given field was assumed if it was recorded at least once during the five counts, whereas in spring the presence of larks was assumed if at least one breeding territory was detected using the territory mapping technique. Winter density was estimated considering the mean count over the five visits (birds 10 ha^{-1}), whereas breeding densities were estimated from territory number (territories 10 ha^{-1}). Prior to statistical analysis, abundance data and skewed habitat 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 other continuous variables (Table 1).

Factors affecting the local occurrence of calandra lark were investigated separately for the wintering and the breeding seasons, using logistic regression. Factors affecting variation in calandra lark density were examined likewise using linear regression. Density analysis excluded fields where calandra lark were absent, thereby focusing on the range of habitat conditions suitable to the species. In all analysis, a binary variable coding the year of sampling was forced into distribution models to account for eventual changes in species prevalence or abundance between years. Modelling involved a two-stage procedure (e.g., Reino et al., 2009; Pita et al., 2009), based on the Information Theoretic Approach (ITA) of Burnham and Anderson (2002). The ITA looks for simplicity and parsimony of several working hypothesis and it is based on the strength of evidence of each candidate predictive model. The AIC 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). Analyses were carried out in R 2.7.2 software (R Development Core Team, 2008).

Model selection started by evaluating alternative response curves of calandra lark to habitat variables, considering linear ($y = K + bx$), square power ($y = K + cx^2$) and quadratic ($y = K + bx + cx^2$) functions (Legendre and Legendre, 1998). For each pair of explanatory and response variables, the best fitting curve was carried forward to subsequent analysis, using Akaike weights (w_i) as the model selection criteria (Burnham and Anderson, 2002). Scatterplots and regression diagnostics were used to check eventual problems resulting from the presence of outliers and influential points (Legendre and Legendre, 1998). A second set of analyses involved the development of multivariate models describing the relationships between each response variable and the explanatory variables. To reduce collinearity problems, Pearson's correlation (R) was computed between each pair of explanatory variables, dropping from subsequent analyses one variable from each pair with $|R| > 0.70$. The variable dropped from each pair was always the one least associated with the dependent variable, as judged from AICc values. Multivariate models were built separately for field, landscape and neighbourhood sets of variables, to assess factors operating at different scales. In each case, models were built from all possible subsets of the predictor variables, and Akaike weights 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 then estimated by summing the Akaike weights of all candidate models where the variable was included (Burnham and Anderson, 2002). Although testing all

possible models is not the best strategy in model selection (Anderson, 2008), this approach is often used when there is not enough *a priori* information to built a more reduced set of plausible candidate models (e.g., Whittingham et al., 2005). In common with other studies (Whittingham et al., 2005), the possibility of finding spurious models was reduced by restricting the analysis to variables that were previously suggested as predictors of open grassland bird distribution and abundance (see Section 2.4).

The most plausible field, landscape and neighbourhood models, as judged from the corresponding Akaike weights, were used in variation partitioning to isolate the unique and shared contributions of factors operating at different scales to the explanatory power of distribution and abundance models (Borcard et al., 1992; Legendre and Legendre, 1998). This was based on an extension to three sets of variables of the method of Borcard et al. (1992), which isolated seven components of explained variation in lark distribution and abundance (e.g., Anderson and Gribble, 1998; Reino et al., 2006): i) pure field effects; ii) pure landscape effects; iii) pure neighbourhood effects; iv) shared field and landscape effects; v) shared field and neighbourhood effects; vi) shared landscape and neighbourhood effects; and vii) shared field, landscape and neighbourhood effects. The Nagelkerke r^2 (Nagelkerke, 1991) was used as a measure of variation explained by each logistic model, whereas the coefficient of determination (R^2) was used for linear regression models.

3. Results

3.1. Overall patterns

In both seasons, calandra larks were found primarily in the northern part of the study area, where they showed the highest local abundances (Fig. 1). In winter, larks occurred in one-third of the sampling fields (33%), with a mean density (±se) in fields where they occurred of 6.0 ± 2.3 birds 10 ha^{-1} (0.5–29.5, $n = 14$). Calandra larks were slightly more widespread in spring (45% of sampling fields), with densities varying less among fields where they occurred (4.5 ± 0.5 territories 10 ha^{-1}, 2.0–9.1, $n = 19$) than in winter. All fields occupied in winter also had larks in spring (Fig. 1), whereas 26% of spring occurrences were recorded in fields unused in winter. Excluding double absences, there was a high correlation between spring and winter densities ($R = 0.77$).

3.2. Determinants of field occupancy

Models of calandra lark occurrence including the year of sampling were always poorer in terms of AICc than the corresponding null models, indicating that species prevalence did not change between years in either spring or winter. In contrast, some field, landscape and neighbourhood variables produced univariate models that performed consistently better than the corresponding null models (Table 2). The presence of trees and shrubs were the field variables showing the strongest negative relation with lark occurrence (Fig. 2), though the latter effect was much weaker in winter (Table 2). Fallow age and the presence of stubbles were highly correlated variables ($|R| > 0.70$), and so only the former was used in multivariate modelling. Analysis of landscape variables underlined strong responses to the amount and fragmentation of favourable habitats, with the prevalence of larks being positively influenced by open farmland cover, local patch size and mean patch size, and negatively so by stream density (Table 2; Fig. 2). The former three variables were highly correlated ($|R| > 0.70$), and so only the open farmland cover and the mean patch size were used in multivariate modelling of spring and winter occupancy data, respectively. Calandra lark occurrence appeared most sensitive to habitat quantity and fragmentation in winter, as the probability of
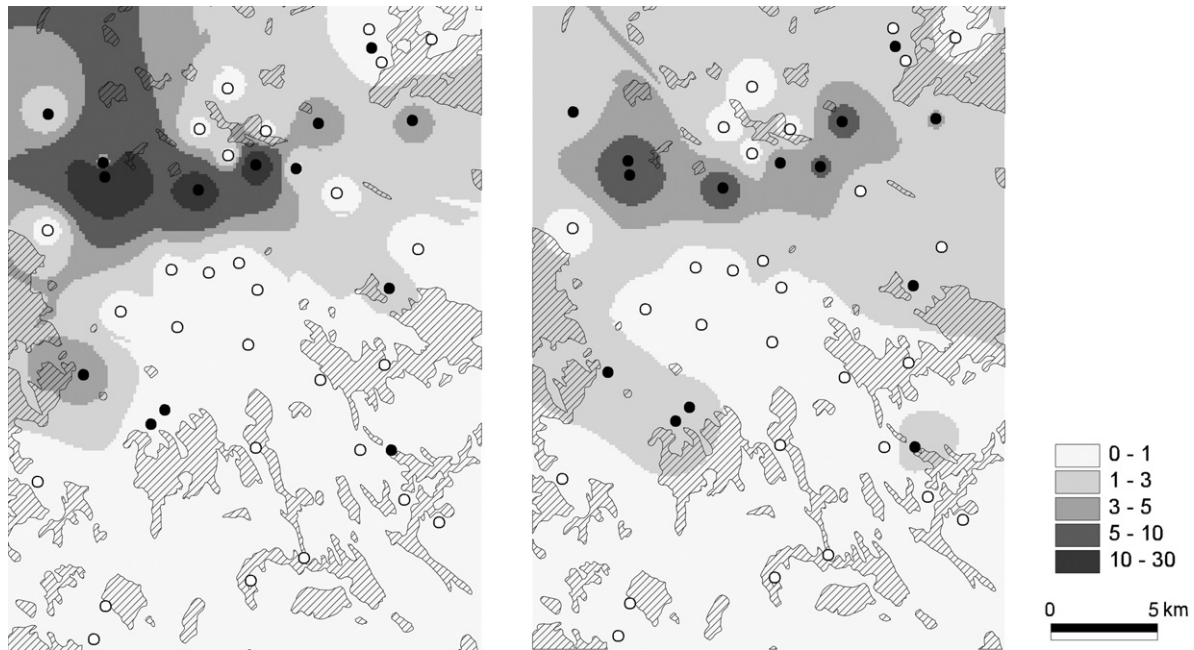
Fig. 1. Interpolated maps, based on inverse-square-distance weighing, of calandra lark densities across the study area in winter (left; birds/10 ha) and spring (right; territories/10 ha). Filled and unfilled dots are sampling fields where larks were present and absent, respectively. Dashed areas represent forest and shrubland habitats that are unsuitable for calandra larks.

larks occurring in fields embedded in landscapes with less and more fragmented habitats tended to be highest in spring (Fig. 2). Models with neighbourhood variables indicated that the local occurrence of calandra lark was positively related with its mean prevalence in surrounding fields, though this effect was much stronger in spring than in winter (Table 2).

In multivariate modelling of spring occupancy data, the landscape effects with the highest selection probabilities were the positive response to the amount of open farmland and the negative response to increasing shape complexity of open farmland patches

Table 2
Summary results of analysis evaluating alternative response curves of calandra lark to habitat variables In each case, the table indicates whether the most plausible response curve was linear (1), square power (2) or quadratic (3), and the corresponding Akaike weights (w_i). The sign of the slope is given for linear and square power response curves, indicating positive ($+$) or negative ($-$) directions of association.

