

Ecological requirements of the threatened  
Ortolan bunting *Emberiza hortulana* in  
temperate Europe (Swiss Alps) and in the  
Mediterranean (Catalonia)

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# Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction

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## Summary

1. The Ortolan Bunting *Emberiza hortulana* has undergone a general decline across much of western Europe in recent decades. In Switzerland, the species is now extinct in farmland, and only one population remains in sub-Mediterranean shrub-steppe habitats on the south-facing slopes of the Rhône Valley (Valais).
2. We aimed to collect data on foraging ecology of the last Swiss Ortolan Buntings during reproduction; however, we found only nine singing males in 2007, and no sign of reproduction. We investigated foraging habitat selection of unpaired males on the meso and micro-scales, and compared patterns of foraging habitat preferences with patterns of food abundance.
3. All radio-tracked birds foraged exclusively on the plain. The adjacent slope, which harboured the former breeding grounds, was used only for territorial song displays. All males showed a preference for conventional corn fields that had been treated with herbicide, while also exhibiting an avoidance of meadows and riparian vegetation.
4. Structurally, it was shown that birds foraged in areas with a high proportion of bare soil, as well as moderately dense overhead vegetation. These areas did not support higher arthropod food supplies, suggesting that food accessibility (and / or vegetation shelter) rather than food abundance dictates habitat selection.
5. *Synthesis and Applications.* It remains to be seen whether these microhabitat preferences also apply to breeding Ortolan Buntings. Further work in southern European breeding grounds should be envisioned to gain

crucial information about the ecological requirements of Ortolan Buntings in Mediterranean and sub-Mediterranean habitats.

246 Words

**Keywords**

*Emberiza hortulana*; Generalised linear mixed models; Habitat selection modelling; Population decline; Prey availability; Species conservation.

## **Introduction**

Changes and intensification of agricultural practices across Europe are considered to be the most important factor affecting the populations of a large number of bird species that utilise agricultural land (Wilson *et al.* 1999; Mason & Macdonald 2000; Donald, Green & Heath 2001). Loss of habitat heterogeneity, changes in culture types and farming regimes, and widespread pesticide application has led to massive drops in food abundance and diversity, especially invertebrates, during the breeding season (Stoate *et al.* 1998; Moreby & Stoate 2001; Robinson, Wilson & Crick 2001; Britschgi, Spaar & Arlettaz 2006). In bird breeding areas, decline in invertebrate populations, whose abundance depends principally on grassland management, can have severe adverse effects on survival of nestlings, which rely on large amounts of protein rich food for growth. Thus, identification of important invertebrate groups in the diet of birds has direct management implications in terms of habitat improvement and conservation (Moreby & Stoate 2000; Di Giulio, Edwards & Meister 2001; Fournier & Arlettaz 2001).

The Ortolan Bunting *Emberiza hortulana* L. is a long-distance passerine migrant that has suffered a major population decline across Europe in recent decades (Stolt 1993; Cramp & Perrins 1994; Dale & Hagen 1997; Goławski & Dombrowski 2002; Revaz *et al.* 2005; Vepsäläinen *et al.* 2005). Causes of decline are often attributed to loss of suitable breeding habitats, possibly through changes in agricultural practices (Revaz *et al.* 2005; Vepsäläinen *et al.* 2005), including intensification of farming away from the more traditional diverse crops (Goławski & Dombrowski 2002) and increased use of pesticides

(Claessens 1992; Steifetten & Dale 2006). Hunting has also been identified as a threat to the species, with birds still being caught in France during the autumn migration: it was estimated that until the 1990's, on average, 50 000 birds were trapped per year (Claessens 1992). The Red List for breeding bird species in Switzerland lists the Ortolan Bunting as vulnerable (Keller *et al.* 2001), whilst the *Artenförderungsprogramm* for birds in Switzerland (Rehsteiner *et al.* 2004) lists it as a top priority. In the early 1980's, the Ortolan Bunting still bred near Geneva and in the canton Graubünden, however, it no longer breeds in these areas (Revaz *et al.* 2005, see also Geroudet 1954 for a review of the historical breeding distribution in Switzerland). Currently, the only remaining breeding population of the Ortolan Bunting in Switzerland is in the canton Valais, on the south-exposed slopes of the Rhône Valley, between 600 and 1400 m above sea level (Rehsteiner *et al.* 2004). In 1978-79, the population in Switzerland was estimated at 243 singing males, whereas in 2004, a total of only 32 singing males were reported, all from the canton Valais (Revaz *et al.* 2005).

Farmland has been determined as an important foraging resource for birds during the breeding season (Dale 2000; Dale & Olsen 2002; Dale & Manceau 2003; Laiolo 2005). Claessens (1992) and Dale (2000) suggest that maintenance of traditional agricultural practices of small parcel farming and increased crop variety is important for the persistence of the Ortolan Bunting. In Switzerland, it is said that the species requires the availability of patchy, structurally diverse habitats, with solitary trees, bushes and rocks, as well as areas with small parcel farming practices in warm, dry areas (Rehsteiner *et al.*

2004), though this is yet to be quantified. In a pre-emptive conservation measure, small parcels of oat were sown on the plain near the slope where the last Swiss Ortolan Buntings reside. Based on expert knowledge, it was proposed that oat is an important resource for Ortolan Buntings upon arrival and before departure on migration (Keusch 1991). Aside from this, very little is known about the foraging habitat requirements of the Ortolan Bunting in Switzerland.

Initially, our aim was to identify the preferred food and foraging habitats of Ortolan Buntings during the breeding season, whilst adults are provisioning nestlings. However, there was an unforeseen population crash, and to our knowledge, the remaining population consisted essentially of bachelor males, with no certified occurrence of breeding in Switzerland in 2007. As a result, habitat selection analysis could only be conducted for unpaired males, which necessitated a revision of the focal questions of the study.

Foraging habitat selection of unpaired male Ortolan Buntings during the breeding season was investigated on two spatial scales: On the meso-scale level, we aimed to identify which habitat types are favoured by foraging Ortolan Buntings; and on the micro-scale level, what are the main structural features required by the Ortolan Bunting for suitable foraging habitat. At the meso-scale level, we also aimed to determine if the locally sown oat fields were used during the breeding season. Finally, we investigated if there is a link between preferred foraging habitat of Ortolan Buntings and prey availability. By recognising basic ecological requirements, we hoped to be able



to formulate habitat management guidelines to possibly rescue this population from the brink of extinction. We did not achieve that goal due to the current non-reproductive status of the population, but think that some of our results could still contribute to shed more light on the ecology of this threatened bird.

## **Methods**

### ***Study Site***

The study was carried out from May to August 2007, on the south-facing slopes of the Rhône valley (46°19'N, 7°40'E) to the East of the town of Leuk in the canton Valais, Switzerland. The study site is characterized by dry, rocky, sub-Mediterranean shrub-steppe, interspersed with tracts of xeric deciduous oak *Quercus pubescens* and coniferous *Pinus sylvestris* forest. The study site also extends onto the plain at the base of the steppe, which nowadays is primarily occupied by intensive agriculture. Much of the study area was burnt by a wildfire in 1979 (Keusch 1991).

The Valais Field Station of the Swiss Ornithological Institute has monitored the population of Ortolan buntings at the study site since 2002 (Revaz *et al.* 2005). Censuses are conducted primarily on the basis of counting singing males.

### ***Capture and Radio-tracking***

Male Ortolan Buntings were captured using mist nets placed within the territory of a target singing male. Males were attracted with playback of the territorial song of the species, obtained from a commercial recording, and

deemed to be most similar to that of the local birds. A stuffed male Ortolan Bunting was positioned over the tape-recorder to act as an additional lure. The stuffed male and tape-recorder were placed on the ground, in view of a singing male, with the net placed between the lure and the target male. Captured birds were ringed with a numbered metal ring, as well as a combination of three colour rings. Birds were fitted with radio-tags (BD-2, 1.4 g, Holohil Systems Ltd., Canada), using a Rappole harness (Rappole & Tipton 1991; Naef-Daenzer 2007). The most appropriate leg-loop size of the Rappole harness was determined to be 55 mm, using the formula and example as presented by Naef-Daenzer (2007). Radio-tracking was conducted using a 3-element antenna and a receiver (Australis 26k Tracking Receiver, Titley Electronics, Australia). Birds were tracked during the day, with a minimum 5 min interval between locations of the same individual to avoid spatio-temporal autocorrelation (Aebischer, Robertson & Kenward 1993). Locations were marked with a Global Positioning System (GPS; Garmin eTrex Summit, Garmin Ltd., USA).

