

A multi-scale analysis of habitat selection in peripheral populations of the endangered Dupont's Lark *Chersophilus duponti*

CRISTIAN PÉREZ-GRANADOS, GERMÁN M. LÓPEZ-IBORRA and JAVIER SEOANE

Summary

Habitat selection of endangered species in peripheral populations must be considered when designing effective conservation plans, as these populations tend to occupy atypical habitats where species-environment relationships are not well understood. We examined patterns of habitat use in peripheral populations of the endangered Dupont's Lark *Chersophilus duponti* using a multi-scale approach and assessed the spatiotemporal transferability of these models to test for their generality. Our results show that at microhabitat (circles of 50-m diameter used by the species versus random points) and macrohabitat (occupied/unoccupied squares of 1 ha) scales the species selected flat and non-forested areas, but at the microhabitat scale the cover of small shrubs was also important. Models developed at patch scale (occupied /unoccupied sites) identified only site size as an important predictor of species occurrence. Habitat models transferred successfully among sites and years, which suggests that these models and our recommendations may be extrapolated over a larger geographic area. A multi-scale approach was used for identifying conservation requirements at different spatial scales. At the patch scale our models confirm it is a priority to maintain or enlarge the extent of habitat patches to ensure the viability of the studied metapopulation. At the macrohabitat scale our results suggest that reducing tree density in low slope areas would be the most effective management action. At the microhabitat scale, encouraging the presence of small and medium-sized shrubs, by clearing certain scrubs (e.g. large brooms *Genista* spp. and rosemary *Rosmarinus officinalis*) or promoting traditional low-level extensive grazing, should increase the availability of high-quality habitats for the species, and thus the number of potential territories within a patch. These recommendations largely coincide with the ones given for core populations at specific scales elsewhere.

Introduction

Habitat selection is a central theme in ecology and conservation biology, since knowledge of the habitat requirements of a species is fundamental to its effective conservation and management. Community interactions and environmental conditions usually vary throughout a species' range (Guo *et al.* 2005), and thus it is advisable to assess habitat preferences in the area where the conservation measures are required (Quevedo *et al.* 2006). More specifically, peripheral populations, considered as those located close to the edge of a species' distribution, often experience less favourable environmental conditions and are smaller, making them more prone to extinction (Sagarin *et al.* 2006, Alda *et al.* 2013).

Peripheral populations might exhibit different genetic features, which deserve particular consideration in conservation planning as evolutionarily significant units (Lesica and Allendorf 1995, Dai and Fu 2011), particularly important for maximising adaptive diversity (Thomassen *et al.* 2010). Moreover, many populations at the edge of a species' range tend to occur in marginal and atypical

habitats, which may lead to local adaptations to particular habitat types (see review in Kawecki 2008). Indeed, the variability of responses by species throughout their ranges has led to considerable interest in the geographical variation in species distribution models and the assessment of their potential transferability among different areas (Randin *et al.* 2006, Torres *et al.* 2015). In this regard, conservation actions based on information obtained from the core area of a species' range are not always applicable, or may even be counterproductive, at the edges of the range (Hampe and Petit 2005). In sum, peripheral populations may require specific conservation assessments.

Dupont's Lark *Chersophilus duponti* is a habitat specialist that mainly inhabits the shrub-steppes and pseudo-steppes of Europe and North Africa (Suárez 2010). In Europe, it is restricted to flat and open areas in Spain, characterised by sparse small shrubs and bare ground (Garza *et al.* 2005, Seoane *et al.* 2006). Its populations have been reduced by over 50% in the last two decades to only about 2,200 pairs and several populations were completely extinguished in this period (Tella *et al.* 2005, Pérez-Granados and López-Iborra 2014). The species is classified as 'Near Threatened' on the IUCN Red List due to its large distribution range (BirdLife International 2015). In Spain it is currently classified as 'Vulnerable'. The main agents responsible for the decline are habitat loss and fragmentation of natural steppes and a much-reduced grazing pressure (which facilitates shrub and tree encroachment of pseudo-steppes; Suárez 2010). Its populations in eastern and southern Spain are small and far away from the core of the species' distribution, located in the Ebro Valley and moorlands in the northern plateau (Figure S1 in the online supplementary material). These populations show ecological differentiation associated with their settlement in marginal and atypical habitats, such as alfalfa grass *Stipa tenacissima* and rosemary *Rosmarinus officinalis* steppes (Suárez 2010, Pérez-Granados and López-Iborra 2013), instead of broom *Genista* spp. or thyme *Thymus* spp. steppes, which constitute the main habitat in the species' core area (Seoane *et al.* 2006, Vögeli *et al.* 2010).

Previous habitat selection studies carried out in the core area of the species in Europe indicate that this lark is a habitat specialist sensitive to patch size and vegetation structure (Garza *et al.* 2005, Seoane *et al.* 2006, Vögeli *et al.* 2010). Such detailed evaluation is lacking for African populations (but see García *et al.* 2008). Thus, research on Spanish peripheral populations of Dupont's Lark could be a good case study to understand habitat preferences of the species at the limit of its range.

With this motivation, we aimed to determine the influence of environmental predictors on the breeding spatial distribution of Dupont's Lark at three different scales (microhabitat, macrohabitat and patch scales) in three isolated and declining populations located in the south of the species' main distribution area in Spain. Multi-scale approaches to identifying habitat preferences of the species are preferable to single-scale studies because they provide a better overview of the gamut of factors determining the presence of a species, and thus better criteria to define effective conservation measures (Leopold and Hess 2013, Traba *et al.* 2013).

We built and transferred habitat models among sites and between sampling years, in order to identify those predictors that affect the occurrence of the study species and whether or not their effects are constant or differ among study sites. The evaluation of the transferability of distribution models among populations is important in deciding whether conservation guidelines can be applied over multiple regions (Vernier *et al.* 2008, Zanini *et al.* 2009, Torres *et al.* 2015). Finally, we provide information for the first time about the habitat selection of this lark in two atypical habitats, including rosemary steppe, a habitat type not previously studied and rarely used by the species, and wooded moorland (Suárez 2010). We use our results to identify the conservation requirements of Dupont's Lark across spatial scales.

Materials and methods

Study area

The study area comprised 13 sites (1,457 ha overall) located in the Rincón de Ademuz region, in the eastern Iberian Peninsula (40°04'N, 1°20'W; Figure 1). These comprised all the potential sites in the region that the species may inhabit, and seven of them are declared as Special Protection Areas

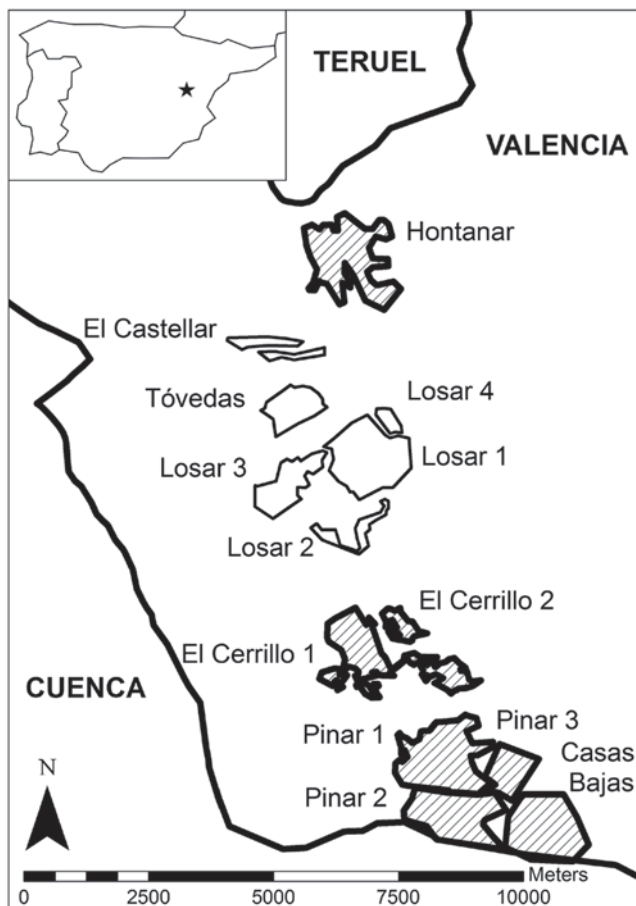


Figure 1. Location of the study area in Rincón de Ademuz (Valencia). Habitat patches identified by name. The inset shows location of the study area (star) in the Iberian Peninsula. Special Protection Areas (SPAs) are marked with black stripes.

(SPA; 1,057 ha, Fig. 1). Potential sites were defined as the areas in which the Dupont's Lark was found in previous studies or all areas in the Rincón de Ademuz that presented flat relief, low scrub and had an extent larger than 10 ha. Sites were surrounded by an unsuitable matrix of forests and agricultural areas (Pérez-Granados *et al.* 2013). Nine sites had been occupied by the species over the last two decades, but currently Dupont's Lark is present in only five of them (Pérez-Granados and López-Iborra 2013). This area is located at an average of 1,100 m. asl, and has a mean annual temperature of about 10°C and a mean annual precipitation of 550 mm. The area exhibits an undulating topography with large flat areas dedicated to crops, especially almond trees *Prunus dulcis*, or scrub. Natural vegetation consists mainly of open and sparse shrub communities dominated by thyme, broom *Genista scorpius* and rosemary, with some interspersed pines *Pinus* spp. and junipers *Juniperus* spp.

Bird data

We surveyed bird abundance from March to June 2011 and 2012 with the territory mapping method over 53–60 sampling days each year (Bibby *et al.* 2000). Unoccupied sites were visited

three times and occupied ones were visited at least five times each year, since four visits are required to detect 98% of the territories within a site (Pérez-Granados and López-Iborra in press). The walking of plots was scheduled to begin at different places on consecutive visits to reduce biases related to time of day or season, and the routes were designed to cover plots completely (considering a 500-m maximum detection band on each side of the observer). Locations of all birds detected on different days were mapped with ArcGIS 9.3 (ESRI 2008) and a territory was defined when two records of a singing male were made within a radius of 100 m, which corresponds to the radius of a circle comprising the average territory core area (3.7 ha) estimated for the species during the breeding season (104.3 m in Layna moorland; Garza *et al.* 2005). We determined the centre of each territory after averaging the locations of clumps of registrations located within a radius of 100 m. Censuses were carried out at dawn by the same person (CPG) walking at a constant and slow speed (1–3 km/h) on dry and windless days. The survey was repeated in 2013 and 2014 to test for temporal transferability of models (see below).

Habitat data

Microhabitat scale (focal points)

The microhabitat structure of the points used by the species during the breeding season across all visits was characterised from May to June in 2011 and 2012 in the three main sites of the study area (Hontanar, Losar 1 and Pinar 1; Figure 1). We selected this subset of the currently occupied sites within the study area because the number of males in the other two occupied sites (Cerrillo 1 and Losar 3) was too low for statistical analyses (mean number of males during the study period was two and five, respectively), despite the large patches they inhabited (125 and 59 ha, respectively). Sites were analysed independently, because they differed in aspects of vegetation that we believed critical for Dupont's Lark. Hontanar was a scrubland dominated by dwarf thyme shrubs with a few trees interspersed, while Pinar 1 was similar but has a much greater density of trees in some areas than the species tolerates in the rest of its distribution range (Seoane *et al.* 2006, Suárez, 2010). In contrast, Losar 1 was a steppe dominated by rosemary rather than thyme shrubs.

In each site, microhabitat features were measured in 25-m radius circles centred on lark locations ("lark points") and in an equal number of control locations ("random points") selected at the end of each breeding season and constrained to be at least 50 m from lark points and to not overlap between years. Within each of those circles habitat variables were estimated in nine 10-m diameter sample circles (Fig. 2) and averaged. For this purpose, and given the difficulty of precisely locating this species by ear, we only considered birds detected closer than 25 m to the observer.

In each 10-m diameter sample circle, we recorded the cover of bare rock, pebble, bare soil, herbaceous plants and scrubs, distinguishing thyme, broom and rosemary (following methods in Prodon and Lebreton 1981). We estimated the cover of grasses and each shrub species considering separately three height categories: low (< 20 cm), medium (20–40 cm), and high (> 40 cm), and mean and maximum vegetation height (see Pérez-Granados *et al.* 2013). We also recorded the slope of terrain in each 10-m circle (in degrees) with an inclinometer (CJQ-1, G.I.S. Iberica, Cáceres; 1° accuracy). Finally, on the total surface area of the 25-m radius circle we counted the number of trees and visually estimated the percentage covered by crops, after previous training.

Macrohabitat scale (home ranges)

At a larger spatial scale, better suited to describe the individual home ranges (macrohabitat scale, hereafter), we divided the whole area of the three selected sites into a grid of 100 x 100 m squares. Each square was surveyed from May to June 2012 to record the cover of crops, bare soil, grass, open scrub formations of rosemary, thyme or broom (visually estimated percentages) and the number of trees. We distinguished between pines and junipers because of their potentially different effects on Dupont's Lark according to their morphological structure (pines tend to be taller while junipers have

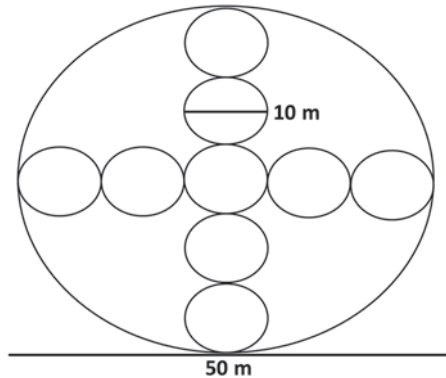


Figure 2. Sampling procedure at microhabitat scale. Predictor variables (see details) were measured in nine circles of 5 m radius located in the centre, at 10 and 20 m from the centre of each sampling point in cardinal directions.

denser foliage), and because pine removal may be authorised as part of habitat management action while junipers are protected under Habitat Directive 92/43/CEE. We further calculated slopes for the 1-ha squares through a Digital Elevation Model obtained from 1:25,000 topographic maps (MDT25) provided by the National Geographic Institute. The mapping of territories carried out in both years of study allowed us to identify occupied and unoccupied squares in each site. A square was considered occupied when at least one territory centre was located within it in any study year.

Patch scale (occupied/unoccupied sites)

We compared habitat variables, from patches occupied or not, in order to identify the main factors that may be related to Dupont's Lark occurrence (assuming that populations at the worst sites disappeared first and the best sites are the last to remain occupied). A patch was considered occupied when at least one Dupont's Lark territory was registered within in any study year. Patch scale habitat data were collected from March to June 2011 in the 13 sites in the study area (Pérez-Granados and López-Iborra 2013; Figure 1). We surveyed 15 randomly selected 25-m radius circles in sites larger than 100 ha, and only 10 in smaller sites. In each of these circles we used the same methodology to estimate the same variables as at the microhabitat scale, except for crop cover and slope. Crop cover was estimated using the freely available images from the Spanish National Aerial Orthophotography Plan (PNOA), while slope was calculated through the digital elevation model used for the macrohabitat scale. These data were recorded at random points selected independently from those at the microhabitat scale. PNOA images were also used to calculate site size, considered as the area of natural vegetation potentially adequate for the species, and the distance among patches to the nearest occupied ones.

Statistical analyses

We studied microhabitat preferences by comparing lark points with random points (Seoane *et al.* 2006). Data from both study years were pooled in this analysis since we consider that the effect of lack of independence in these data should be negligible. Lark points considered for each year to estimate habitat use were spaced at least by 50 m and their number (around 20 per year, see Table 1) is less than the double the number of territories in each site (11–13, Pérez-Granados and López-Iborra 2013). Thus, and given that most, but not all, birds were identified as males, a given individual would have contributed on average with less than two lark points per year.

Table 1. Mean \pm SD of the microhabitat variables measured in lark and random points in the three main populations of the study area. Number of points of each type are shown in parentheses. The p column shows the significance level of the One-way ANOVA tests when difference among points was significant ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$). Significances were calculated from One-way ANOVA analysis in each site, corrected by False Discovery Rate.

Variable	Hontanar			Losar 1			Pinar 1		
	Lark (N=40)	Random (N=40)	P	Lark (N=45)	Random (N=45)	P	Lark (N=40)	Random (N=40)	P
Slope $^{\circ}$	2.0 \pm 1.4	5.3 \pm 3.5	***	2.3 \pm 0.81	5.2 \pm 3.1	***	1.5 \pm 0.7	2.8 \pm 2.0	***
Crops %	0 \pm 0	7.1 \pm 23.6	**	0 \pm 0	0 \pm 0		0 \pm 0	3.0 \pm 9.4	
Bare rock %	10.2 \pm 4.4	8.2 \pm 5.6		8.1 \pm 5.0	18.1 \pm 9.0	***	15.4 \pm 4.0	15.4 \pm 12.7	
Pebble %	11.5 \pm 3.2	9.6 \pm 4.0	*	10.2 \pm 4.6	8.0 \pm 5.1	*	9.6 \pm 3.7	11.6 \pm 5.6	
Bare soil %	4.6 \pm 2.3	4.8 \pm 3.4		12.8 \pm 7.6	5.4 \pm 2.4	***	4.8 \pm 2.3	7.6 \pm 8.6	
Herb. < 20 cm %	9.8 \pm 4.8	9.9 \pm 5.2		8.1 \pm 3.6	6.1 \pm 2.4	**	19.6 \pm 3.9	20.0 \pm 12.5	
Herb. 20-40 cm %	3.8 \pm 1.9	11.1 \pm 18.6	*	1.4 \pm 1.3	1.9 \pm 2.9		4.8 \pm 1.8	5.9 \pm 3.7	
Herb. > 40 cm %	0.1 \pm 0.2	1.5 \pm 4.9		0.1 \pm 0.4	0.2 \pm 0.7		0 \pm 0	2.6 \pm 3.6	***
Rosemary < 20 cm %	0.5 \pm 1.3	2.0 \pm 3.1	**	10.0 \pm 5.2	8.8 \pm 5.3		0 \pm 0	0 \pm 0	
Rosemary 20-40 cm %	0.4 \pm 1.1	2.4 \pm 3.8	**	9.8 \pm 4.6	11.2 \pm 5.6		0 \pm 0	0 \pm 0	
Rosemary > 40 cm %	1.4 \pm 4.1	7.1 \pm 10.9	**	15.1 \pm 7.9	24.9 \pm 8.6	***	0 \pm 0	0 \pm 0	
Broom < 20 cm %	8.2 \pm 3.6	4.9 \pm 2.9	***	2.9 \pm 2.6	1.8 \pm 1.5		6.3 \pm 2.4	4.7 \pm 3.8	**
Broom 20-40 cm %	9.2 \pm 5.6	8.0 \pm 4.8		2.1 \pm 2.3	1.6 \pm 2.2		5.9 \pm 4.0	5.0 \pm 5.1	
Broom > 40 cm %	5.7 \pm 4.4	11.0 \pm 10.7		0.1 \pm 0.3	0.6 \pm 1.7		0.7 \pm 1.2	4.6 \pm 11.5	*
Thyme < 20 cm %	25.1 \pm 9.2	13.1 \pm 7.1	***	18.5 \pm 6.0	10.1 \pm 4.6	***	22.6 \pm 5.0	17.7 \pm 10.34	**
Thyme 20-40 cm %	8.5 \pm 5.0	5.8 \pm 4.3	**	2.6 \pm 2.6	1.2 \pm 2.5	***	8.9 \pm 2.4	4.9 \pm 3.1	***
Thyme > 40 cm %	0.6 \pm 1.3	0.3 \pm 1.0		0.2 \pm 0.6	0.1 \pm 0.4		0.9 \pm 2.2	0.4 \pm 1.3	
Maximum height cm	43.7 \pm 5.5	72.3 \pm 29.8	***	74.4 \pm 100.4	95.8 \pm 30.6		52.0 \pm 12.5	105.0 \pm 67.8	***
Mean height cm	27.4 \pm 5.6	38.2 \pm 8.0	***	34.5 \pm 7.5	38.3 \pm 4.9	**	24.9 \pm 4.1	28.5 \pm 8.0	***
Number of trees	0 \pm 0	2.9 \pm 6.0	**	0.9 \pm 0.3	9.9 \pm 9.5	***	1.9 \pm 2.0	12.2 \pm 13.5	***

In addition, data were recorded along the whole breeding season, which means that the eventual duplicate records for a bird would be separated by weeks or months, and then these separate records may be considered as independent events of habitat choice. For records obtained in different years of study, it should be taken into account that only about a half of the adult birds may survive between successive years (Laiolo *et al.* 2007), which would further decrease the effect of non-independence of data. We tested differences between sampling points using one-way analysis of variance at each site, with *P*-values adjusted using the False Discovery Rate (FDR, Benjamini and Hochberg 1995). To identify the main vegetation gradients at this scale we applied a varimax rotated Principal Components Analysis (PCA; Dormann *et al.* 2013, Pérez-Granados *et al.* 2013) to the lithological and natural vegetation cover variables (arcsine transformed) of the three sites together. We selected the axes of this PCA that had eigenvalues higher than one, and used them as explanatory factors in subsequent analyses. At the macrohabitat scale we tested the differences between environmental variables in occupied and unoccupied squares in each site by one-way analysis of variance corrected by FDR.

At each site we used Hierarchical Partitioning (HP) analyses to identify the environmental variables with greater influence on habitat use (microhabitat scale) and home ranges (macrohabitat scale) during the breeding season. This method allowed us to identify those predictors with an important independent – as opposed to partial – relationship with the occurrence of Dupont's Lark in one point or square (Mac Nally 2002; and see applications in bird studies in López-Iborra *et al.* 2011, Reis *et al.* 2012). We used logistic regression and log-likelihood as the goodness-of-fit measure and tested statistical significances of the independent contribution of each variable by a randomization procedure with 999 bootstraps (Mac Nally 2002). We reduced the potential impact of collinearity among variables by removing those with Spearman rank correlation coefficients above a cut-off of $|0.7|$ (Randin *et al.* 2006, Dormann *et al.* 2013).

To take into account spatial autocorrelation in our HP analyses we included an autocovariate in analyses at microhabitat and macrohabitat scales (Lichstein *et al.* 2002). At the microhabitat scale, we choose the radius of a circle including the average territory core area reported for the species during the breeding season (about 100 m according to Garza *et al.* 2005) and we quantified the autocovariate as the total number of lark points within a 100-m radius buffer around a lark or random point. At the macrohabitat scale we estimated the autocovariate as the number of 1-ha squares occupied by the species among the eight neighbouring squares around each grid cell (Segurado *et al.* 2006).

To evaluate whether there is regional or temporal variation in habitat preferences, taking into account model uncertainty, we built habitat models for each site at the macrohabitat scale following a model averaging strategy (Cade 2015). We addressed the transferability of habitat models in space and time by both a spatial and a temporal cross-validation strategy. We used presence/absence of the species in a 100 × 100 m square as a dependent variable and habitat measurements as potential predictor variables. First, we ranked the possible models according to their Akaike's information criterion adjusted for small samples (AICc) and selected the subset of models having $\Delta\text{AICc} \leq 2$ (Burnham and Anderson 2002). Then, we averaged the suitability estimates for each square weighting the predictions of the models by their AICc (Cade 2015). We used these predictions to assess the discrimination ability of the models using AUC (Sing *et al.* 2005). Large AUC values are associated with higher estimation-observation agreement (Fielding and Bell 1997). For the spatial cross-validation, we applied the set of models developed for each site to the data sets of the other populations. For the temporal validation, we applied models built with presence-absence data collected during 2011–2012 to a set of data of the same site collected during 2013–2014 by the same observer.

At patch scale we employed Generalized Linear Models (GLM, binomial error distribution; logit-link function) to test the relationship of selected environmental predictors estimated at the site level to species occurrence (presence/absence at each site as a dependent variable). Due to the low sample size ($n = 13$ potential sites), models were kept simple (just building univariate models). Models were ranked according to their AICc, and we considered a concrete variable to have an effect on Dupont's Lark occurrence when the model including this variable had an AICc at least two units lower than the null model (Burnham and Anderson 2002). Given previous knowledge

of the species, we hypothesised that the probability of presence of Dupont's Lark at a given site may be positively affected by size (larger sites are more likely to be occupied; Vögeli *et al.* 2010), and negatively by slope (since the species is largely cursorial; Suárez 2010), population isolation (because of the species' very low annual dispersal movements; Laiolo *et al.* 2007) and tree cover (which the species avoids even if the trees are small; Seoane *et al.* 2006). In addition, habitat structure has an important effect on Dupont's Lark presence (Garza *et al.* 2005, Seoane *et al.* 2006), so we developed univariate models for each scrub species, which differ in their height, foliage density and main cover (Dupont's Lark prefer the smaller and sparser thyme to the other species). Similarly, we hypothesised that herbaceous and bare soil cover could be related to lark occurrence by affecting foraging success (we expected to find the species in patches with lower herbaceous cover and higher bare soil cover).

We conducted the data analysis with R 3.1.1 (R Development Core Team 2009) using specialised packages when needed (hier.part for HP, Walsh and Mac Nally 2008; MASS for AICc estimates; Venables and Ripley 2002; MuMIn for model averaging; Barton 2011; and ROCR for AUC calculations; Sing *et al.* 2005). We conducted GIS analysis (random point placement, surface covered by crops, Digital Elevation Model and distance to nearest occupied patch) in ArcGIS 9.3 (ESRI 2008).

Results

Microhabitat scale (focal points)

Dupont's Lark microhabitat preferences were similar among sites, and lark points differed from random points in a number of predictor variables (Table 1). In the three study sites the slope, vegetation height and number of trees were significantly lower in lark than in random points (Table 1). Larks were only detected in points with slopes lower than 7.7° and with a low number of trees (a maximum of eight trees per sampling point). Likewise, larks were never detected in crops in any of the studied populations (Table 1), and tended to occupy areas with higher cover of small-shrubs (Table 1). This general pattern was independent of the vegetation type of the study sites.

Soil and vegetation characteristics of the study sites were summarised in four PCA axes (69.1% of total variance of data; see Table S1). The first axis (PCA I; 31.0% of the variance) contrasted rosemary-dominated scrub with broom or thyme communities. The second (PCA II; 14.1% of the variance) describes a gradient of grass cover, while the third axis (PCA III; 14.4% of data variability) defined a gradient of broom cover. The fourth axis (PCA IV, 9.6% of the variance) distinguished areas dominated by bare rock and vegetated areas.

PCA II and crops showed a high correlation ($R_s = 0.72$). Thus, we excluded crops in HP analyses due to their low presence in the study area (Table 1). Slope, PCA I and PCAII Axis, number of trees and the spatial term had a significant and similar effect on Dupont's Lark territory selection among study sites (Table 2). However, the independent contribution of the remaining predictors varied greatly among populations (Table 2).

Macrohabitat scale (home ranges)

In general, the species inhabited non-cultivated squares with gentler slopes, more small chamaephytes (thyme) and fewer trees, independent of the vegetation type of the study sites (Table 3). However, HP analyses showed less consistency among study sites at this scale than at a microhabitat scale, since only the number of pines and the spatial term was significant in all sites (Table 4).

A large number of similarly plausible models was found for each site. The number of candidate models and the number of times each predictor was selected in those models for each site can be found in Table S2. Predictions agreed with the observed occurrence according to AUC (Fig. 3), and their transferabilities (as measured by AUC) were very high both in space and time (Fig. 3).

Table 2. Habitat variables related to species preference according to hierarchical partitioning (HP) analyses at the microhabitat scale. PCA axes come from a varimax rotated Principal Components Analysis performed with the lithological and vegetation variables. Individual contribution of each variable is shown as a percentage (1%) of the total deviance explained by the variables. The sign of the effects are obtained from univariate regression models. The z-test column shows the significance level of the randomization tests for the independent contributions (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). % Dev is the percentage of deviance accounted by a logistic regression model including all variables.

	Hontanar			Losar 1			Pinar 1		
	Sign	1%	z-test	Sign	1%	z-test	Sign	1%	z-test
Spatial term	+	21.9	***	+	15.3	***	+	22.3	***
Slope	-	14.4	***	-	12.7	***	-	11.0	***
PCA I	+	7.3	***	+	6.1	**	+	15.8	***
PCA II	+	14.4	***	+	4.6	*	+	11.8	***
PCA III	+	1.8		+	28.8	***	+	8.7	***
PCA IV	+	1.0		+	12.4	***	+	2.8	
Maximum height cm	-	17.7	***	-	0.6		-	11.0	***
Mean height cm	-	11.8	***	-	2.3		-	6.2	***
Number of trees	-	9.9	***	-	16.7	***	-	10.5	***
%Dev		100			69.9			100	

Patch scale (occupied/unoccupied sites)

Only one univariate model for the probability of occurrence across sites was clearly better than the null model (AICc = 19.3). This model describes a positive relationship between site size (AICc = 17.1) and Dupont's Lark presence. Dupont's Larks were detected on average in patches two times larger than unoccupied ones, with a minimum site size of 59 ha (Table 3).

Discussion

We found that Dupont's Lark show similar habitat preferences between the core area and peripheral populations at all scales analysed. Slope degree, density of trees and crop cover seem to be good environmental predictors in both population types, filtering the distribution of the species throughout its range (Garza *et al.* 2005, Seoane *et al.* 2006). It is revealing that there were similar fine-grained preferences for focal points, even among sites whose habitat configuration differed notably. In our view, this indicates that birds are able to find their preferred niche within arguably atypical habitats (e.g. rosemary shrubs and sparse woodlands), which contrasts with the classical view of Dupont's Lark as a strict low-shrub steppe specialist.

Along these lines, an enlightening result of our study is the first description of the microhabitat preferences of Dupont's Lark in rosemary steppe. Rosemary is a well-distributed shrub species in Spain (López 2007). However, there are only five known populations of Dupont's Lark in this habitat type, most of them located in peripheral areas where the species cannot find more typical habitats (Suárez 2010). Our results suggest that the species successfully occupies alternative habitats, similar to those preferred in its core areas, by exploiting favourable microhabitat features. Specifically, the species had a strong preference for thyme-dominated areas even at sites where rosemary was the dominant vegetation.

Dupont's Lark is reported to be intolerant of trees in its core areas in the Iberian Peninsula (Seoane *et al.* 2006, Suárez 2010). Thus, we were surprised to find that the larks completely avoided trees at focal points, but they tolerated a higher density of trees within their home ranges than previously described. However, we attribute this tolerance to the clumped spatial distribution of trees, which allows the birds to exploit the open areas found within home ranges. The natural encroachment of the study sites –which were formerly heavily grazed – is likely to be squeezing the regional distribution of Dupont's Larks into the ever-diminishing natural and semi-natural

Table 3. Mean \pm SD of the habitat features measured in occupied and unoccupied 1-ha squares (macrohabitat scale) and habitat patches (landscape scale) by Dupont's Lark in the three main populations of Valencia. At the macrohabitat scale the *p* column shows the significance level of the One-way ANOVA tests, corrected by False Discovery Rate, when difference among type 1-ha square was significant, whereas at the landscape scale *P* shows the significance of the logistic regression models. In both cases (**P* < 0.05, ***P* < 0.01, ****P* < 0.001).

	MACROHABITAT SCALE									LANDSCAPE SCALE		
	Hontanar			Losar 1			Pinar 1			Occupied	Unoccupied	<i>P</i>
	Occupied	Unoccupied	<i>P</i>	Occupied	Unoccupied	<i>P</i>	Occupied	Unoccupied	<i>P</i>			
(N=43)	(N=149)		(N=43)	(N=133)		(N=32)	(N=159)		(N=5)	(N=8)		
Site size (ha)										155.1 \pm 62.3	80.8 \pm 58.0	*
Distance occupied patch (m)										785.6 \pm 833.6	334.0 \pm 382.5	
Slope $^{\circ}$	4.2 \pm 2.6	8.8 \pm 5.1	***	4.0 \pm 1.0	7.5 \pm 6.0	***	2.7 \pm 0.7	2.9 \pm 2.0		4.1 \pm 2.2	2.7 \pm 1.4	
Crops %	1.5 \pm 5.8	8.6 \pm 27.4		0	0.3 \pm 2.7		0	2.1 \pm 10.9		7.5 \pm 11.9	9.1 \pm 16.2	
Bare ground %	13.6 \pm 6.3	17.4 \pm 9.7		30.6 \pm 10.2	28.5 \pm 12.3		19.7 \pm 7.7	14.7 \pm 7.8	**	33.2 \pm 13.1	27.3 \pm 7.5	
Herbaceous %	26.4 \pm 10.7	27.3 \pm 11.2		13.7 \pm 5.9	14.3 \pm 7.3		23.9 \pm 9.6	31.1 \pm 13.6	**	19.5 \pm 8.4	29.1 \pm 13.5	
Rosemary %	4.5 \pm 8.9	7.7 \pm 15.7		31.1 \pm 10.3	35.9 \pm 11.6	**	0	0		14.5 \pm 18.4	9.9 \pm 18.2	
Broom %	31.1 \pm 15.3	27.2 \pm 16.1		6.7 \pm 3.4	6.9 \pm 3.8		23.6 \pm 10.4	38.1 \pm 19.3	***	13.2 \pm 7.6	15.9 \pm 8.1	
Thyme %	24.4 \pm 10.7	20.5 \pm 11.8		17.9 \pm 8.5	14.4 \pm 5.7	*	32.8 \pm 13.7	16.1 \pm 12.6	***	19.5 \pm 5.9	17.8 \pm 6.1	
Maximum height (cm)										79.2 \pm 22.9	87.0 \pm 23.9	
Mean height (cm)										33.0 \pm 10.2	27.2 \pm 9.8	
N $^{\circ}$ Pines	0.0 \pm 0.1	2.1 \pm 7.1		0.5 \pm 1.0	1.9 \pm 2.4	***	5.1 \pm 10.7	54.9 \pm 64.1	***			
N $^{\circ}$ Junipers	1.3 \pm 2.1	4.6 \pm 6.3	***	5.8 \pm 7.7	44.0 \pm 37.1	***	35.2 \pm 17.6	21.1 \pm 21.1	***			
Number of trees (N $^{\circ}$ /ha)										40.9 \pm 26.8	56.8 \pm 32.2	

Table 4. Habitat variables related to species distribution according to hierarchical partitioning (HP) analyses at a macrohabitat scale. The individual contribution of each variable is shown as a percentage (%I) of the total deviance explained by the variables. The signs of the effects are obtained from univariate regression models. In analyses that included more than 9 variables (Hontanar and Losar), with results sensitive to the ordering of variables (see Olea *et al.* 2010), the table shows the mean of %I and mean of variable ranking calculated from 10 HP runs with variables randomly ordered, while in Pinar only 1 HP was run since it was not sensitive to the ordering of variables. Numbers in parentheses show the range found in the 10 runs. The z-test column shows the significance level of the randomization tests for the independent contributions (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Rosemary % was not used in the Pinar analysis since this shrub was lacking this area. % Dev is the percentage of deviance accounted by a logistic regression model including all variables.

	Hontanar				Losar 1				Pinar 1		
	Sign	I% (range)	z-test	Rank (range)	Sign	I% (range)	z-test	Rank (range)	Sign	I%	z-test
Spatial term	+	51.4 (48.3–55.5)	***	1 (1–1)	+	38.9 (34.4–43.0)	***	1.2 (1–2)	+	48.9	***
Slope °	-	19.1 (17.3–19.6)	***	2 (2–2)	-	11.2 (10.7–11.5)	***	3.2 (3–4)	-	2.1	
Crops %	-	3.3 (2.3–5.0)		6 (5–7)	-	0.6 (0.3–1.1)		9 (9–9)	-	1.4	
Bare ground %	-	2.9 (1.9–3.8)		6.1 (5–7)	+	1.0 (0.6–1.3)		7.8 (7–8)	+	3.4	
Herbaceous %	+	1.2 (0.4–1.9)		9 (8–10)	-	1.4 (1.2–1.7)		7 (6–8)	-	4.5	**
Rosemary %	-	1.3 (0.8–2.5)		8.7 (5–10)	-	2.0 (1.7–2.5)		5.9 (5–6)			
Broom %	+	1.1 (0.5–1.7)		9 (8–10)	-	0.4 (0.2–0.9)		10 (10–10)	-	5.3	***
Thyme %	+	2.9 (1.9–3.8)		6.2 (5–8)	+	2.3 (1.8–2.9)		5.2 (5–7)	+	14.4	***
N° Pines	-	7.2 (5.9–9.6)	***	4 (4–4)	-	9 (7.6–13.0)	***	3.9 (3–4)	-	17.5	***
N° Junipers	-	9.6 (8.7–13.9)	***	3 (3–3)	-	33.2 (29.0–37.6)	***	1.8 (1–2)	+	2.5	
%Dev	53.4				65.3				62.5		

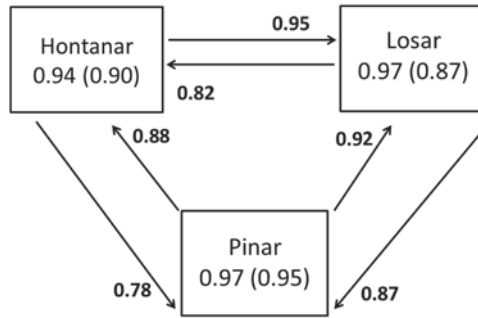


Figure 3. Summary of AUC values of the plausible models for each study site. Arrows indicate the direction of the spatial cross-validation of the models to the other sites, while brackets indicate the temporal transferability of the models calculated with an independent set of data collected during 2013–2014 at the same sites.

open areas. Indeed, and contrary to our assumptions, the abundance of juniper trees had a positive effect on the species' distribution in the wooded moorland. We think that this is due to the fact that junipers segregate spatially from pines, which are taller and strictly avoided by larks, and thus male territories end up in areas with a relatively high density of junipers.

The high habitat model performance and transferability among sites provide evidence against local habitat specialisation in the studied peripheral populations. Similarly, transferability across time suggests inter-annual stability of habitat preferences. Thus, we think our models would likely be useful for conservation planning and management over a larger geographic area, including reserve design and assessment (Guisan and Thuiller 2005, Tuanmu *et al.* 2011). Such a high transferability could be favoured by the aggregated distribution of the species, since clumped occurrence patterns make it easier to predict spatial distributions than sparse ones (Vallecillo *et al.* 2010). If so, we suspect that our model performance would decrease if transferred to areas inhabited by Dupont's Larks in other climatic regions, with less aggregated distribution or different land uses (Pearson *et al.* 2004, Luoto *et al.* 2005).

At the larger scale, the size of habitat patches was the only relevant variable explaining current Dupont's Lark distribution, as has been found elsewhere (e.g. Nogués-Bravo and Aguirre 2006, Vögeli *et al.* 2010). This is not surprising given that our studied populations are declining and occupy a highly fragmented and isolated landscape (Pérez-Granados and López-Iborra 2013). Indeed, all of the studied plots might fulfil the fundamental habitat requirements of the species, and therefore those currently unoccupied sites could be colonised in future if the total population grows (Vögeli *et al.* 2010).

Conservation implications

Multi-scale habitat studies offer important tools for identifying requirements of rare and elusive species at different scales (Razgour *et al.* 2011), which are essential to guide conservation management practices (Gonthier *et al.* 2014). Different processes may drive the population trends of endangered species at the different scales, and thus specific strategies should be adopted at each scale (Marty *et al.* 2014). Our patch scale results show that less than half of the potential habitat patches were occupied by Dupont's Lark, and thus a first objective must be to increase the number of patches occupied. Site size is related to occupation probability, but crop development and shrub and tree encroachment are ongoing processes in the study area that are reducing patch sizes to critical thresholds. Indeed, those phenomena seem to have resulted in species extinction in some previously occupied patches in the study area (Pérez-Granados and López-Iborra 2013). Thus, our main recommendation at this scale is to avoid further reduction in the size of the remnant patches and to

study the possibility of returning some of them to their previous extension. Interestingly, the distance to occupied patches has not been found to have a significant effect on the species' occurrence, despite the fact that Dupont's Lark is considered to be a poor disperser (Laiolo *et al.* 2008). Therefore, facilitating connectivity among patches, which has been commonly proposed to ensure the viability of the species (Tella *et al.* 2005, Suárez 2010, Vögeli *et al.* 2010), does not appear to be a priority in this region, and the emphasis should be placed on increasing the extent of the patches.

Population viability is related to its size (Mills 2007), and thus habitat should be managed to favour the settlement of new territories, especially within the larger sites. Slope is an important environmental predictor at both macrohabitat and microhabitat scales. Slope is usually out of the reach of habitat management actions, but should be taken into account in proposed management measures only in areas with the appropriate slope. The vegetation feature most important at the macrohabitat scale is the density of trees, especially pines. Thus, we expect that reducing their number, at least to a density similar to that found in occupied squares in our study patch with more pines (five pines/ha), should increase the habitat suitability for the species, and thus the number of potential territories within a patch. Likewise, reforestation should be prohibited within all potential sites, since it would be detrimental for the species (Seoane *et al.* 2006).

At the microhabitat scale, vegetation management may act to increase the availability and quality of preferred places for feeding, nesting, etc. At this scale our results have shown that although the species may tolerate rosemary, it favours areas dominated by small and medium-sized thymes, and to a lesser extent small brooms. Therefore, these features could be promoted by clearing specific scrubs or promoting traditional low-level extensive grazing. In broad terms, our recommendations coincide with those proposed for core populations at specific scales elsewhere (Seoane *et al.* 2006, Vögeli *et al.* 2010). Unfortunately, to our knowledge, these measures have never or rarely been put into practice (own data) and the decline of the Dupont's Lark populations continues in Spain (Pérez-Granados and López-Iborra 2014). Our multi-scale analysis of habitat selection has provided a multi-scale strategy for planning the conservation of this species that should be tested as soon as possible in the field. Likewise, this approach may also be useful for designing conservation strategies in other species.

Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270916000356>

Acknowledgements

This study was supported by a pre-doctoral fellowship, financed by Levantina y Asociados Minerales, S.A. within the project "Estudios aplicados a la conservación de las poblaciones de alondra ricotí (*Chersophilus duponti*) en el entorno del municipio de Vallanca". We are grateful to Eva Serrano-Davies for her collaboration during field-work. We also thank two anonymous referees and Paul Donald whose helpful comments contributed to improving the paper. We wish to thank the Servicio de Vida Silvestre of Conselleria D'infraestructures, Territori i Medi Ambient (Generalitat Valenciana) for supporting our work and to Sarah Young for help with the English manuscript. This research is part of the doctoral thesis of C.P.G. at the University of Alicante.

References

- Alda, F., González, M. A., Olea, P. P., Ena, V., Godinho, R. and Drovetski, S. V. (2013) Genetic diversity, structure and conservation of the endangered Cantabrian Capercaillie in a unique peripheral habitat. *Eur. J. Wild. Res.* 59: 719–728.
- Barton, K. (2011) MuMIn: Multi-model inference. R package version 1.0.0. Available at: <http://CRAN.R-project.org/package=MuMIn>.
- Benjamini, Y. and Hochberg, Y. (1995) Controlling the false discovery rate: a practical

- and powerful approach to multiple testing. *J. Roy. Stat. Soc. B.* 5: 289–300.
- Bibby, C. J., Burgess, N. D., Hill, D. A. and Mustoe, S. (2000) *Bird census techniques*. London, UK: Academic Press.
- BirdLife International (2015) *Chersophilus duponti*. In The IUCN Red List of Threatened Species. Version 2015.3. <www.iucnredlist.org>. Accessed 23 October 2015.
- Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel inference: a practice information-theoretic approach*. New York, USA: Springer.
- Cade, B. S. (2015) Model averaging and muddle multimodel inferences. *Ecology* 96: 2370–2382.
- Dai, Q. and Fu, J. Z. (2011) When central populations exhibit more genetic diversity than peripheral populations: A simulation study. *Chinese Sci. Bull.* 56: 2531–2540.
- Dormann, F. C., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitao, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.
- ESRI (2008) *ArcGIS 9.3*. Redlands, CA, USA: Environmental Systems Research Institute.
- Fielding, A. H. and Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24: 38–49.
- García, J. T., Suárez, F., Garza, V., Justribó, J. H., Oñate, J. J., Hervás, I., Calero, M. and García de la Morena, E. L. (2008) Assessing the distribution, habitat, and population size of the threatened Dupont's lark *Chersophilus duponti* in Morocco: lessons for conservation. *Oryx* 42: 592–599.
- Garza, V., Suárez, F., Herranz, J., Traba, J., García de la Morena, E. L., Morales, M. B., González, R. and Castañeda, M. (2005) Space use and habitat selection of the endangered Dupont's Lark (*Chersophilus duponti*) in Spain: the breeding and postbreeding periods. *Ardeola* 52: 133–146.
- Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H. Y., Iverson, A. L., Batáry, P., Rudolphi, J., Tscharrantke, T., Cardinale, B. J. and Perfecto, I. (2014) Biodiversity conservation in agriculture requires a multi-scale approach. *Proc. R. Soc. B.* 281: 20141358.
- Guisan, A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8: 993–1009.
- Guo, Q., Taper, M., Schoenberger, M. and Brandle, J. (2005) Spatial-temporal population dynamics across species range: from centre to margin. *Oikos* 108: 47–57.
- Hampe, A. and Petit, R. J. (2005) Conserving biodiversity under climate change: The rear edge matters. *Ecol. Lett.* 8: 461–467.
- Kawecki, T. J. (2008) Adaptation to marginal habitats. *Ann. Rev. Ecol. Evol. Syst.* 39: 321–342.
- Laiolo, P., Vögeli, M., Serrano, D. and Tella, J. L. (2007) Testing acoustic versus physical marking: two complementary methods for individual-based monitoring of elusive species. *J. Avian Biol.* 38: 672–681.
- Leopold, C. R. and Hess, S. C. (2013) Multi-scale habitat selection of the endangered Hawaiian Goose. *Condor* 115: 17–27.
- Lesica, P. and Allendorf, F. W. (1995) When are peripheral populations valuable for conservation? *Conserv. Biol.* 9: 753–760.
- Lichstein, J. W., Simons, T. R., Shriener, S. A. and Franzreb, K. E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.* 72: 445–463.
- López, G. (2007) *Guía de los árboles y arbustos de la península Ibérica y Baleares*. Madrid: Mundi-Prensa Libros.
- López-Iborra, G. M., Limiñana, R., Pavón, D. and Martínez-Pérez, J. E. (2011) Modelling the distribution of short-toed eagle (*Circaetus gallicus*) in semi-arid Mediterranean landscapes: Identifying important explanatory variables and their implications for its conservation. *Eur. J. Wild. Res.* 57: 83–93.
- Luoto, M., Pöyry, J., Heikkinen, R. K. and Saarinen, K. (2005) Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Global Ecol. Biogeogr.* 14: 575–584.
- Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. *Biodivers. Conserv.* 11: 1397–1401.

- Marty, P. Daeden, J. Moutet, R., Vogiatzakis, I., Mathevet, R., Potts, S. G. and Tzanopoulos, J. (2014) Conceptual framework and typology of drivers. Pp. 25–30 in K. Henle, S. G. Potts, W. E. Kunin, Y. G. Matsinos, J. Similä, J. D. Pantis, V. Grobelnik, L. Penev and J. Settele, eds. *Scaling in ecology and biodiversity conservation*. Sofia, Bulgaria: Pensoft Publishers.
- Mills, L. S. (2007) *Conservation of wildlife populations: demography, genetics and management*. Malden, Massachusetts: Blackwell.
- Nogués-Bravo, D. and Aguirre, A. (2006) Patrón y modelos de distribución espacial de la alondra ricotí *Chersophilus duponti* durante el periodo reproductor en el LIC de Ablitas (Navarra). *Ardeola* 53: 55–68.
- Olea, P. P., Mateo-Tomás, P. and de Frutos, Á. (2010) Estimating and Modelling Bias of the Hierarchical Partitioning Public-Domain Software: Implications in Environmental Management and Conservation. *PLoS ONE* 5(7): e11698.
- Pearson, R. G., Dawson, T. P. and Liu, C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27: 285–298.
- Pérez-Granados, C. and López-Iborra, G. M. (2013) Census of breeding birds and population trends of the Dupont's Lark (*Chersophilus duponti*) in Eastern Spain. *Ardeola* 60: 143–150.
- Pérez-Granados, C. and López-Iborra, G. M. (2014) ¿Por qué la alondra ricotí debe catalogarse como "En peligro de Extinción"? *Quercus* 337: 18–25.
- Pérez-Granados, C. and López-Iborra, G. M. (2015) Baja dispersión adulta y baja tasa de recaptura juvenil de la alondra ricotí (*Chersophilus duponti*) en el Rincón de Ademuz (Valencia, España). XIX Spanish Congress of Bird Ringing. Oral communication. Ceuta, Spain.
- Pérez-Granados, C. and López-Iborra, G. M. (in press) Assessment of counting methods used for estimating the number of territorial males in the endangered Dupont's lark.
- Pérez-Granados, C., López-Iborra, G. M., Serrano-Davies, E., Nogueras, V., Garza, V., Justribó, J. H. and Suárez, F. (2013) Short-term effects of a wildfire on the endangered Dupont's Lark *Chersophilus duponti* in arid central Spain. *Acta Ornithol.* 48: 201–210.
- Prodon, R. and Lebreton, J. D. (1981) Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series Pyrenees. I. Analysis and modelling of the structure gradient. *Oikos* 37: 21–38.
- Quevedo, M., Bañuelos, M. J., Sáez, O. and Obeso, J. R. (2006) Habitat selection by Cantabrian capercaillie *Tetrao urogallus cantabricus* at the edge of the species' distribution. *Wildl. Biol.* 12: 267–276.
- R Development Core Team. (2009) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Randin, C. F., Dirnbock, T., Dullinger, S., Zimmerman, N. E., Zapper, M. and Guisan, A. (2006) Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33: 1689–1703.
- Razgour, O., Hanmer, J. and Jones, G. (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: the grey long-eared bat as a case study. *Biol. Conserv.* 144: 2922–2930.
- Reis, E., López-Iborra, G. M. and Pinheiro, R. T. (2012) Changes in bird species richness through different levels of urbanization: Implications for biodiversity conservation and garden design in Central Brazil. *Landscape Urban Plan.* 107: 31–42.
- Sagarin, R. D., Gaines, S. D. and Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol. Evol.* 21: 524–530.
- Segurado, P., Araújo, M. B. and Kunin, W. E. (2006). Consequences of spatial autocorrelation for niche-based models. *J. Appl. Ecol.* 43: 433–444.
- Seoane, J., Justribó, J. H., García, F., Retamar, J., Rabadán, C. and Atienza, J. C. (2006) Habitat-suitability modelling to assess the effects of land-use changes on Dupont's lark *Chersophilus duponti*: A case study in the Layna Important Bird Area. *Biol. Conserv.* 128: 241–252.
- Sing, T., Sander, O., Beerenwinkel, N. and Lengauer, T. (2005) ROCR: visualizing

- classifier performance in *R. Bioinformatics* 21: 3940–3941.
- Suárez, F. (2010) La alondra ricotí *Chersophilus duponti*. Madrid, Spain: Dirección General para la Biodiversidad. Ministerio de Medio Ambiente y Medios Rural y Marino.
- Tella, J. L., Vögeli, M., Serrano, D. and Carrete, M. (2005) Status of the threatened Dupont's lark in Spain: overestimation, decline, extinction of local populations. *Oryx* 39: 1–5.
- Thomassen, H. A., Buermann, W., Milá, B., Graham, C. H., Cameron, S. E., Schneider, C. J., Pollinger, J. P., Saatchi, S., Wayne, R. K. and Smith, T. B. (2010) Modeling environmentally associated morphological and genetic variation in a rainforest bird, and its application to conservation prioritization. *Evol. Appl.* 3: 1–16.
- Torres, L. G., Sutton, P. J. H., Thompson, D. R., Delord, K., Weimerskirch, H., Sagar, P. M., Sommer, E., Dille, B. J., Ryan, P. J. and Phillips, R. A. (2015) Poor transferability of species distribution models for a pelagic predator, the Grey Petrel, indicates contrasting habitat preferences across ocean basins. *PLoS ONE* 10(3): e0120014. doi:10.1371/journal.pone.0120014.
- Traba, J., Acebes, P., Malo, J. E., García, J. T., Carriles, E., Radi, M. and Znari, M. (2013) Habitat selection and partitioning of the Black-bellied Sandgrouse (*Pterocles orientalis*), the Stone Curlew (*Burhinus oedecnemus*) and the Cream-coloured Courser (*Cursorius cursor*) in arid areas of North Africa. *J. Arid Environ.* 94: 10–17.
- Tuanmu, M., Viña, A., Roloff, G. J., Liu, W., Ouyang, Z., Zhang, H. and Liu, J. (2011) Temporal transferability of wildlife habitat models: implications for habitat monitoring. *J. Biogeogr.* 38: 1510–1523.
- Vallecillo, S., Brotons, L. and Osborne, P. E. (2010) Geographical variation in the distributional constraints along a gradient of population aggregation. *Acta Oecol.* 36: 666–674.
- Venables, W. N. and Ripley, B. D. (2002) *Modern applied statistics*. New York, USA: Springer.
- Vernier, P. R., Schmiegelow, F. K., Hannon, S. and Cumming, S. G. (2008) Generalizability of songbird habitat models in boreal mixed wood forests of Alberta. *Ecol. Model.* 211: 191–201.
- Vögeli, M., Serrano, D., Pacios, F. and Tella, J. L. (2010) The relative importance of match habitat quality and landscape attributes on a declining steppe-bird metapopulation. *Biol. Conserv.* 143: 1057–1067.
- Walsh, C. and Mac Nally, R. (2008) hier.part: hierarchical partitioning. R package version 1.0.3. Vienna, Austria: R Foundation for Statistical Computing.
- Zanini, F., Pellet, J. and Schmidt, B. R. (2009) The transferability of distribution models across regions: an amphibian case study. *Divers. Distrib.* 15: 469–480.

CRISTIAN PÉREZ-GRANADOS*¹, GERMÁN M. LÓPEZ-IBORRA^{1,2}

¹Multidisciplinary Institute for Environmental Studies “Ramón Margalef”, Universidad de Alicante, PO Box 99, 03080. Alicante, Spain.

²Department of Ecology /IMEM “Ramón Margalef”, PO Box 99, Universidad de Alicante, 03080. Alicante, Spain.

JAVIER SEOANE

Terrestrial Ecology Group, Department of Ecology, Universidad Autónoma de Madrid. C/Darwin, 2, 28049, Madrid, Spain.

*Author for correspondence; e-mail: cristian.perez@ua.es

Received 22 July 2015; revision accepted 28 July 2016;
Published online 17 October 2016