Variable	Occurrence		Abundance	
	Winter	Spring	Winter	Spring
Field variables				
Livestock	0.31 $(+)^2$	0.30 $(+)^2$	0.20 $(+)^1$	0.19 $(-)^1$
Fallow age	0.35 $(+)^2$	0.42 $(+)^2$	0.32 $(+)^1$	0.18 $(+)^1$
Stubbles	0.24 $(-)^1$	0.24 $(+)^1$	0.23 $(-)^1$	0.18 $(+)^1$
Vegetation height	0.27 $(-)^1$	0.28 $(-)^2$	0.22 $(+)^1$	0.64 $(+)^2$
Bare ground	0.44 $(-)^1$	0.25 $(+)^2$	0.23 $(+)^1$	0.21 $(+)^1$
Shrubs	0.71 $(-)^1$	0.90 $(-)^1$	0.63 $(-)^1$	0.33 $(-)^1$
Trees	0.92 $(-)^1$	0.94 $(-)^1$	0.29 $(-)^1$	0.66 $(-)^1$
Landscape variables				
Open farmland cover	0.96 $(+)^1$	0.99 $(+)^1$	0.78 $(+)^1$	0.80 $(+)^2$
Farmland patch	0.94 $(+)^1$	0.98 $(+)^1$	0.80 $(+)^1$	0.90 $(+)^2$
Mean patch size	0.98 $(+)^1$	0.95 $(+)^1$	0.89 $(+)^2$	0.99 $(+)^2$
Patch shape index	0.41 $(-)^1$	0.43 $(-)^2$	0.23 $(-)^1$	0.21 $(-)^2$
Drainage density	0.71 $(-)^1$	0.62 $(-)^2$	0.72 $(-)^1$	0.87 $(-)^1$
Road density	0.25 $(-)^1$	0.25 $(+)^1$	0.27 $(-)^1$	0.93 $(-)^2$
Neighbourhood				
Mean occurrence	0.72 $(+)^2$	1.00 $(+)^2$	–	–
Mean abundance	–	–	0.18 $(+)^1$	0.58 $(+)^2$

(AWMSI), both of which were included in most plausible model (Table 3). The best field model included the negative influences of tree and shrub presence, and that of increasing vegetation height (Fig. 2), though with much higher selection probabilities for the former two variables (Table 3). The amount of explained variation in spring occurrence by field and landscape models was similar, whereas that of neighbourhood models was slightly lower (Table 3). Variation partitioning isolated relatively high proportions of unique field and landscape effects on calandra lark occurrence, whereas most variation explained by neighbourhood effects was shared with that of field and landscape sets of variables (Fig. 3).

In winter, landscape variables with the highest selection probabilities were the mean size and the complexity (AWMSI) of open farmland patches, with the former variable and river drainage density being included in the most plausible model (Table 3). The presence of trees was the field variable with the highest selection probability, though the presence of shrubs was also included in the most plausible model (Table 3). The amount of explained variation in field winter occupancy by landscape models was slightly higher than that of field models, whereas that of neighbourhood models was much lower than that of landscape and field models (Table 3). Variation partitioning showed that a relatively large proportion of explained variation in the distribution model was accounted for unique field and landscape effects, whereas there were virtually no unique neighbourhood effects. Like in spring, there were relatively large amounts of explained variation shared among sets of variables, particularly between field and landscape effects (Fig. 3).

3.3. Determinants of lark density

Models of calandra lark abundance including the year of sampling were always poorer in terms of AICc than the corresponding null models, indicating that species density did not change between years in either spring or winter. Landscape variables produced univariate models that performed consistently better than null models, whereas the support for field and neighbourhood effects was much weaker
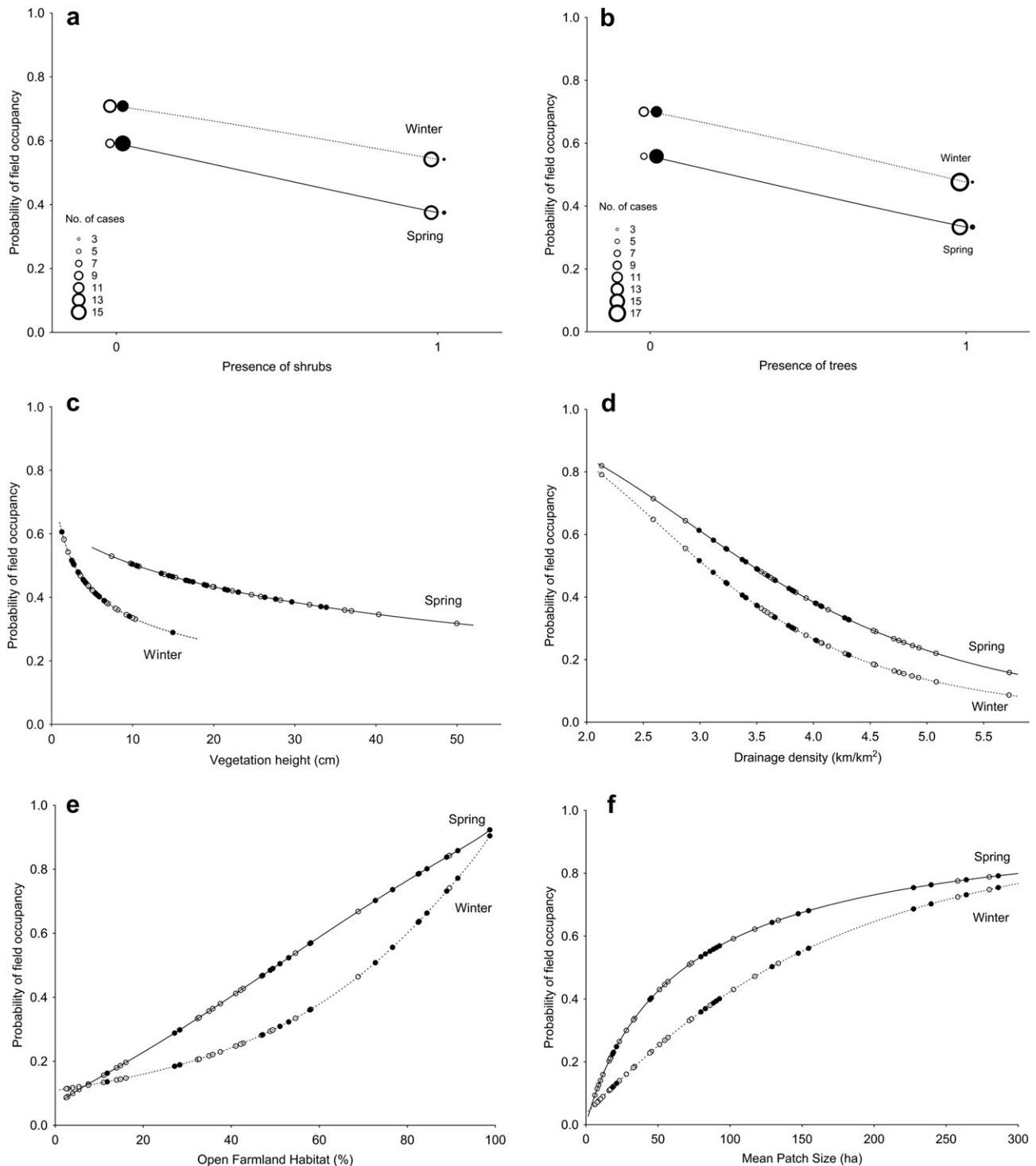
Fig. 2. Variation in spring (solid line) and winter (dashed line) probabilities of calandra larks occurrence estimated from logistic regression modelling, as a function of variables describing the characteristics and landscape context (1-km radius buffer) of fallow fields in southern Portugal. Closed and open circles indicate the predicted probabilities of occupancy for sites with and without calandra larks, respectively. For binary variables (presence of shrubs and trees), the size of symbols is proportional to the number of sites with or without calandra larks, and data points are slightly displaced along the XX axis to enhance readability. Models were fitted on transformed data (Table 1) but are depicted on the original scale.

($w_i < 0.70$) (Table 2). The presence of shrubs in winter and the presence of trees in spring were the field variables with the strongest negative relation with lark densities (Fig. 4). Spring densities tended to increase along with vegetation height, but support to this effect was relatively low (Table 2). Fallow age and the presence of stubbles

were highly correlated variables ($|R| > 0.70$), so only the former effect was used in multivariate modelling (Fig. 4). In both seasons, lark densities were strongly influenced by variables reflecting the amount and fragmentation of open farmland at the landscape scale, increasing with the total cover, local patch size and mean patch size

Table 3
Summary results of information-theoretic model selection for the relationships between calandra larks and field, landscape and neighbourhood sets of variables. For each response variable, the table provides the model selection probabilities of individual explanatory variables, and the Akaike weights (w_i) and percentage of explained variation (R^2) for each of the most plausible field, landscape and neighbourhood models. Akaike weights for variables included in the best models are underlined. Abbreviations of variables are given in Table 1 and directions of associations between response and explanatory variables are given in Table 2.