Birds were located and actual locations determined by approaching and attempting to observe the bird. As Ortolan Buntings typically forage on the ground (Cramp & Perrins 1994), birds that were on the ground were considered to be foraging. Home ranges for each individual were estimated using the minimum convex polygon (MCP) method (Mohr 1947; White & Garrott 1990), calculated using ArcView v3.3 GIS software (Environmental Systems Research Institute Inc., California) with the Animal Movement extension v2.0 (Hooge, Eichenlaub & Solomon 1999), using all locations for

each bird, either foraging or perched. Within each home range, an equivalent number of random locations as observed locations were generated. A 5 m buffer was placed around the visited locations when generating the random locations so as to prevent overlap, as well as allowing a minimum of 5 m between random points.

### ***Meso-scale Habitat Selection***

At each location, broad-scale habitat type was recorded. Nine distinct habitat types were present in the foraging areas of the male Ortolan Buntings, these were: Corn fields treated with herbicide, untreated Corn fields, Meadow, Lucerne, Riparian vegetation, Rye, Oats, Ploughed field, and Other (which includes infrastructure, road works and river). Preliminary observations in the field suggested that the two different types of Corn fields (those with obvious use of herbicide, and those without) were used to a different extent by foraging birds, thus, these are treated as separate habitat types. The habitat type Other is not considered as available foraging habitat for the birds, therefore it is not included in any further analysis. As a result, the remaining area within the MCP is considered as the total area. The actual cover of the different habitat types was determined by superimposing the home ranges over an orthophoto using ArcView v3.3. Actual locations and boundaries of changing habitat types, such as crops were verified by mapping in the field with the use of a GPS.

### ***Micro-scale Habitat Selection***

In addition to habitat type, at each of the recorded foraging and random locations, a number of habitat variables were recorded within a 2 x 2 m square around the location. The habitat variables recorded were: Soil cover, Vegetation cover at 0.5-1 m and at 1–2 m (all in %, 5-10% accuracy). Only those males with  $\geq 40$  foraging locations were used in the analysis.

### ***Prey Availability***

Availability of ground-dwelling invertebrate prey was sampled by pitfall trapping. Only ground-dwelling invertebrates were sampled, as the Ortolan Bunting is a ground-foraging species, and ground-dwelling invertebrate fauna feature prominently in the diet during the breeding season (Cramp & Perrins 1994). It has been observed that adult Ortolan Buntings may revert to a diet of seeds towards the end of the breeding season (Cramp & Perrins 1994; Glutz von Blotzheim & Bauer 1997), however, at the time the study took place, the crops and grasses were still green. This indicated a very low availability of seed material, thus, it was considered that the birds were still feeding on invertebrates, which could be confirmed by in situ observations of foraging birds. Pitfall trapping was employed in the three main habitat types, Corn fields treated with herbicide, untreated Corn fields, and Meadow. Pit traps consisted of small plastic (yoghurt) containers, 9 cm high with a top diameter of 7 cm, placed within a piece of PVC pipe (7 cm diameter) in the ground. Traps were half-filled with ethylene glycol, with a plastic cover (11 cm<sup>2</sup>) placed approximately 5 cm above the trap. Traps were installed in two

rows of three, with 2 m between traps and rows. Four of these trapping grids were placed at randomly selected locations within each habitat type, within the overall area used by the foraging Ortolan Buntings. Traps were emptied three times, at three-day intervals between 4<sup>th</sup> and 14<sup>th</sup> August 2007.

Invertebrate samples were preserved in 70% Ethanol and stored in sealed plastic bags. Invertebrate samples were sorted to Order level with the use of a dissecting microscope. Samples were then dried in an oven at 60°C for a period of 72 hours. The number of individuals in each category was counted and then weighed using a precision balance (Mettler Toledo PB303-L Delta Range, Switzerland) to an accuracy of  $\pm 0.001$  g. Only invertebrates longer than 2 mm were considered as potential prey.

### ***Statistical Analyses***

Meso-scale habitat preference was assessed by using both a  $\chi^2$  approach with 95% Confidence Intervals (Neu Statistic; as described in Neu, Byers & Peek 1974; Byers, Steinhorst & Krausman 1984), and a randomised contingency table procedure (Estabrook & Estabrook 1989; Arlettaz 1999; Estabrook *et al.* 2002). The Neu statistic was calculated as a comparison between the visited foraging locations, and the actual cover of each habitat type within the foraging area of each male. As the Neu statistic is governed by  $\chi^2$  limitations, some habitat types had to be combined in order to avoid very small expected values (Neu, Byers & Peek 1974). Randomised contingency tables were calculated based on a comparison between the habitat types of the visited foraging locations and the random locations within the foraging area of each

male.

Micro-scale habitat requirements were assessed using binomial logistic regression, comparing habitat variables of visited locations to random locations. Continuous variables were first tested for pair-wise correlation, using Spearman's Rank Correlation Coefficient ( $r_s$ ) before inclusion in the modelling. An  $r_s = 0.7$  was used as the acceptable lower limit of correlation and variables exceeding this were excluded from further analysis. Presence of multicollinearity between the variables was tested for, using Variance Inflation Factors (VIF) (Faraway 2004). In addition to the variables recorded, quadratic functions of all variables were also tested to determine if there is an optimum level governing the likelihood of occurrence of foraging Ortolan Buntings. A Generalised Linear Mixed Model (GLMM) procedure (Broström 2003) was applied, including the individual bird as a random factor in the models. Models were defined prior to running the analysis. Models were ranked based on Akaike's Information Criterion, corrected for small samples ( $AIC_C$ ) (Burnham & Anderson 1998; Johnson & Omland 2004). A total of 18 pre-defined models were tested. The models with AIC weights ( $AIC_w$ ) summing to 0.95 were defined as the most parsimonious set of models. The model with the highest  $AIC_w$  was selected as the most parsimonious model from which to make predictions.

Relationships between habitat type and invertebrate abundance and dry biomass were tested using linear mixed-effects models (Crawley 2007), deriving the effect of habitat from comparing a model with habitat as the explanatory variable, and a null model (Crawley 2007). The relationship

between abundance and biomass of the two major invertebrate groups and habitat was also tested. Site and habitat were included as random factors in the models, with site nested within habitat. The mean of the three sampling replicates for each pit-trap was used for the analysis. In order to satisfy the assumption of normality, the variables Total abundance, Total biomass, Aranaea abundance and Coleoptera abundance had to be log transformed, and the variable Aranaea biomass had to be square root transformed.

Randomised contingency tables were calculated using the program ACTUS2 (Estabrook & Estabrook 1989), with 10 000 simulations. All modeling was carried out using the program R v2.5.1 (The R Development Core Team, 2006). The library glmmML was used for Generalised Linear Mixed Models, and the library nlme for linear mixed-effects models (both available at <http://cran.r-project.org>).

## **Results**

### ***Capture and Radio-tracking***

A total of six males were captured. Of these six males, four could be successfully radio-tracked. Only one female was observed during the study period. This female constructed the only nest known from this population during the 2007 breeding season; unfortunately, the nest was abandoned soon after construction for unknown reasons. From the 25<sup>th</sup> of June, males abandoned their singing territories on the steppe (foothill slope) and moved to the fields on the plain below, where they remained throughout the rest of the season. For each of Males 3, 5 and 6, 40 foraging locations were recorded

from the plain. Male 1 returned for a short period, allowing collection of eight foraging locations, altogether totaling 128 foraging locations across four males. Area of each habitat type within the foraging range of Males 1, 3, 5 and 6 is presented in Table 1. The most abundant habitat type (disregarding Other) within the foraging ranges of the males was Meadow (mean = 33.7%; range = 29.9 – 41.7%), followed by Corn fields treated with herbicide (mean = 24.9%; range = 11.7 – 34.2%), Rye (mean = 11.3%; range = 3.8 – 16%), untreated Corn fields and Riparian vegetation (mean = 8.3% for each; range = 2.8 – 11.9%, 3.7 – 10.9%, respectively), Lucerne (mean = 4.8%; range = 2.0 – 10.6%) and Oat (0.8%) which was only present within the foraging area of Male 3. The most commonly used habitat, based on foraging locations, was Corn fields treated with herbicide (mean = 88.13%; range = 77.5 – 95%), followed by Rye and Meadow (mean = 10%; range = 7.5 - 12.5%, for each), and untreated Corn fields (mean = 3.75%; range = 2.5 – 5%). The remaining five habitat types were not visited by foraging birds.

### ***Meso-scale Habitat Selection***

Results from the randomised contingency tables show strong positive selection for Corn fields treated with herbicide, for all four birds (Fig. 1, Males 5 and 6,  $P < 0.001$ ; Male 3,  $P < 0.01$ ; Male 1,  $P < 0.05$ ), and avoidance of meadows for three out of the four males (Fig. 1, Males 5 and 6,  $P < 0.001$ ; Male 3,  $P < 0.01$ ). Male 6 avoided untreated Corn fields (Fig. 1,  $P < 0.05$ ).

For the Neu statistic, some habitats had to be combined to avoid small expected values: Rye, Oat and Ploughed field were combined to give Cereals,



and Meadow and Lucerne were combined to give Meadow. Only birds with at least 40 foraging locations were used in the analysis. All three males showed disproportionate use of habitats compared to availability within the foraging areas (Table 2,  $\chi^2$ -tests,  $P < 0.001$ , all males). Results show a preference across all birds for Corn fields treated with herbicide, and a general avoidance of Meadows and Riparian vegetation (Table 2). Response to untreated Corn fields was statistically non-significant for Males 3 and 5, and avoided by Male 6. Male 6 also avoided Cereals (Table 2).

### ***Micro-scale Habitat Selection***

Multicollinearity was not a serious problem ( $VIF = \leq 1.15$ ), thus all variables were retained in the modeling. Four models had a combined AICw of 0.95 (Table 3). The most parsimonious model contained only the variables Bare soil, Vegetation to 1 m and the square of Vegetation to 1 m (Table 3), thus these are considered to be important for determining foraging habitat selection of Ortolan Buntings. The inclusion of an interaction between Bare soil and Vegetation to 1 m did not improve the AIC<sub>C</sub> of the most parsimonious model. Parameter estimates for the variables included in this model showed an increasing probability of occurrence, with percentage cover of Bare soil (Fig. 2a). Soil cover above 70% exceeded the 0.5 level of probability, indicating positive selection (Fig. 2a). The quadratic function of Vegetation to 1 m exceeded the 0.5 level of occurrence probability at a cover between 20 - 70% and showed an optimum for occurrence at 50%, with an occurrence probability of 0.8 (Fig. 2b).

### **Prey Availability**

A total of 5404 invertebrates were collected from 14 Orders, totaling 52.48 g dry biomass. As Ortolan Buntings feed on a wide variety of invertebrates (Cramp and Perrins 1994; Glutz von Blotzheim and Bauer 1997), all orders sampled were considered as potential prey. The most abundant Orders were: Aranaea (45.9%), Coleoptera (35.4%) and Diptera (9.4%). The Orders contributing most to dry biomass were: Coleoptera (78.5%), Aranaea (12.3%) and Orthoptera (6.7%) (Fig. 3).

The total abundance of invertebrates differed significantly between habitat types (Table 4,  $P = 0.004$ ). The highest abundance was recorded from Meadow (Fig. 3). Total dry biomass did not differ significantly between habitat types (Table 4,  $P = 0.43$ ). Total abundance and biomass of Aranaea were significantly correlated ( $R^2 = 0.88$ ,  $n = 70$ ,  $P < 0.001$ ), thus, only dry biomass was used for the analysis. Dry biomass of Aranaea differed significantly between habitat types (Table 4,  $P < 0.001$ ), with Meadow providing the highest value (Fig. 3). Total abundance and total dry biomass of Coleoptera were not significantly correlated, so they were analysed separately. Dry biomass of Coleoptera did not differ significantly between habitats (Table 4,  $P = 0.64$ ), conversely, abundance showed a significant difference (Table 4,  $P = 0.018$ ), with the highest abundance occurring in meadow (Fig. 3).

## **Discussion**

### ***Remaining Population***

This population appears to have undergone a considerable decline in recent years, with the current state of the Ortolan Bunting in Switzerland being much direr than was previously expected. It was assumed that there were approximately 32 singing males remaining in Switzerland in 2004, and that the core of these, around 20 males, was situated within our study site (Revaz *et al.* 2005). Survey results from 2006 recorded 20 territories within the bounds of the study area (E. Revaz pers. comm.). Based on these results, it was assumed that the population was still functioning as a breeding population, although declining and in need of conservation measures. From this study, it is clear that the population is much smaller than previously thought (8-9 singing males, 1 female), and is possibly now functionally extinct as a breeding population. It appears that this phenomenon of a high number of unpaired males has been previously observed in declining Ortolan Bunting populations elsewhere (Dale 2001; Dale, Lunde & Steifetten 2005), as well as in other passerine species (Donald 2007) Either the population has declined by 50% since the previous year, or it was overestimated in the past, which is conceivable, considering male Ortolan Buntings can be highly mobile when holding territories (Dale, Lunde & Steifetten 2005; Dale *et al.* 2006).

Ultimate reasons for the observed decline in this population are still unclear, whilst the recent crash is likely linked to a lack of recruitment in the quasi absence of females. Cause for the lack of females in declining Ortolan Bunting populations has previously been linked to female biased natal

dispersal (Dale 2001; Dale *et al.* 2006; Steifetten & Dale 2006). Though this may be a contributing factor, it is likely that adult females hold a much lower site fidelity than males, and move throughout the landscape more freely, abandoning areas no longer suitable, and establishing in areas with more favorable conditions. It is also of interest to note, that the time when the males abandoned singing territories on the steppe and moved to the plain coincides with the peak laying date for this population, reported by an earlier study (Keusch & Mosimann 1984). Dale, Lunde & Steifetten (2005) and Dale *et al.* (2006) have shown that male Ortolan Buntings can exhibit rapid long-distance breeding dispersal if no female is attracted early in the breeding season, moving to prospect other habitat patches. This may explain the rapid disappearance of some males in our study, with the return of one individual later on in the season.

### ***Meso-scale Habitat Selection***

The male Ortolan Buntings showed a clear preference for Corn fields that had been treated with herbicide, and an avoidance of meadows. Additionally, there was an avoidance of riparian vegetation, and one male even avoided untreated Corn fields. Most previous studies have not typically identified corn fields as important foraging areas (Dale 2000; Dale & Olsen 2002; Dale & Manceau 2003), but, Bellenhaus (2007) has mentioned that Ortolan Buntings of unknown breeding status favoured corn fields. To our knowledge, this is the only other study that describes the use of corn fields by unpaired Ortolan Buntings.

Berg (2008) determined that foraging Ortolan Buntings preferred habitats with patches of bare ground, or sparse ground vegetation. At the study site, there was no other habitat type that was structurally similar to the corn fields that had been treated with herbicide. These differed from untreated corn fields, by the high proportion of bare soil in the former, compared to large amounts of herbaceous plants covering the soil in the latter. It is most probable that this structure is what is favoured by foraging Ortolan Buntings.

Unfortunately, these results can only give us insight into the favoured foraging habitat type of unpaired males, and not of breeding birds. We predict that habitat type preferences would actually be totally different when adults are provisioning nestlings, because the latter have a high reliance on protein-rich arthropod food due to an extremely rapid growth and very early fledging (Keusch 1991; Cramp & Perrins 1994). Otherwise, Ortolan Buntings would still thrive throughout Europe where corn remains a widespread crop. These results are of course also limited regarding generalisations about the species due to the small sample size, comprising only four individuals.

### ***Micro-scale Habitat Selection***

To our knowledge, this is the only study to date that investigates micro-scale habitat selection patterns of foraging Ortolan Buntings on the individual level. Micro-scale habitat selection analysis showed that foraging unpaired male Ortolan Buntings have a preference for a high percentage cover of bare soil, as well as overhead vegetation cover: corn fields treated with herbicide were

strongly favoured. Actually, this habitat was structurally unlike any other available at the study site, in having high proportions of bare soil, with moderately dense overhead vegetation cover. Bare soil has previously been shown as an important requirement for a number of other terrestrially foraging bird species (Maurer 2006; Ioset 2007; Weisshaupt 2007). Preference for the shelter effect of the vegetation is probably a predator avoidance strategy, although the presence of vegetation could also promote the presence of arthropod prey for the birds.

Santos, Tellería & Carbonell (2002) studied the effect of vegetation structure on the presence of Ortolan Buntings, and showed a negative relationship between occurrence and cover of herbaceous plants, and a positive relationship for patch size and number of tree species present within the habitat, however, this study was conducted only for species presence, based on visual surveys.

### ***Prey Availability***

The general diet of Ortolan Buntings comprises both plant and animal material, but animal material predominates during reproduction, with chicks fed almost exclusively on arthropods (Keusch & Mosimann 1984; Cramp & Perrins 1994; Glutz von Blotzheim & Bauer 1997). Even though the highest invertebrate abundance (as well as the dominant groups, Aranaea and Coleoptera) occurred in meadows, this habitat was avoided by foraging Ortolan Buntings. Conversely, corn fields were shown to harbour a comparatively lower abundance of potential invertebrate prey but were still

the favoured habitat. This suggests that prey accessibility, here in an easy-walking terrain created by systematic herbicide application, is a more important habitat feature than prey abundance itself, at least for bachelor males. Breeding Ortolan Buntings may show different habitat requirements (Bellenhaus 2007), to cope with the high protein demand of rapidly growing nestlings. Further studies of habitat selection and diet composition are required to quantify this. With the increase of agricultural intensification across Europe, invertebrate prey availability and accessibility has become a growing issue for management of birds dependent on agricultural land (Donald, Green & Heath 2001; Vickery *et al.* 2001; Benton, Vickery & Wilson 2003; McCracken & Tallowin 2004; Atkinson *et al.* 2005).

### ***Implications for Conservation***

Based on the current situation of this last remaining Swiss population of Ortolan Buntings, it is recommended that the conservation significance of the species be upgraded within Switzerland, from Vulnerable to Critically Endangered. Monitoring of this population should continue in following years, considering also that most of the singing males present in 2007 were colour marked. This will allow observers to determine if birds are returning to the site, as well as if individuals may be changing territories throughout the breeding season, resulting in more accurate counts.

Unfortunately, little can be drawn from this study regarding general comments on habitat requirements of Ortolan Buntings. However, it can be said that the birds, although only unpaired males, showed a strong preference

for corn fields with a high proportion of bare soil. As this habitat did not harbor a high abundance or biomass of invertebrates, compared to other available habitats, it indicates that the birds are not drawn to high prey availability. More likely, the birds are selecting for the high proportion of bare soil, which likely provides enhanced prey accessibility. The extent to which this may drive the habitat selection of breeding Ortolan Buntings necessitates further investigation in reproducing populations. Regarding the study population, it may be that progressive closing of the steppe vegetation, due to natural vegetation succession, after a fire which burnt the whole area 29 years ago in 1979 (Keusch 1991) may have changed the ecological conditions so drastically that suitable foraging habitat is no longer available today. In this case, the high site fidelity, as seen in older male Ortolan Buntings (Dale, Lunde & Steifetten 2005) could explain the persistence of a bachelor population. Foraging in agricultural land could thus result simply from the unavailability of crucial foraging habitat (Fonderflick, Thévenot & Guillaume 2005). Ortolan Buntings breeding in northern Europe do so in quite different habitat types compared to those breeding in southern Mediterranean Europe (Small 1992; Cramp & Perrins 1994). Much of the research on habitat selection of Ortolan Buntings to date has been focused on regions in northern Europe. The habitats that Ortolan Buntings occupy in these areas, which appears to be primarily agricultural land, do not reflect that which is occupied by the species in and around the Mediterranean (Small 1992; Cramp & Perrins 1994). Investigations in the Mediterranean, where some populations appear to be thriving (Pons 2004), would be essential to understand the decline of



the last Swiss population, which inhabits a sub-Mediterranean landscape. This could also provide decisive insights into understanding the decline of northern populations.

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## Tables

**Table 1.** Area (ha) and percentage of each habitat type within the foraging range of each of the four radio-tracked male Ortolan Buntings (represented by ring number). Foraging area was determined by the minimum convex polygon determined from the radio-tracking study. Other includes infrastructure, road works and river.

Bird	Ring number	Corn herbicide		Corn no herbicide		Meadow		Lucerne		Riparian vegetation		Rye		Oats		Other		Total area	
		ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Male 1	N228454	1.8	30.0	-	-	2.5	41.7	0.2	3.8	0.6	10.2	0.9	14.5	-	-	-	-	6.0	100
Male 2	N228455*																		
Male 3	N228456	5.0	11.7	1.2	2.8	12.7	29.9	1.2	2.8	4.6	10.9	1.6	3.8	0.3	0.8	20.4	48.2	42.4	100
Male 4	N228457*																		
Male 5	N228458	1.8	23.8	0.9	11.9	2.4	31.6	0.8	10.6	0.3	3.7	0.8	11.0	-	-	0.8	11.2	7.6	100
Male 6	N228459	2.2	34.2	0.7	10.2	2.0	31.6	0.1	2.0	-	-	1.0	16.0	-	-	0.4	6.1	6.4	100
	Mean		24.9		8.3		33.7		4.8		8.3		11.3		0.8		21.8		

\* Insufficient data for foraging habitat selection analysis (see text for details).

**Table 2.** Habitat selection analysis for three male Ortolan Buntings, 95% Confidence Intervals are derived from the method as described in Neu, Byers & Peek (1974). MCP = minimum convex polygon.

Bird	Ring number	Habitat	Proportion of Habitat within MCP	Observed number of locations	Expected number of locations	$\chi^2$	Proportion of observed locations	95% Confidence Intervals	Direction of Selection
Male 3	N228456	Corn H <sup>1</sup>	0.187	31	7.47	53.345	0.775	0.605-0.945	Preferred
		Corn NH <sup>2</sup>	0.045	1	1.79	0.623	0.025	-0.039-0.089	-
		Cereals	0.073	5	2.93	0.582	0.125	-0.010-0.260	-
		Meadow	0.522	3	20.87	19.597	0.075	-0.032-0.182	Avoided
		Riparian	0.173	0	6.93	6.927	0	0	Avoided
		Total	1	40	40	81.074***	1		
Male 5	N228458	Corn H <sup>1</sup>	0.258	38	10.31	74.382	0.95	0.861-1.039	Preferred
		Corn NH <sup>2</sup>	0.129	2	5.16	1.938	0.05	-0.039-0.139	-
		Cereals	0.118	0	4.74	4.738	0	0	Avoided
		Meadow	0.455	0	18.20	18.203	0	0	Avoided
		Riparian	0.040	0	1.59	1.587	0	0	Avoided
		Total	1	40	40	100.848***	1		
Male 6	N228459	Corn H <sup>1</sup>	0.364	37	14.57	34.532	0.925	0.821-1.029	Preferred
		Corn NH <sup>2</sup>	0.108	0	4.30	4.303	0	0	Avoided
		Cereals	0.170	3	6.81	2.127	0.075	-0.029-0.179	-
		Meadow	0.358	0	14.32	14.323	0	0	Avoided
		Riparian	0.364	0	14.57	34.532	0	0	Avoided
		Total	1	40	40	55.285***	1		

\*\*\*  $P < 0.001$

<sup>1</sup> Corn fields treated with herbicide

<sup>2</sup> Untreated Corn fields

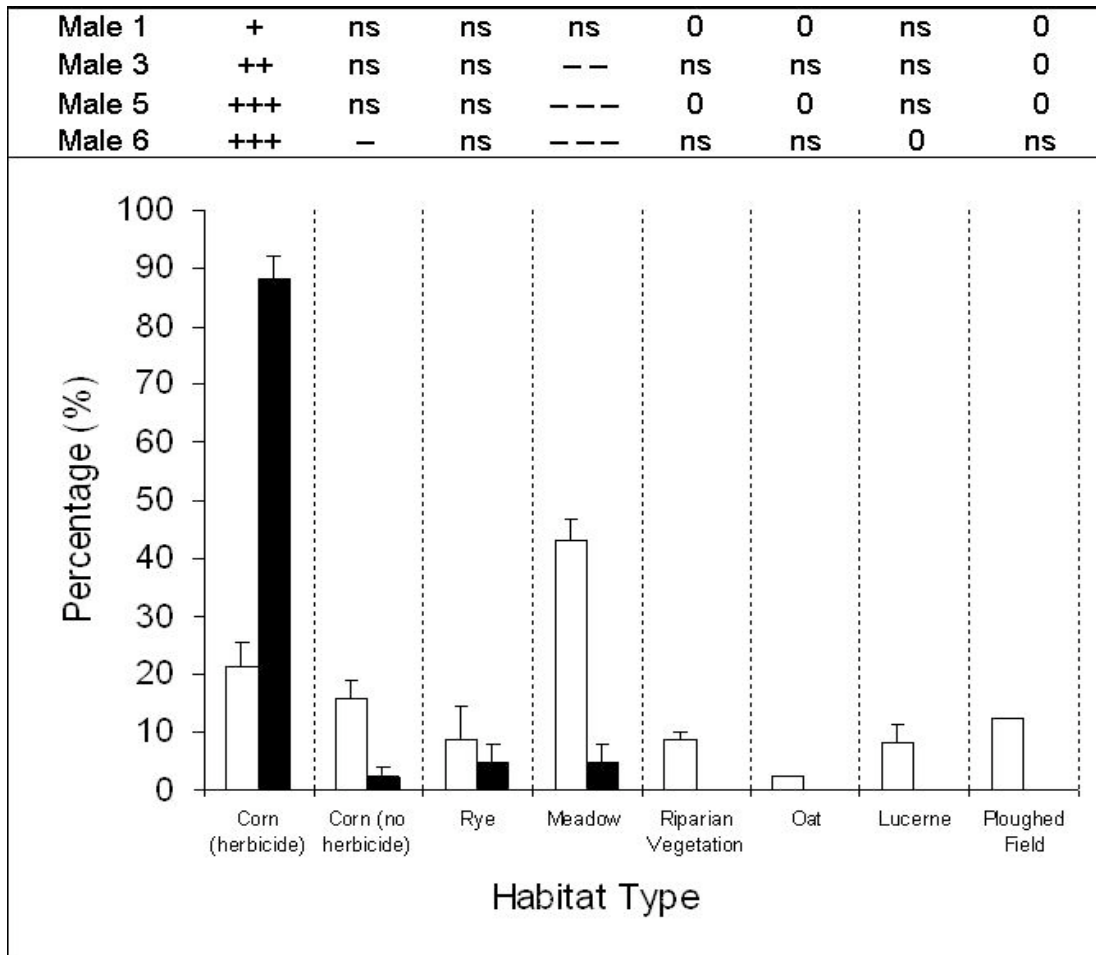
**Table 3.** Generalised Linear Mixed Model results and parameter estimates ( $\pm$  s.e) for microhabitat variables modeled for three male Ortolan Buntings. Est. = Estimate; Veg1m = Vegetation cover between 0.5 – 1 m; Veg2m = Vegetation cover between 1 – 2 m; AIC<sub>C</sub> = Akaike’s Information Criterion corrected for small samples;  $\Delta_i$  = change in AIC<sub>C</sub>;  $w_i$  = Akaike weight; Dev. = Residual Deviance; Par. = number of parameters.

Model	Variables														$\Delta_i$	$W_i$	Dev.	Par.
	Intercept		Soil		Soil <sup>2</sup>		Veg1m		Veg1m <sup>2</sup>		Veg2m		Veg2m <sup>2</sup>					
	Est.	s.e	Est.	s.e	Est.	s.e	Est.	s.e	Est.	s.e	Est.	s.e	Est.	s.e				
6	-2.764	0.426	0.025	0.005	-	-	0.096	0.027	-0.001	0.000	-	-	-	-	0	0.499	234.4	6
5	-2.609	0.461	0.005	0.026	0.000	0.000	0.099	0.027	-0.001	0.000	-	-	-	-	1.5	0.236	232.7	7
3	-2.605	0.473	0.004	0.027	0.000	0.000	0.122	0.037	-0.002	0.001	-0.010	0.001	-	-	2.02	0.182	232.5	8
1	-2.572	0.474	0.005	0.027	0.000	0.000	0.122	0.037	-0.001	0.001	-0.025	0.031	0.000	0.000	3.96	0.069	245.6	4
7	-2.475	0.387	0.033	0.005	-	-	0.019	0.007	-	-	-	-	-	-	8.61	0.007	245.5	5
12	-2.448	0.391	0.033	0.005	-	-	0.019	0.008	-	-	-0.002	0.005	-	-	10.60	0.002	245.6	5
4	-2.464	0.459	0.032	0.025	0.000	0.000	0.019	0.008	-	-	-	-	-	-	10.70	0.002	251.1	3
10	-2.166	0.348	0.035	0.004	-	-	-	-	-	-	-	-	-	-	12.44	0.001	245	7
13	-2.145	0.351	0.036	0.005	-	-	-	-	-	-	-0.003	0.005	-	-	14.21	0	251.4	4
2	-2.454	0.465	0.029	0.025	0.000	0.000	0.021	0.009	-	-	0.013	0.023	0.023	0.000	14.32	0	251.2	4
8	-2.080	0.410	0.026	0.024	0.000	0.000	-	-	-	-	-	-	-	-	14.41	0	251	5
14	-2.049	0.413	0.026	0.024	0.000	0.000	-	-	-	-	-0.003	0.005	-	-	16.10	0	251	5
16	-2.147	0.351	0.036	0.005	-	-	-	-	-	-	-0.012	0.023	0.000	0.000	16.10	0	250.8	6
15	-2.059	0.416	0.028	0.025	0.000	0.000	-	-	-	-	-0.012	0.023	0.000	0.000	18.00	0	262.4	4
9	-1.824	0.322	-	-	-	-	0.150	0.024	-0.002	0.000	-	-	-	-	25.41	0	309.6	3
11	-0.725	0.207	-	-	-	-	0.031	0.007	-	-	-	-	-	-	70.54	0	325.5	3
18	-0.295	0.171	-	-	-	-	-	-	-	-	0.011	0.004	-	-	86.44	0	323.8	4
17	-0.335	0.174	-	-	-	-	-	-	-	-	0.033	0.017	0.000	0.000	86.81	0	234.9	5

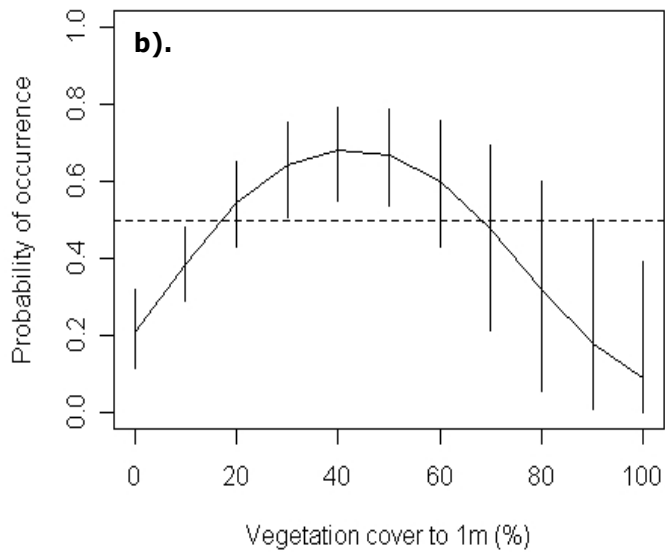
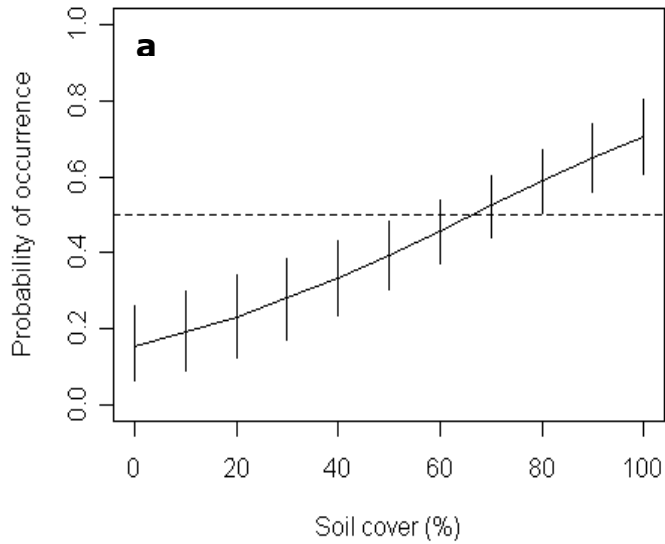
**Table 4.** Linear mixed-effects model results for the effect of Habitat on biomass and abundance of invertebrates. df = degrees of freedom; AIC = Akaike’s Information Criterion; LogLik = Log Likelihood; L.Ratio = Log ratio.

Source of variation	df	AIC	LogLik	L.Ratio	<i>P</i>
Total Biomass					
Full model	5	129.48	-59.74		
Habitat effect	4	128.37	-60.19	0.90	0.344
Coleoptera Biomass					
Full model	5	-106.99	58.49		
Habitat effect	4	-108.77	58.38	0.22	0.638
Aranaea Biomass					
Full model	5	274.59	-132.30		
Habitat effect	4	285.51	-138.75	12.91	<0.001
Total Abundance					
Full model	5	79.21	-31.61		
Habitat effect	4	85.58	-38.79	8.36	0.004
Coleoptera Abundance					
Full model	5	106.65	-48.33		
Habitat effect	4	110.21	-51.01	5.55	0.018
Aranaea Abundance					
Full model	5	111.65	-50.82		
Habitat effect	4	123.98	-57.99	14.33	<0.001

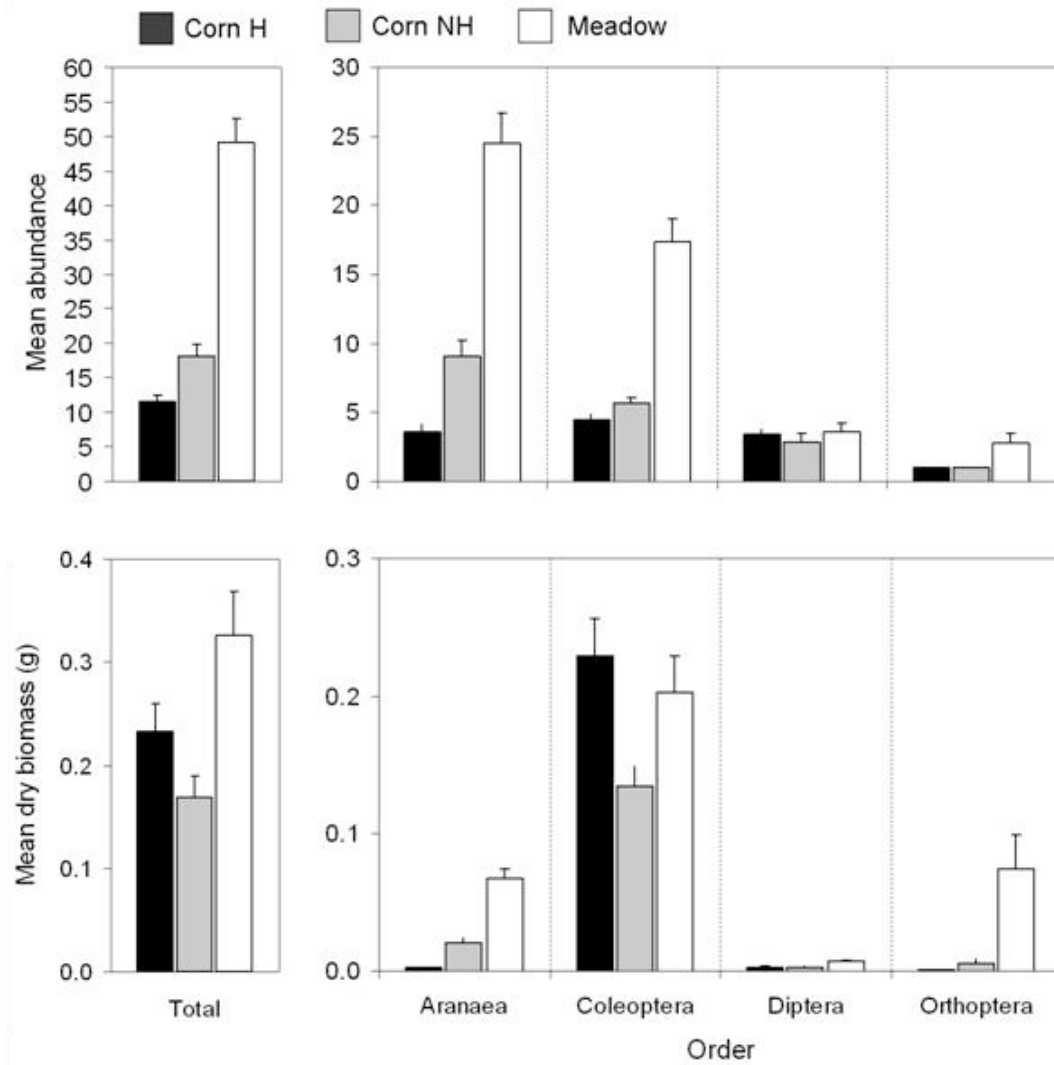
## Figures



**Figure 1.** Results of randomised contingency tables for foraging habitat preferences of four male Ortolan Buntings. Presented are mean values (+ s.e.). Comparisons were made between absolute frequencies of visited (filled bars) versus random (open bars) locations within the foraging minimum convex polygon (MCP) for each male. +/- indicates direction of selection; one symbol:  $P < 0.5$ ; two symbols:  $P < 0.01$ ; three symbols:  $P < 0.001$ ; ns: not significant; 0: habitat not present in MCP.



**Figure 2.** Parameter estimates of microhabitat variables included in the most parsimonious model, derived from a Generalised Linear Mixed Model (GLMM) procedure: (a) estimates of occurrence probability in relation to percentage cover of Bare soil; (b) estimates of occurrence probability in based on a quadratic function of percentage cover of vegetation up to 1 m in height. Values above the 0.5 level of occurrence probability are indicative of selection, whereas values below this level indicate avoidance



**Figure 3.** Mean (+ s.e) abundance and biomass (g) of invertebrates captured in the three main habitat types, Corn fields treated with herbicide (Corn H), untreated Corn fields (Corn NH) and Meadow. Also presented are mean (+ s.e) abundance and biomass (g) of the four dominant invertebrate Orders.



# The Ortolan bunting, a pioneer colonizer of post-fire vegetation succession in the Mediterranean: wider implications for halting its dramatic decline across Europe?

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## Summary

1. The Ortolan Bunting *Emberiza hortulana* is a long-distance passerine migrant that has suffered major population declines across much of its European breeding range. Contrary to northern populations which are bound to farmland, Mediterranean populations mostly inhabit natural habitats subject to recurrent wildfires.
2. We investigated habitat selection patterns of the Ortolan bunting in a recently burnt area in Catalonia, in the Western Mediterranean, with the hope to recognize essential habitat features which may provide guidance for conservation management beyond the Mediterranean. Habitat selection was studied on two spatial scales: landscape and microhabitat. We used a Zero-inflated Poisson procedure to model the abundance of birds encountered along 101 census transects, in relation to habitat variables.
3. The most parsimonious landscape-scale models predicted the highest number of birds in more southerly-facing areas, as well as areas with a moderate slope, above 10°. The most parsimonious microhabitat model showed a positive quadratic effect of bare ground and regenerating *Quercus* spp., with predicted optima for Ortolan bunting abundance around 20-30% and 20% cover, respectively.
4. *Synthesis and Applications.* This study establishes that there is a clear relationship between predicted abundance of the Ortolan Bunting and post-fire regenerating Oak *Quercus* spp. shrubs, that south-facing, moderately sloping areas are favoured, and that bare ground is a key feature of species' habitat. Management should be directed towards maintaining open habitats

representative of early stages in vegetation succession after disturbance, preferably on shallow south-exposed slopes. A matrix combining patches of sparse shrub vegetation (especially in the form of rejuvenating oaks) and surfaces of bare ground may be essential to guarantee the persistence of suitable breeding habitat, possibly also well beyond the Mediterranean. Further studies are needed to define which stage of vegetation succession is favoured, and the spatial scale at which habitat management must be implemented.

299 words

**Keywords**

Conservation; *Emberiza hortulana*; Fire mosaics; Habitat selection; Mediterranean landscapes; Vegetation succession; Zero-inflated Poisson.

## Introduction

In numerous ecosystems, succession after natural disturbance maintains habitat heterogeneity, and in turn, biodiversity (Duncan *et al* 2008; Gardner & Engelhardt 2008). In river systems, for instance, inundations recurrently initiate vegetation succession. Riparian ecosystem dynamics, however, has been greatly simplified due to damming, which reduces the occurrence of natural disturbance events such as flooding and natural flow regimes (Bunn & Arthington 2002; Maingi & Marsh 2002; Poff *et al.* 2007; Rader, Voelz & Ward 2008). As a result, the structural heterogeneity and integrity of the river bed is reduced (Choi, Yoon & Woo 2005), whilst the dynamics of the water column itself is altered (Friedl & Wüest 2002). This inevitably impacts on community diversity. Agroecosystems, on the other hand, are currently being affected by widespread agricultural intensification which reduces the heterogeneity of the agricultural landscape (Fuller, Hinsley & Swetnam 2004), but here a fast turnover of habitat succession is induced (Donald *et al.* 2001; Benton, Vickery & Wilson 2003; Öckinger, Eriksson & Smith 2006). Natural disturbances in an ecosystem thus allow for colonisation events, as well as the presence of differing successional stages, which in turn supports a more diverse community. Removal of the natural dynamics of an ecosystem, either by slowing down or accelerating the processes, will therefore inevitably result in an overall decrease of biodiversity.

Fire is another major process shaping landscapes and ecological communities (Moreira *et al.* 2001; Herrando & Brotons 2002; Brotons, Pons & Herrando 2003; Rodrigo, Retana & Picó 2004). Alteration of habitat and

landscape structure by fire may increase the overall habitat heterogeneity of an area, in turn affecting the heterogeneity of faunal assemblages (Izhaki & Adar 1997; Herrando & Brotons 2002; Brotons, Herrando & Martin 2004). In birds, for instance, opening of habitat through removal of vegetation by fire may allow colonisation by open-habitat specialists and boost their populations locally (Herrando, Brotons & Llacuna 2003; Brotons, Pons & Bas 2005; Pons & Herrando 2005; Brotons, Herrando & Pons 2008). Persistence of these species in an area will depend on the regeneration characteristics of the vegetation, which predominantly determine the post-fire habitat structure. Vegetation regeneration post-fire can vary markedly regarding tree and shrub species (Rodrigo, Retana & Picó 2004). Closing of the understorey as a result of natural vegetation succession will for instance be detrimental to the persistence of ground-foraging bird species. Thus, presence of a mosaic of vegetation at different stages of post-fire regeneration can provide support to a rich and varied bird community. Herrando *et al.* (2002) mention that 5-6 years after fire appears to be the best period regarding avifaunal species diversity in the Mediterranean.

The Ortolan Bunting *Emberiza hortulana* L. is a ground-foraging, long-distance passerine migrant typical of open habitats and favouring warm, dry areas with sparse vegetation (Cramp & Perrins 1994; Glutz von Blotzheim & Bauer 1997). The species may occupy quite different breeding habitats, depending on the geographical region. Breeding areas in northern and central Europe appear to be primarily or closely associated with agricultural land (Conrads 1969; Small 1992; Berg & Pärt 1994; Cramp & Perrins 1994; Dale

& Olsen 2002; Goławski & Dombrowski 2002; Steifetten & Dale 2006).

Whereas in the Mediterranean regions, the species occurs mainly in open shrubland and steppe-like habitat (Cramp & Perrins 1994; Glutz von Blotzheim & Bauer 1997).

In recent decades, the species has suffered a dramatic population decline across much of its European breeding range (Stolt 1993; Cramp & Perrins 1994; Dale & Hagen 1997; Goławski & Dombrowski 2002; Revaz *et al.* 2005; Vepsäläinen *et al.* 2005). Causes of decline regarding habitat loss and alteration are mainly considered to result from changing agricultural practices (Claessens 1992; Laiolo 2005; Revaz *et al.* 2005; Vepsäläinen *et al.* 2005), particularly intensification of agriculture away from the more traditional diverse crops and heterogeneous farming regimes (Lang *et al.* 1990; Goławski & Dombrowski 2002), and possibly closing of vegetation through natural processes of succession (Sirami, Brotons & Martin 2007; Zozaya & Brotons 2007).

In contrast to most other Ortolan bunting populations in Europe, the Catalanian population has increased over the past 20 years (Pons 2004). This expansion has been attributed to the presence of large-scale wildfires in the area, increasing the availability of suitable habitat (Brotons, Herrando & Pons 2008). Previous studies on habitat selection of the Ortolan bunting in Mediterranean habitats have primarily included the species within studies of post-fire bird communities, and have typically focused on community assemblage and habitat-species relationships at the landscape level (Pons & Prodon 1996; Santos, Tellería & Carbonell 2002; Brotons, Herrando & Martin

2004; Pons & Bas 2005; Sirami, Brotons & Martin 2007; Zozaya & Brotons 2007; Vallecillo, Brotons & Herrando 2008). The Mediterranean Ortolan bunting has been observed to occur in areas with sparse vegetation (Cramp & Perrins 1994; Fonderflick, Thévenot & Guillaume 2005) and poor tree regeneration, particularly recently burnt areas (Pons & Prodon 1996; Brotons, Herrando & Pons 2008), but has been noted to disappear from these habitats in later stages of vegetation succession (Sirami, Brotons & Martin 2007; Zozaya & Brotons 2007). Santos, Tellería & Carbonell (2002) described a negative relationship between occurrence of the Ortolan bunting and cover of herbaceous plants, and a positive relationship for habitat patch size and number of tree species present within the habitat. The association with recently and historically burnt areas has also been observed in other parts of the species' breeding range (Dale & Hagen 1997; Dale 2000; Dale & Olsen 2002; Dale & Manceau 2003; Dale 2004; Revaz *et al.* 2005).

Altogether, however, we still lack a comprehensive and detailed analysis of habitat selection patterns in this endangered species. The present study thus aims at exploring the habitat requirements of the Ortolan bunting in a vast forested area, in which the species became abundant after an extensive wildfire episode which took place in Catalonia, Central Western Mediterranean, in 1998 (Brotons, Herrando & Pons 2008). Applying a rigorous statistical procedure, we extracted specific habitat requirements of this species at two spatial scales: 1) landscape scale and; 2) microhabitat scale, using zero-inflated Poisson models. In this approach, we specifically model the *abundance* of the species against habitat variables, instead of

focusing on factors explaining its mere *occurrence*. This method was chosen due to the breeding ecology of the Ortolan bunting. Breeding groups have been shown to be particularly important in this species (Vepsäläinen *et al.* 2007), with male birds sometimes moving long distances in search of areas with available females (Dale, Lunde & Steifetten 2005; Dale *et al.* 2006). It has also been observed that older singing males will persist in areas where there are very few or no females (Dale 2001; Dale, Lunde & Steifetten 2005). For these reasons we consider that areas with higher densities of Ortolan buntings are likely to be most suitable in terms of habitat quality. Thus, there is less chance that the results will be confounded by observations which may consist of only unpaired singing males.

The ultimate goal of this study is to recognize essential ecological niche features of this endangered species, so as to better figure out the mechanism of its widespread and dramatic decline across most of Europe and to propose sound recommendations for optimal conservation management, hopefully beyond the Mediterranean.

## **Methods**

### ***Study Area***

The study area is located in the Solsonès county (between 41° 59' and 41° 44' N and 1° 21' and 1° 39' E, Lleida, north-eastern Iberian Peninsula) in an area affected by a wildfire which occurred in July 1998 and which burned ca. 26,000 ha (Fig. 1). The burnt area is located between 450 to 950 m above sea level. According to the data collected in 1993 by the Ecological Forest



Inventory of Catalonia (IEFC) (Gracia *et al.* 2000), 67% of the total burnt area affected forest, with the rest composed of agricultural fields. The primary forest species' affected include Black Pine *Pinus nigra* (74%) and Aleppo Pine *P. halepensis* (11%), with Holm Oak *Quercus ilex* and deciduous *Quercus* spp. (Lusitanian Oak *Q. faginea* and Downy Oak *Q. humilis*) extensively present in the understorey.

Since the seeds of *P. nigra* are released in spring, summer fires prevent the regeneration and recovery of *P. nigra* stands, leading to «non-direct regeneration» of the forest, dominated by resprouting species such as oaks (see Habrouk, Retana & Espelta 1999; Rodrigo *et al.* 2004). In the case of *P. nigra* stands in Catalonia, forest landscapes typically change toward a mosaic of different states dominated by different *Quercus* species, shrubland and open grasslands, with some remains of unburned *P. nigra* (Retana *et al.* 2002).

### **Censuses**

Line transects were used to estimate presence and abundance of the Ortolan bunting (Bibby, Burgess & Hill 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 belts on both sides of the track. 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 one month between visits to the same transect. The

maximum number of birds observed on the two visits to each transect was used in the modeling.

Transects were distributed within the burnt area using a random stratified sampling design. Initially, we randomly placed 25 points within the fire perimeter. At each of these points (approximately 2 km radius), we designated 4 survey transects. The criteria used to select transect locations around each random point were as follows: 1) Transects were only conducted across burnt natural habitat and therefore were not placed in patches of non-burnt forest or farmland within the fire perimeter; 2) Transects had to be easily accessible from walking trails; 3) Transects had to represent the main burnt habitat types occurring near the random point. We considered burnt habitat at a landscape scale to be associated with aspect and amount of non-burnt and agricultural patches in the surroundings. Therefore we used these factors as cues to place transects; 4) The minimum distance between transects was 150 m. All bird surveys were performed by the same observer (LB) to avoid between-observer variation; they were always conducted in good weather conditions, without rainfall or strong wind. All transects were conducted within 3 hours of sunrise.

### ***Habitat Selection***

Habitat selection can be measured on a number of spatial and temporal scales (Cousin 2004). The importance of this is that factors affecting the distribution of a species can act differently on varying spatial scales (Steele 1992; George & Zack 2001). Major complexity in terms of habitat selection

exists at the microhabitat level (George & Zack 2001). Indeed, variables describing habitat features take on a finer resolution, and generally fall into four categories: vegetation structure, vegetation composition, topographic features and specific habitat elements (George & Zack 2001). It has been said that species tend to respond more to vegetation structure than species composition (George & Zack 2001), though some species are deemed to be associated with certain plant assemblages (Wiens, Rotenberry & Van Horne 1987). In consideration of the reasons given above, we explore habitat selection of the Ortolan bunting on different spatial scales, in order to gain a broader understanding of the species' habitat requirements.

### ***Landscape Variables***

All landscape and microhabitat variables were recorded by the same observer (LB) 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 scale variables recorded for each transect are as follows: Proportion of south-facing pixels and Slope were calculated using a Digital Elevation Model (DEM, 30 m resolution) generated from 1:50,000 topographic maps. Proportion of south-facing pixels gives a direct measure of the aspect of the transect. The percentage cover of surrounding agricultural fields was estimated within a 500 m belt surrounding the transect based on 1:50,000 topographic maps. Cover of unburnt patches was determined in the field (categorical, 0-3 with increasing cover). Finally, the stream character of the transect (the degree to which there were streams along or near the

transect) was recorded (categorical, 0-5 ascending), as it has been previously observed that these areas often exhibit specific, higher vegetation recovery rates.

### ***Microhabitat Variables***

We recorded variables relating to vegetation and microhabitat structure along each transect, using a modification of the cover estimation method proposed by Prodon & Lebreton (1981). Variables were estimated for the whole length of the transect, including a 100 m belt on either side of the transect.

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. For each variable, the relative 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. Cover values of continuous variables were recorded to an accuracy of 5–10%.

### ***Statistical Analysis***

Due to the nature of survey count data, excess zeros were present in the data set, more than would be expected from a typical Poisson distribution (Fig. 2). In order to account for over-dispersion of the data and the excess zeros, a Zero-inflated Poisson (ZIP) modelling procedure was applied

(Lambert 1992; Martin *et al.* 2005; Potts & Elith 2006). As mentioned in the introduction, we chose to model the abundance of the species against habitat variables, instead of focusing on factors describing the occurrence. This method was chosen, as breeding groups are known to be important regarding the distribution of the Ortolan Bunting (Vepsäläinen *et al.* 2007), thus, we consider that areas where Ortolan Buntings are more abundant are most likely to be optimal habitat. Modelling was conducted using the maximum count of Ortolan Buntings from the two visits, for each transect.

Continuous variables were first tested for pair-wise correlation, using Spearman's Rank Correlation Coefficient ( $r_s$ ) before inclusion in the modelling. An  $r_s = |0.7|$  was used as the acceptable lower limit of correlation and variables exceeding this were excluded from further analysis. Presence of multicollinearity between the continuous variables was tested for, using Variance Inflation Factors (VIF) (Faraway 2004).

Modelling was conducted in two stages: landscape scale and microhabitat scale. All models were defined prior to running the analysis (see Burnham & Anderson 1998): 27 models were defined based on the microhabitat variables and 27 models were defined based on the landscape scale variables. Quadratic functions of the variables appearing in the most parsimonious models were also tested to determine if there is an optimum level of these variables relating to increased abundance of Ortolan buntings. Models were ranked based on Akaike's Information Criterion, corrected for small samples ( $AIC_C$ ) (Burnham & Anderson 1998; Johnson and 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 1 000 repeats. All analyses were carried out using the program R v2.6.2 (R Development Core Team 2008) using the packages *zicounts* for ZIP (Mwalili 2008) and *car* for calculating variance inflation factors (Fox 2007; both packages available at <http://cran.r-project.org>).

## **Results**

### ***Landscape scale Habitat Selection***

A summary of the results (coefficients  $\pm$  s.e.) from the most parsimonious set of landscape-scale habitat models are presented in Table 1.

Multicollinearity was not a serious problem ( $VIF \leq 1.45$ ). Four models were included in the most parsimonious set of models (combined  $w_i = 0.961$ ; Table 1). The most parsimonious Landscape scale model contained only the variables Percentage of south-facing pixels and the quadratic function for Slope ( $w_i = 0.767$ ). 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 Figures 3a-b. Predictions derived from the most parsimonious model show a clear optimal level predicting the highest abundance of Ortolan Buntings on moderate slopes between 15-20°. A predicted abundance of more than one individual is indicated for Slopes between 10-25° (Fig. 3a.). Results from predictions of abundance compared to Proportion of south-facing pixels are predict the occurrence of more than

one individual for almost completely north-facing slopes, though predicted abundance increases steadily with increasing proportion of south-facing pixels (Fig. 3b.). This shows that although there is no clear avoidance of north-facing areas, birds are predicted to be more abundant in south-facing areas.

### ***Microhabitat Selection***

A summary of the results (coefficients  $\pm$  s.e.) from the most parsimonious set of microhabitat models are presented in Table 2. Multicollinearity was not a serious problem ( $VIF \leq 1.49$ ). Five models were included in the most parsimonious set of models (combined  $w_i = 0.966$ ). All of the top models included only the variables Bare ground and Regenerating *Quercus* spp., with various combinations of the quadratic terms (Table 2). 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 2). The inclusion of an interaction between these variables did not improve the  $AIC_c$  of the model. Predictions made from this model are presented in Figures 4a-b. Results clearly show an optimal level for occurrence of the Ortolan Bunting at around 20% cover of Regenerating *Quercus* spp (Fig. 4b.). More than one individual is predicted to occur between 0-45% cover of Regenerating *Quercus* spp. (Fig. 4b.). Results from predictions indicate an optimum level of Bare ground at around 20-30% cover (Fig. 4a.), with more than one individual predicted to occur between 10-50% cover. The large level

of uncertainty surrounding predictions between 40-80% cover, is most likely due to the paucity of data points within this cover range.

## **Discussion**

This study establishes, for the first time empirically, a preference of Ortolan buntings in postfire areas of the Mediterranean for shallow South-facing slopes offering a habitat matrix consisting of rejuvenating Oak shrubland interspersed with patches of bare ground. This habitat configuration is amply provided by the early stages of vegetation succession in burnt shrubland and woodland.

Cramp & Perrins (1994) already mentioned species' inclination towards dry, south-facing, sunny areas, but this has recently been questioned by Fonderflick, Thévenot & Guillaume (2005). Actually, our results show no evidence for avoidance of north-facing areas, but are indicative of a clear increase in predicted abundance of the species with more southerly-facing areas. This trend may stem from a greater availability of bare ground surfaces in the warmest aspect in Mediterranean biomes (Dale 2000), i.e. may be constrained mainly by foraging constraints (see below the discussion about patches of bare ground). The same explanation would hold for the low probability of occurrence of the species on flat areas found in this study. Flat areas are more likely to be densely vegetated, i.e. less suitable to Ortolan buntings, due to lower soil drainage (Fonderflick, Thévenot & Guillaume 2005). Several studies have already pointed out a preference of the species for dry, well drained soils (Mildenberger 1968; Cramp & Perrins 1994;



Kupczyk 1997; Glutz von Blotzheim & Bauer 1997; Dale 2000; Fonderflick, Thévenot & Guillaume 2005; Deutsch 2007) and avoidance of wet areas (Kuzniak 1997).

Previous studies have reported a link between the occurrence of the Ortolan bunting and burnt areas (Dale & Hagen 1997; Dale & Olsen 2002; Dale & Manceau 2003; Revaz *et al.* 2005; Brotons, Herrando & Pons 2008), with a progressive disappearance from these areas in later stages of vegetation succession (Sirami, Brotons & Martin 2007; Zozaya & Brotons 2007). Our study is the first to explore in detail the relationship between the abundance of the species and post-fire vegetation community on a microhabitat scale. It shows a clear relationship between predicted abundance of the Ortolan bunting and regenerating Oak *Quercus* spp. shrubs. Other studies conducted in Mediterranean habitats have recorded that Ortolan buntings favour open shrubland, without mentioning oak explicitly, with most territories present in areas with shrub cover between 5-24% and 10-40% (Fonderflick & Thévenot 2002; Fonderflick, Thévenot & Guillaume 2005, respectively). This is consistent with our results, which predict the highest abundance of Ortolan buntings is to occur in open regenerating oak shrubland with between 0-40% cover. The exact reasons behind this link between the Ortolan bunting and open shrubland in general, and oak shrubland in particular, are still unclear. For shrubland, the most commonly given reason is that isolated shrubs and small trees provide song-posts (Lang *et al.* 1990; Fonderflick, Thévenot & Guillaume 2005). As per the link between the species and oaks, recognized earlier by von Bülow (1990)

and Lang *et al* (1990), it may be attributed to the fact that in some areas, early in the nestling season, chicks are fed largely on defoliating caterpillars gleaned from the foliage of oak trees (Conrads 1969). Indeed, caterpillars are especially abundant in the foliage of oaks, compared to other deciduous tree species, providing an essential source of proteins for a number of breeding birds (Blondel *et al* 1991; Blondel *et al* 1998; Naef-Daenzer & Keller 1999; Naef-Daenzer 2000; Naef-Daenzer, Naef-Daenzer & