Habitat selection by Ortolan Buntings *Emberiza hortulana* in post-fire succession in Catalonia: implications for the conservation of farmland populations

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The Ortolan Bunting *Emberiza hortulana* is a long-distance migrant that has suffered major population declines across much of its European breeding range. While northern populations are bound largely to farmland, Mediterranean populations are largely confined to habitats subject to recurrent wildfires. Habitat selection of the Ortolan Bunting was assessed in a recently burnt area in Catalonia at landscape and habitat scales. A Zero-inflated Poisson procedure was used to model the abundance of birds in relation to landscape and habitat variables. The most parsimonious landscape model predicted the highest abundance on south-facing slopes, with a gradient above 10°. The most parsimonious habitat model showed a positive quadratic effect of bare ground and regenerating oak *Quercus* spp., with predicted optima for abundance around 20–30% and 20% cover, respectively. There was a clear relationship between predicted abundance of the Ortolan Bunting and post-fire regenerating oak shrubs. South-facing, moderately sloping areas were favoured and bare ground was a key feature of the species' habitat. A matrix combining patches of sparse oak shrubs and patches of bare ground appears to be the optimal breeding habitat in the Mediterranean. The maintenance or provision of similar habitat features, especially patches of bare ground, may prove crucial for the conservation of rapidly declining Ortolan Bunting populations on farmland across temperate Europe.

Keywords: farmland, fire mosaics, Mediterranean landscapes, Zero-inflated Poisson.

Fire is an important process in shaping landscapes and ecological communities (Moreira *et al.* 2001, Herrando & Brotons 2002, Stuart-Smith *et al.* 2002, Rodrigo *et al.* 2004, Andersen *et al.* 2005, Brotons *et al.* 2005). Alteration of habitat and landscape structure by fire may increase the overall habitat heterogeneity of an area and the associated faunal assemblages (Herrando & Brotons 2002, Brotons *et al.* 2004, Andersen *et al.* 2005). The opening of habitat through removal of vegetation by fire may allow colonization by open-habitat specialist birds and boost their populations (Herrando *et al.* 2003, Brotons *et al.* 2005, 2008, Pons & Bas 2005). Persistence of such species depends on the regeneration characteristics of the vegetation, which predominantly determine post-fire habitat structure and can vary

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markedly depending on tree and shrub species (Rodrigo *et al.* 2004). Closing of the understorey as a result of natural vegetation succession will be detrimental to the persistence of ground-foraging bird species. Thus, presence of a vegetation mosaic at different stages of regeneration can support a rich and varied bird community.

The Ortolan Bunting *Emberiza hortulana* is a ground-foraging, long-distance migrant typical of open habitats and favouring warm, dry areas with sparse vegetation (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). The species appears to occupy quite different breeding habitats in different parts of its range. Breeding areas in temperate northern and central Europe are closely associated with richly structured, semi-open agricultural land (Conrads 1969, Cramp & Perrins 1994, Dale & Olsen 2002, Goławski & Dombrowski 2002, Berg 2008), whereas in Mediterranean regions the species occurs mainly in open and semi-open shrubland and steppe-like habitats (Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997).

In recent decades, the Ortolan Bunting has suffered a dramatic population decline across much of its temperate European breeding range (BirdLife International 2004). Declines are ascribed to habitat loss and alteration resulting from changing agricultural practices (Revaz *et al.* 2005, Vepsäläinen *et al.* 2005), particularly the intensification of traditional heterogeneous farming regimes (Lang *et al.* 1990, Goławski & Dombrowski 2002) and possibly vegetation closure through natural succession (Sirami *et al.* 2007).

In contrast to most other European populations, some Mediterranean populations have increased over the past 20 years (Pons 2004). This expansion has been attributed to the presence of large-scale wildfires, increasing the availability of suitable habitat (Brotons *et al.* 2008). Previous assessments of habitat selection by Ortolan Buntings in Mediterranean habitats have focused on community assemblage and habitat–species relationships at the landscape level (e.g. Pons & Prodon 1996, Santos *et al.* 2002, Brotons *et al.* 2004, Pons & Bas 2005, Sirami *et al.* 2007). In the Mediterranean region, Ortolan Buntings occur in areas with sparse vegetation (Cramp & Perrins 1994, Fonderflick *et al.* 2005) and poor tree regeneration, particularly recently burned areas (Prodon 1988, Pons & Prodon 1996, Herrando *et al.* 2002, Brotons *et al.* 2008), and disappear from these habitats in the later stages of vegetation succession (Sirami *et al.*

2007). The association with recently and historically burnt areas has also been observed in other parts of the species' breeding range in temperate and sub-Mediterranean Europe (Dale & Hagen 1997, Dale 2000, Dale & Olsen 2002, Dale & Manceau 2003, Revaz *et al.* 2005). The Ortolan Bunting appears thus to be a typical pioneer colonizer of the early stages of vegetation succession.

The present study aims to assess in detail the habitat requirements of the Ortolan Bunting in a large forested area in Catalonia, northeast Spain, where the species became abundant after several extensive wildfires that occurred in 1998 (Brotons *et al.* 2008). The study attempts to assess habitat requirements of Ortolan Buntings, considering both landscape and habitat variables, and to identify correlates of abundance that might be useful in developing conservation recommendations for declining farmland populations in other parts of Europe.

METHODS

Study area

The study area is located in Solsonès county (41°59′–41°44′N and 1°21′–1°39′E, Lleida, northeastern Spain), in an area in which around 26 000 ha were burned by several wildfires in July 1998 (Fig. 1). The burnt areas were located between 450 and 950 m asl. Data collected in 1993 by the Ecological Forest Inventory of Catalonia (IEFC; Gracia *et al.* 2003) suggested that 67% of the total burnt area was forest, with the rest composed of agricultural fields. Of the forest areas burnt, the majority comprised Black Pine *Pinus nigra* (74%) and Aleppo Pine *Pinus halepensis* (11%), with the remainder including Holm Oak *Quercus ilex* and the deciduous species Lusitanian Oak *Quercus faginea* and Downy Oak *Quercus humilis*.

As the seeds of Black Pine are released in spring, summer fires prevent the regeneration and recovery of stands of this species, leading to regeneration of a different type of forest dominated by resprouting species such as oaks (Habrouk *et al.* 1999, Rodrigo *et al.* 2004). In the case of burnt Black Pine stands in Catalonia, forest landscapes typically develop into a mosaic of different states dominated by different *Quercus* species, shrubland and open grasslands, with some remains of unburnt Black Pine (Retana *et al.* 2002).

Figure 1. Map of the study area showing locations of transects surveyed (*n* = 101) for the Ortolan Bunting in 2005, in the area affected by the Solsonès wildfires from 1998. Filled circles of increasing size represent abundance of the species in three classes: 0, 1–2 and 3–6 individuals. The area shown represents burnt habitats, with grey representing burnt forests and white accounting for agricultural areas (mainly cereals).

Data collection

Line transects were used to estimate presence and abundance of the Ortolan Bunting (Bibby *et al.* 1992). Each census lasted for 20 min and covered about 700 m in length (range 602–850 m). Birds were counted as present when heard or seen within 100 m either side of the transect. Censuses were conducted in 2005, 7 years after the fire. Each transect was surveyed twice, with one visit in the early breeding season (19 April–24 May) and one in the middle of the breeding season (24 May–24 June), allowing approximately 1 month between visits to the same transect. The higher of the two counts of birds was used as the dependent variable in the modelling.

Transects were distributed within the burnt areas using a random stratified sampling design. Initially, 25 points were randomly placed within the fire perimeter. At each of these points (approximately 2-km radius), four survey transects were defined. The criteria used to select transect locations around each random point were: (1) transects were only conducted across burnt natural habitat and therefore were not placed in patches of

unburnt forest or farmland within the fire perimeter, (2) transects were easily accessible from walking trails, (3) transects represented the main regenerating habitat types occurring near the random point and (4) the minimum distance between transects was 150 m. All bird surveys were performed by the same observer, to avoid between-observer variation, and were always conducted in good weather conditions, without rainfall or strong wind. All transect counts were conducted within 3 h of sunrise.

All explanatory landscape and habitat variables were recorded by the same observer, to reduce observer error in the data. Variables recorded in the field were estimated during the period of the first census and applied to the results from both censuses.

Landscape variables were estimated within 100 m of the transects. Aspect and slope were estimated from a Digital Elevation Model (DEM, 30-m resolution) generated from 1 : 50 000 topographical maps. The proportion of south-facing pixels was used as a measure of the aspect of transects. Cover of unburnt patches was determined in the field (categorical, 0–3 with increasing cover). The stream character of transects (the relative abundance of streams within the 100-m belt at each side of the transect) was recorded (categorical, 0–5 ascending), as it has been previously observed that these areas often exhibit higher vegetation recovery rates. Finally, the percentage cover of surrounding agricultural fields was estimated within a 500-m belt surrounding transects, based on 1 : 50 000 topographical maps.

Explanatory variables relating to habitat were recorded along each transect using a modification of the cover estimation method proposed by Prodon and Lebreton (1981), which involves a visual estimation of the relative percentage cover of each variable within a defined area, in this case the transect. Variables were taken to be representative of the whole length of transects, including a 100-m belt on either side. Variables recorded were bare ground, rocky outcrops, shrubby vegetation (0.25–1 m) and an overall assessment of the cover of three regenerating tree species: *P. halepensis*, *Q. ilex* and *Q. faginea*. Cover of regenerating *Q. ilex* and *Q. faginea* were combined, as both species appear to exhibit similar patterns of regeneration (Rodrigo *et al.* 2004). For each variable, the relative percentage cover value was defined as the projection of the foliage volume of the layer

(or rock and bare ground layer) onto a horizontal plane. Rocky outcrops was the only categorical variable, with values (0–5) increasing with surface area covered. Although the accuracy of the Prodon and Lebreton (1981) method has been argued to be around 5–10%, its application was initially meant for the description of point count stations and could therefore potentially be less appropriate for its use over a longer surface, linked to a transect-based method. Repeatability (r_i; Lessells & Boag 1987) of our method between the two visits was calculated, and found to be high for the recorded variables (r_i = 0.71–0.78). Furthermore, the relationship between bare ground and regenerating oak was estimated indirectly from satellite Landsat data (Normalized Difference Vegetation Index, NDVI, Pettorelli *et al.* 2005), matching the area sampled in the field visits. Measured concordance (explained variability, r^2) ranged from 0.65 to 0.68, suggesting that our field vegetation cover estimates indeed reliably represented major components of variability in vegetation cover along the transects.

Data analysis

We applied a Zero-inflated Poisson (ZIP) modelling procedure to allow for overdispersion and the high proportion of zero observations in the data (38.6%; Lambert 1992, Cunningham & Lindenmayer 2005, Martin *et al.* 2005). ZIP models are two-part models that comprise a mixture of a Bernoulli distribution and a Poisson distribution, which allows both occurrence and abundance to be modelled simultaneously (Lambert 1992, Cunningham & Lindenmayer 2005). Because of the semi-colonial nature of the species' breeding, with males moving large distances to find aggregations of females (Dale *et al.* 2005, 2006) and sometimes persisting in the absence of females (Dale 2001, Vepsäläinen *et al.* 2007), models were developed to explain abundance in relation to co-variates, whereas occurrence was constant and not dependent on covariates. The dependent variable taken for each transect was the maximum count of Ortolan Buntings over the two visits.

Continuous variables were first tested for pairwise correlation, using Spearman's coefficient (r_s) before inclusion in the modelling. A value of r_s = |0.7| was used as the acceptable lower limit of correlation. None of the landscape or the habitat variables were significantly correlated ($r_s \le 0.36$ and 0.57, respectively), so all variables were retained for the modelling.

Modelling was conducted in two stages: landscape variables and habitat variables. All models were defined *a priori* to running the analysis (Burnham & Anderson 2002): 27 models were defined based on the habitat variables (Table 1) and 27 models were defined based on the landscape variables (Table 2). Quadratic functions of the variables appearing in the most parsimonious models were also fitted to assess non-linear relationships. Models were ranked using Akaike's Information Criterion, corrected for small samples (AIC_C; Burnham & Anderson 2002, Johnson & Omland 2004). Models with Akaike weights (w_i) summing to 0.95 were defined as the most parsimonious set of models. The model with the highest w_i was selected as the most parsimonious model from which to make predictions. Predictions are bounded with 95% confidence intervals, calculated by bootstrapping, using 1000 repeats. All analyses were carried out using the program R v. 2.6.2 (R Development Core Team 2008) using the package 'zicounts' for ZIP (Mwalili 2008; package available at http://cran.r-project.org).

RESULTS

Landscape-scale habitat selection

A summary of the results (regression coefficients ± 1 se) from the most parsimonious set of landscape models is given in Table 3. Four models were included in the most parsimonious set of models (combined w_i = 0.961; Table 2). The most parsimonious landscape model contained only the variables percentage of south-facing pixels and quadratic function of slope (w_i = 0.767; Table 2). Inclusion of an interaction between these variables did not improve the AIC_C of the most parsimonious model. Predictions from the most parsimonious model are presented in Figure 2(a,b). Predictions derived from the most parsimonious model predicted the highest abundance of Ortolan Buntings on moderate slopes between 15° and 20°. A predicted abundance of more than one individual per transect is indicated for slopes of 10–25° (Fig. 2a). Results from predictions of abundance compared with proportion of south-facing pixels predict the occurrence of more than one individual for almost completely north-facing slopes, although predicted abundance increases steadily

Table 1. Zero-inflated Poisson regression models describing the abundance of Ortolan Buntings in relation to habitat variables. Covariates included are average values along each transect surveyed; all variables refer to percentage cover values, apart from outcrops, which is categorical.

No.	Covariates	Deviance	K	ΔAIC_C	w_i
17	Bare ground, bare ground^2, rquercus, rquercus^2	293.6	6	0.00	0.64
16	Bare ground, rquercus, rquercus^2	298.7	5	2.84	0.15
18	Bare ground, bare ground^2, rquercus	299.2	5	3.34	0.12
20	Bare ground, bare ground^2	304.1	4	6.02	0.03
3	Bare ground, rquercus	304.7	4	6.62	0.02
22	Bare ground, shrubs, rquercus	303.0	5	7.14	0.02
1	Bare ground, rpinus, rquercus	304.1	5	8.24	0.01
24	Bare ground, shrubs	309.5	4	11.42	0.00
5	Bare ground	312.6	3	12.35	0.00
2	Bare ground, rpinus	312.0	4	13.92	0.00
19	Rquercus, rquercus^2	313.0	4	14.92	0.00
23	Shrubs, rquercus	315.5	4	17.42	0.00
10	Bare ground, rquercus, outcrops	297.5	12	18.55	0.00
7	Rquercus	319.5	3	19.25	0.00
21	Bare ground, shrubs, rquercus, outcrops	295.9	13	19.59	0.00
8	Bare ground, rpinus, rquercus, outcrops	296.4	13	20.09	0.00
4	Rpinus, rquercus	318.9	4	20.82	0.00
26	Bare ground, shrubs, rquercus, rpinus, outcrops	295.0	14	21.77	0.00
12	Bare ground, outcrops	303.3	11	21.77	0.00
9	Bare ground, rpinus, outcrops	302.1	12	23.15	0.00
14	Rquercus, outcrops	309.6	11	28.07	0.00
11	Rpinus, rquercus, outcrops	308.4	12	29.45	0.00
25	Shrubs	332.1	3	31.85	0.00
27	Shrubs, rpinus	332.1	4	34.02	0.00
15	Outcrops	324.1	10	40.05	0.00
6	Rpinus	341.6	3	41.35	0.00
13	Rpinus, outcrops	323.3	11	41.77	0.00

For each model, the number of parameters (K), difference between Akaike's Information Criterion adjusted for small samples (ΔAIC_C) between each model and the most parsimonious model, and Akaike weight (w_i) are given. Rquercus, regenerating oaks; rpinus, regenerating pine; shrubs, regenerating shrubs 0.25–1 m.

with increasing proportion of south-facing pixels (Fig. 2b). Therefore, although there was no clear avoidance of north-facing areas, birds were predicted to be more abundant in south-facing areas.

Habitat selection

A summary of the results (coefficients ± 1 se) from the most parsimonious set of habitat models is presented in Table 4. Five models were included in the most parsimonious set of models (combined w_i = 0.966; Table 1). All of the top models included only the variables bare ground and regenerating *Quercus* spp., with various combinations of the quadratic terms (Table 1). The most parsimonious model describing the abundance of Ortolan Buntings contained the variables bare ground (% cover) and regenerating *Quercus* spp. (% cover), as well as the quadratic terms for both variables (w_i = 0.638; Table 1). The inclusion of an interac-

tion between these variables did not improve the AIC_C of the model. Predictions made from this model are presented in Figure 3(a,b). Results show a peak level of abundance at around 20% cover of regenerating *Quercus* spp. (Fig. 3a). More than one individual is predicted to occur per transect between 0 and 45% cover of regenerating *Quercus* spp. (Fig. 3a). Results from predictions indicate an optimum level of bare ground at around 20–30% cover (Fig. 3b), with more than one individual predicted to occur per transect between 10% and 50% cover. The high degree of uncertainty surrounding predictions between 40% and 80% cover results from the paucity of data points within this cover range.

DISCUSSION

Although previous studies have reported a link between the occurrence of Ortolan Buntings and

Table 2. Zero-inflated Poisson regression models describing the abundance of Ortolan Buntings in relation to landscape variables. Covariates slope, sthslopes and farmland are continuous, stream and unburnt are categorical.

No.	Covariates	Deviance	K	ΔAIC_C	w_i
23	Slope, slope^2, sthslopes	314.6	5	0.00	0.77
12	Sthslopes, slope	320.2	4	3.39	0.14
11	Sthslopes, farmland	323.3	4	6.49	0.03
21	Slope, slope^2, farmland	321.6	5	7.00	0.02
16	Sthslopes	326.9	3	7.92	0.02
22	Slope, slope^2, farmland, farmland^2	320.8	6	8.46	0.01
20	Sthslopes, sthslopes^2	326.7	4	9.89	0.01
17	Slope	329.1	3	10.12	0.01
6	Stream, sthslopes, farmland	320.7	8	13.03	0.00
25	Stream, sthslopes	324.7	7	14.67	0.00
9	Unburnt, sthslopes	318.0	10	15.21	0.00
8	Unburnt, sthslopes, slope	315.5	11	15.23	0.00
7	Unburnt, sthslopes, farmland	315.7	11	15.43	0.00
26	Stream, slope	327.3	7	17.27	0.00
18	Farmland	341.2	3	22.22	0.00
19	Farmland, farmland^2	339.6	4	22.79	0.00
13	Unburnt, slope	325.6	10	22.81	0.00
3	Stream, unburnt, sthslopes, slope	313.0	15	23.42	0.00
1	Stream, unburnt, sthslopes, slope, farmland	311.1	16	24.34	0.00
14	Stream	337.7	6	25.36	0.00
27	Stream, farmland	337.2	7	27.17	0.00
15	Unburnt	333.0	9	27.75	0.00
5	Stream, unburnt, slope	321.4	14	29.05	0.00
10	Unburnt, farmland	332.8	10	30.01	0.00
24	Stream, unburnt	325.1	13	30.05	0.00
2	Stream, unburnt, slope, farmland	321.4	15	31.82	0.00
4	Stream, unburnt, farmland	325.1	14	32.75	0.00

For each model, the number of parameters (K), difference between Akaike's Information Criterion adjusted for small samples (AIC_C) between each model and the most parsimonious model, and Akaike weight (w_i) are given. Sthslopes, average number of south-facing pixels.

Table 3. Zero-inflated Poisson model results and parameter estimates (± 1 se) for the most parsimonious set of landscape models describing the abundance of Ortolan Buntings. Z = intercept of the Bernoulli distribution.

	Variable											
	Intercept		Slope		Slope^2		Southern pixels		Farmland		Z	
Model	Coef.	se	Coef.	se	Coef.	se	Coef.	se	Coef.	se	Coef.	se
23	−3.345	1.205	0.422	0.158	−0.012	0.005	0.010	0.004	–	–	−1.649	0.539
12	−0.835	0.407	0.066	0.025	–	–	0.010	0.003	–	–	−1.657	0.576
11	0.127	0.210	–	–	–	–	0.015	0.003	−0.021	0.011	−1.729	0.652
21	−3.875	1.397	0.522	0.176	−0.014	0.005	–	–	0.006	0.012	−1.208	0.338

burnt areas (Prodon 1988, Dale & Hagen 1997, Dale & Olsen 2002, Dale & Manceau 2003, Revaz *et al.* 2005, Brotons *et al.* 2008), this is the first time that habitat preferences within burnt areas have been quantified. Birds selected shallow, south-facing slopes offering a habitat matrix consisting of regenerating oak shrubland interspersed with patches of bare ground. This habitat configuration is abundant in the early stages of vegetation succession in burnt shrubland and woodland.

There was no evidence of avoidance of north-facing areas, but there was an increase in predicted abundance in more south-facing areas, supporting previous assertions of the species' preference for
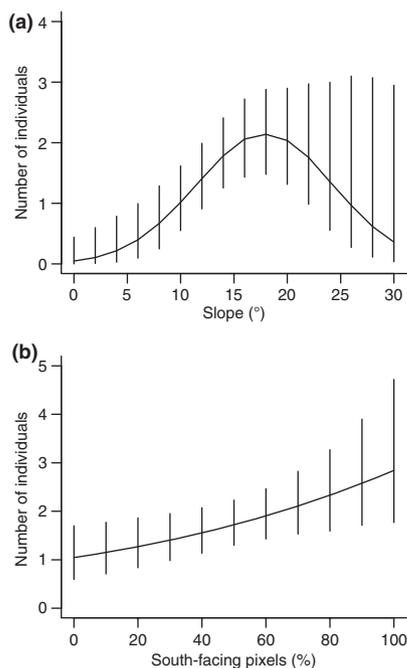
Figure 2. Estimates of abundance of Ortolan Buntings in relation to landscape variables from the most parsimonious Zero-inflated Poisson model: (a) estimate of abundance in relation to slope and (b) estimate of abundance in relation to percentage of south-facing pixels.
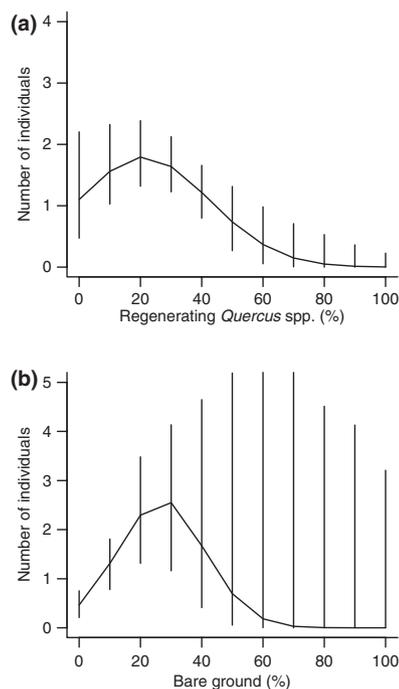

Figure 3. Estimates of abundance of Ortolan Buntings in relation to habitat variables from the most parsimonious Zero-inflated Poisson model: (a) estimate of abundance in relation to percentage cover of regenerating *Quercus* spp. and (b) estimate of abundance in relation to percentage cover of bare ground.

Table 4. Zero-inflated Poisson model results and parameter coefficients (± 1 se) for the most parsimonious set of habitat models describing the abundance of Ortolan Buntings. Regen. = regenerating; Z = intercept of the Bernoulli distribution.

| | Variable | | | | | | | | | | | |
| | Intercept | | Bare ground | | Bare ground^2 | | Regen. oaks | | Regen. oaks^2 | | Z | |
Model	Coef.	se	Coef.	se	Coef.	se	Coef.	se	Coef.	se	Coef.	se
17	−0.699	0.713	0.125	0.038	−0.002	0.001	0.040	0.038	−0.001	0.000	−2.191	0.905
16	−0.143	−0.636	0.045	0.012	–	–	0.040	0.036	−0.001	0.000	−2.104	0.959
18	0.026	0.455	0.127	0.037	−0.002	0.001	−0.018	0.008	–	–	−2.282	0.906
20	−0.747	0.312	0.159	0.036	−0.003	0.001	–	–	–	–	−1.796	0.593
3	0.643	0.341	0.045	0.011	–	–	−0.022	0.008	–	–	−2.272	1.016

dry, south-facing, sunny areas (Cramp & Perrins 1994). This may be due to a greater availability of bare ground surfaces on warmer, south-facing areas (Dale 2000). The same explanation holds for the low predicted abundance of the species on flat areas, as shown in this study. Flat areas are more likely to be densely vegetated due to poorer soil drainage (Fonderflick *et al.* 2005) and thus less suitable for Ortolan Buntings. Several studies have already pointed to a preference of the species for dry, well-drained soils (Dale 2000, Fonderflick

et al. 2005) and avoidance of wet areas (Conrads 1968, Deutsch 2007).

The results show a clear relationship between predicted abundance of the Ortolan Bunting and regenerating oak shrubs, with optimal predicted shrub cover reinforcing estimates from previous work in other areas (Fonderflick & Thévenot 2002, Fonderflick *et al.* 2005), although in these studies, oak was not mentioned explicitly. The reasons for this link with open shrubland, specifically oaks, remain unclear, although it has been suggested that

isolated shrubs and small trees provide song-posts (Lang *et al.* 1990, Fonderflick *et al.* 2005). A link with oaks has been reported elsewhere (von Bülow 1990, Lang *et al.* 1990) and may be due to the relatively high abundance of defoliating caterpillars on oak trees, compared with other deciduous trees, providing an essential food source for a number of breeding birds (Naef-Daenzer & Keller 1999). Ortolan Buntings have been observed to feed chicks largely on defoliating caterpillars gleaned from the foliage of oaks, particularly early in the nesting season (Conrads 1969).

There was a positive relationship between the predicted abundance of Ortolan Buntings and bare ground cover. Bare ground has previously been identified as an important variable in habitat selection of the species (Menz 2008), as well as for other terrestrially foraging insectivorous birds (Moorcroft *et al.* 2002, Butler & Gillings 2004, Maurer 2006, Ioset 2007, Weisshaupt 2007). Ortolan Buntings have been shown to avoid areas with dense ground-level vegetation (Nævra 2002, Santos *et al.* 2002, Berg 2008, Menz 2008), which is likely to be a result of reduced food accessibility. However, in areas where bare ground is not a limiting factor, it has little effect on habitat suitability (Fonderflick *et al.* 2005). Availability of bare ground may well be the principal driver of the Ortolan Bunting's habitat selection pattern, with the other factors discussed above (southern aspect, shallow slopes, shrubland regrowth) being subordinate.

Due to our static approach, with all forest fragments investigated being burned in the same year, it is difficult to determine the optimal stage in post-fire oak regeneration, or the ideal spatial mosaic offering patches of burnt vegetation at different stages of regeneration. We assume that in a semi-natural, fire-driven habitat mosaic, it is likely that there will be patches of vegetation near to an optimal stage of regeneration available at any one time. Our methodology and that of Fonderflick *et al.* (2005) are based primarily on data from singing males, which is limiting regarding information on foraging habitat requirements. Resolution of this requires fine-grained habitat selection studies at the individual level, to determine whether these birds forage in close proximity to singing areas and the exact nature of these foraging grounds.

The observed increase in the Catalan population may offer some suggestions regarding potential causes of decline of Ortolan Buntings outside the Mediterranean. The increase in Catalonia has been attributed to the presence of wildfires increasing available suitable habitat (Brotons *et al.* 2008), which, as has been quantified here, consists structurally of open oak shrubland and the presence of large areas of bare ground. This mosaic structure can be likened to that of traditional European agricultural areas, characterized by extensive farming practices involving small-parcel farming and abundant structural elements such as tree rows and hedges. The onset of agricultural intensification has reduced overall habitat heterogeneity (Fuller *et al.* 2004) through an increase in monocultures and large-scale cropping, and an abandonment of traditional practices such as managed burning. Furthermore, the intensification of grassland management has led to matrices dominated by a dense sward, which dramatically affects both arthropod abundance and accessibility to ground-foraging insectivores (Vickery *et al.* 2001, Atkinson *et al.* 2004, Butler & Gillings 2004). These progressive land-use changes may be affecting Ortolan Bunting populations elsewhere in Europe through a reduction in optimal habitat structure and food accessibility, although there is need for further work to shed more light on these proposed causes of decline.

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