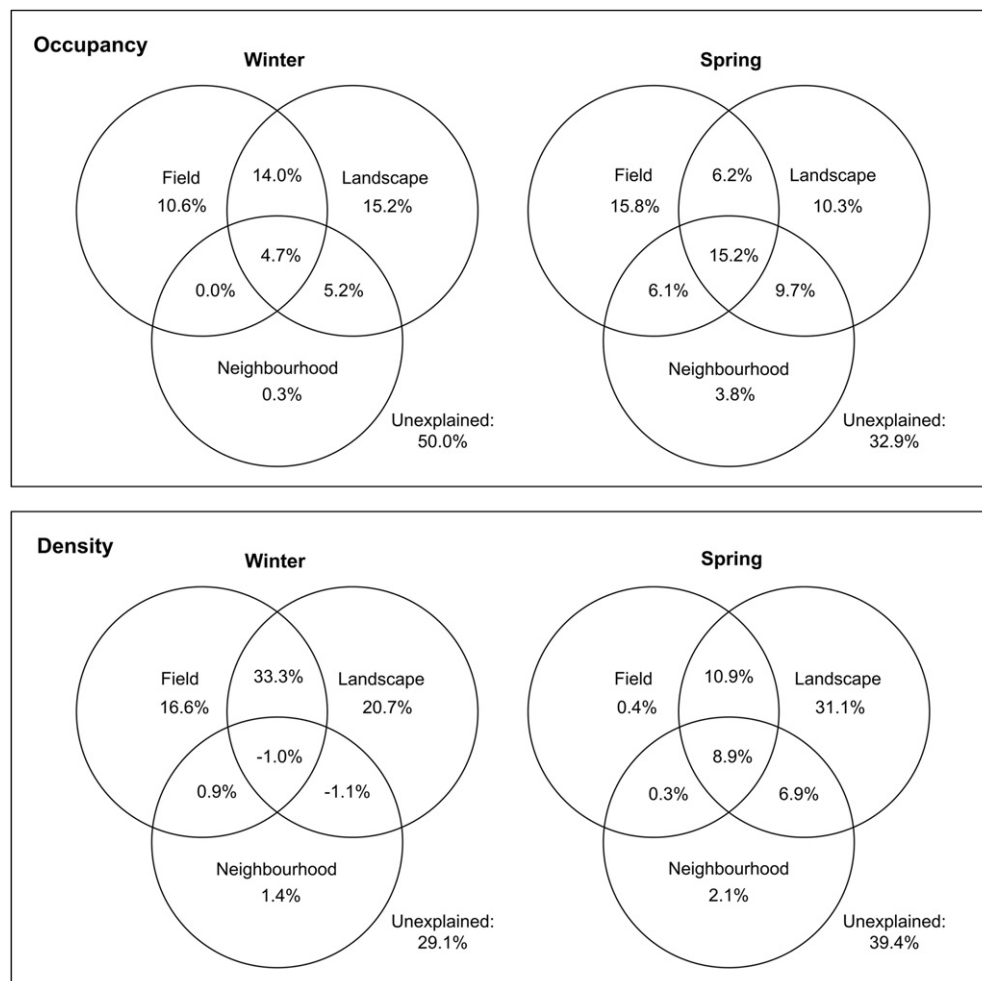|	Field								Landscape						Neighbourhood		
	R^2	w_i	AGE	VEGH	BARE	SHRUB	TREE	LVSTOCK	R^2	w_i	MPS/FARM	AWMSI	RIVER	ROAD	R^2	w_i	NEIGH
Occurrence																	
Winter	29.3	0.09	0.29	0.33	0.49	0.56	0.86	0.29	39.1	0.34	0.97[a]	0.65	0.35	0.27	10.2	0.61	0.61
Spring	43.3	0.19	0.31	0.51	0.24	0.82	0.92	0.23	41.4	0.44	0.99[b]	0.73	0.28	0.23	34.8	0.99	0.99
Abundance																	
Winter	49.8	0.23	0.53	0.32	0.14	0.77	0.18	0.13	51.9	0.40	0.84[a]	0.51	0.28	0.12	0.3	0.18	0.18
Spring	20.5	0.10	0.24	0.49	0.35	0.20	0.63	0.16	57.8	0.23	0.75[a]	0.21	0.52	0.77	18.2	0.59	0.59

[a] Analysis carried out using MPS.
[b] Analysis carried out using FARM.

of open farmland, and declining with stream density. The former three variables were highly correlated ($|R| > 0.70$), and so only the mean patch size was used in multivariate modelling, as this showed the strongest association with lark densities in both winter and spring. The negative effect of habitat fragmentation appeared strongest in winter, when lark densities tended to be lower than in spring in landscapes with low proportion of open farmland ($<60\%$) and relatively small mean patch sizes (<120 ha), but to be much higher than spring densities in less fragmented landscapes (Fig. 4). In

the breeding season, but not in winter, road density showed a very strong negative effect on lark density (Table 2; Fig. 4). There was essentially no support for neighbourhood effects on winter densities, whereas local breeding densities were positively related with that in surrounding fields (Table 2).

In multivariate modelling of spring densities, the landscape effects with the highest selection probabilities were the positive response to the mean size of open patches and the negative response to road density, both of which were included in the most

Fig. 3. Variation partitioning Venn diagrams representing the unique and shared contributions of field, landscape and neighbourhood sets of variables to explained variation in field occupancy and local densities of calandra larks, in 42 fallow fields of an open farmland landscape in southern Portugal, in both winter and spring.
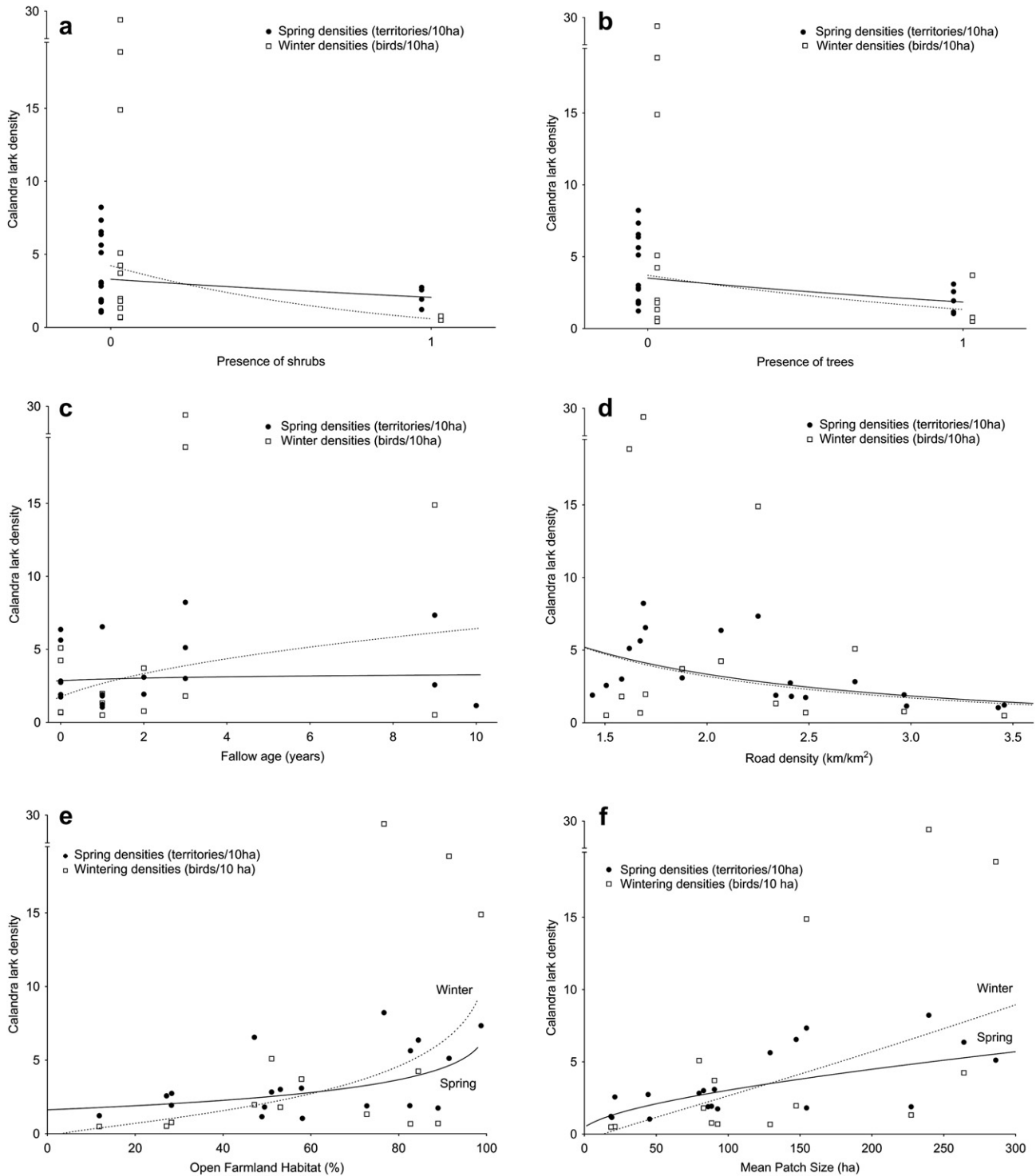
Fig. 4. Variation in spring (solid line) and winter (dashed line) densities of calandra larks estimated by linear regression modelling, as a function of variables describing the characteristics and landscape context (1-km radius buffer) of fallow fields in southern Portugal. For binary variables (presence of shrubs and trees), data points are slightly displaced along the XX axis to enhance readability. Models were fitted on transformed data (Table 1) but are depicted on the original scale. Note the scale break at 19–28 birds/10 ha.

plausible model (Table 3). The presence of trees was the only variable included in the best field model, albeit with a relatively low selection probability (Table 3). The landscape models explained almost three times as much variation as either the field or neighbourhood models (Table 3). Variation partitioning further emphasized the importance of landscape effects, showing that a large proportion of explained variation resulted from unique landscape effects, whereas that of field and neighbourhood variables was shared with landscape effects (Fig. 3).

In winter, only the mean patch size had a high selection probability, and this and the patch shape index (AWMSI) were the only variables included in the best landscape model (Table 3). The best field model included the effects of shrub presence and fallow age, though the latter variable showed a relatively low selection probability (Table 3).

The amounts of explained variation by landscape and field models were similar, whereas the neighbourhood model explained virtually no variation in lark winter densities (Table 3). Variation partitioning confirmed this pattern, indicating that a large proportion of explained variation was accounted for by the unique and shared contributions of field and landscape sets of variables (Fig. 3).

4. Discussion

This study supports preliminary observations indicating that habitat fragmentation is one of the key factors affecting the distribution and abundance of calandra larks in Mediterranean farmland (Moreira et al., 2005a; Reino et al., 2009), as suggested by their strong positive responses to the amount and patch size of open farmland habitats at the landscape scale, and their marked negative responses to the presence of trees and shrubs at the field scale. Fragmentation effects seemed stronger during winter, when calandra larks were gregarious and appeared to concentrate solely in large and continuous expanses of open habitat. Calandra larks were also sensitive to habitat fragmentation during the breeding season, though they also occurred at low density in more fragmented habitats than in winter, which may reflect the effect of territorial conspecifics in the surrounding landscape. These strong negative responses to habitat fragmentation are similar to that reported for a range of bird species inhabiting natural and agricultural grasslands (Wilson et al., 1997; Helzer and Jelinski, 1999; Winter and Faarborg, 1999; Johnson and Igl, 2001; Hamer et al., 2006), suggesting that the calandra lark is an area-sensitive species and a true grassland specialist. However, several non-exclusive hypotheses may be put forward to explain the ecological mechanisms underlying these marked fragmentation effects, which need testing in future studies.

In common with other grassland birds, it is possible that calandra larks avoid fragmented landscapes due to increased predation risks at habitat edges (Burger et al., 1994; Vickery et al., 1999), as predator density is frequently higher near edges (Flaspohler et al., 2001) and predators may use edges as travel corridors (Small and Hunter, 1988; Renfrew et al., 2005). Furthermore, mammalian carnivores in Mediterranean farmland landscapes tend to be most diverse and abundant where open habitats are fragmented by forest and shrubland patches and corridors (Pita et al., 2009). This predation hypothesis is supported to some extent by a recent study showing that calandra larks strongly avoid woody edges, only reaching densities equivalent to core open habitats at > 200 m from forest plantations (Reino et al., 2009). It is uncertain, however, whether predation risk is always lower in the interior of open areas, due to the ease with which predators can move within these habitats and the presence of open area specialized predators (Renfrew et al., 2005). This idea is supported by preliminary findings on predation patterns and predator distribution in the study area, suggesting that nest predation rates are not necessarily highest near wooded edges, and that reductions in the abundance of mammalian carnivores in open farmland landscapes may be compensated at least partly by increased abundances of some avian predators (L. Reino, R. Morgado and P. Beja, unpublished data). Irrespective of the actual predation risk, however, it is also possible that calandra larks avoid small patches bordered by woody vegetation due to reduced foraging efficiency, as it has been found that granivorous passerines tend to show higher vigilance levels and shorter food-search periods in patches with obstructed views compared to ones with clear views (Whittingham and Evans, 2004). The preference for large, continuous patches of open farmland habitat may also be related to higher resource density and lower risk of movement to exploit those resources (Söderström and Pärt, 2000; Hamer et al., 2006). This may be particularly important in this study area, because at any given time only part of the farmland habitat is available to calandra larks, as they mostly use fallow fields and

pastures in a landscape otherwise made up of cereal and ploughed fields (Delgado and Moreira, 2000). Finally, the avoidance of fragmented landscapes may have at present no adaptive value, resulting from the evolution of grassland birds in open, extensive prairies and steppes, which resulted in a strong aversion to less familiar features (Renfrew et al., 2005). Clearly, further information is needed to clarify which of these hypotheses, if any, underlie the strong responses of calandra larks to habitat fragmentation, as different mechanisms may imply different conservation options.

At the field scale, the strong avoidance of trees and shrubs by calandra larks resembles that reported for other specialist grassland birds (Coppedge et al., 2001; Ribic and Sample, 2001), and it is usually interpreted as reflecting the evolved or immediate avoidance of actual or perceived predation risk (Lima and Valone, 1991; Lima, 1993). Trees and shrubs are often used as look-out perches by avian predators, whereas shrubs frequently provide adequate cover and stalking sites to many mammalian predators. For instance, in the study area, various potential avian predators of nests or adult birds, such as birds of prey, carrion crows *Corvus corone*, azure-winged magpies *Cyanopica cyanus* and southern grey shrikes *Lanius meridionalis*, often breed and perch in isolate trees, groups of trees and small shrub patches. Another field variable affecting calandra larks was the height of herbaceous vegetation, which was negatively related with the presence of the species in spring, corroborating the strong preference for short swards shown by Moreira (1999). However, when analysing only fields where calandra larks were present, there was a tendency, albeit weak, for densities increasing with the height of herbaceous vegetation. This may be a consequence of the confounding effect of tree presence, the strongest negative correlate of breeding lark density at the field scale, as vegetation height tended to be shorter in fields with trees (14.9 ± 5.6 cm) than without trees (20.4 ± 7.6 cm). The weak positive response of calandra larks to fallow age during winter was consistent with the pattern previously described by Moreira et al. (2005a) for seed-eating passerines in the same study area. Reasons for this are unclear at present, but they may reflect a higher availability or accessibility of seeds in old grazed fallows (Moreira et al., 2005a).

In both seasons field occupancy by calandra larks increased with the occurrence of conspecifics in neighbouring fields, and spring densities were also higher where conspecifics were more abundant nearby. This pattern may partly be a consequence of spatial autocorrelation in habitat conditions, as calandra larks were locally more prevalent and abundant in large, continuous expanses of open farmland, which also favoured conspecifics in neighbouring fields. This view is supported by the generally low contribution of neighbourhood effects to the explanatory power of occurrence and abundance models, when field and landscape features were statistically controlled. Nevertheless, the relatively high proportion of explained variation on local occurrence of breeding larks that was shared among landscape, field and neighbourhood effects, may reflect some kind of density-dependent habitat selection. During this period intraspecific competition and territorial behaviour is usually responsible for a more evenly spaced distribution, which may exclude some individuals from the best habitats once a given threshold density is passed (Newton, 1992; Tellería and Pérez-Tris, 2003) and force these birds to use marginal, less favourable habitats (Jensen and Cully, 2005). This could cause the positive relationship between local occupancy and conspecific occurrence in neighbouring fields, within landscapes and fields meeting the species requirements.

In winter, neighbourhood effects were weaker, probably due to the seasonal shift of social behaviour from spring territoriality to winter gregariousness. Flocking behaviour in winter allows birds to concentrate in the most favourable areas, thereby decreasing the potential for density-dependent habitat selection. In the calandra lark, winter gregariousness may be favoured by the overabundance of seed resources in Mediterranean farmland (Diáz and Telleria,

1994), whereas the invertebrate resources used to feed the chicks may put tight limits to breeding densities. These views are supported by the observed spatial distribution patterns, with larks occupying a more restricted area in winter than in spring. The winter area probably corresponded to the best habitats, as suggested by the strong correlations between winter and spring local densities, with few birds breeding in fields that were unused in the previous winter. Furthermore, calandra larks in spring were able to settle in more fragmented landscapes than in winter, albeit at lower density than in large and continuous open farmland areas. The possibility that calandra larks use suboptimal habitats during the breeding season due to density-dependent mechanisms deserves further investigation, as this may have far-reaching consequences for the regulation of population size (Rodenhouse et al., 1997).

Consistent with other analysis of Mediterranean grassland birds (Moreira et al., 2005a; Brotons et al., 2005; Laiolo and Tella, 2006; Reino et al., 2009), this study underlined the strong detrimental effect of habitat fragmentation on calandra larks, thus pointing out the need to maintain large expanses of open farmland. This is challenging, because several factors are contributing to the rapid loss and fragmentation of open farmland across the Iberian Peninsula, most notably the long-term trends for rural depopulation and agricultural abandonment in poorly productive areas, generally followed by scrub encroachment and afforestation (Moreira et al., 2005a; Santos et al., 2006; Van Doorn and Bakker, 2007). Furthermore, fears have been expressed that the latest CAP reform will exacerbate these trends, due to a potential reduction of gross profit margins under the new CAP mechanisms in comparison to the previous support system and a derived risk of activity cessation (Oñate et al., 2007), though it is very uncertain what will be the actual extent of such effects (Tranter et al., 2007; Stoate et al., in press). Although it might be argued that abandonment is beneficial to allow land to revert to a more natural condition, there is strong evidence that maintaining agricultural landscapes is essential for biodiversity conservation in Mediterranean Europe (Santos, 2000; Moreira et al., 2005b). Agri-environment schemes provide at present the main mechanisms to support conservation farming in particularly important bird areas (Stoate et al., in press), though effectiveness greatly varies among countries (Kleijn et al., 2006). In the case of calandra lark and other grassland birds, it is essential that these schemes are targeted at sustaining the rotational cereal farming system, using for instance the guidelines suggested in the Cereal Steppes Agri-environmental Programme of Oñate et al. (2007). However, the strong fragmentation effects observed in this and other studies suggest that these schemes need to be implemented over sufficiently large and continuous areas, because maintaining relatively small patches of suitable habitat may be largely worthless (Brotons et al., 2005; Moreira et al., 2005a). Because of this, voluntary schemes such as the agri-environmental programmes may need to be combined with legal regulations preventing detrimental land use changes, as disparate decisions by neighbouring farmers might result in totally unsuitable landscape mosaics. This is particularly important, because agri-environmental incentives to maintain favourable farming practices often compete within the same territory with funding schemes encouraging incompatible land uses such as farmland afforestation, with strong negative consequences for grassland birds (Diáz et al., 1998; Moreira et al., 2005a; Santos et al., 2006; Reino et al., 2009).

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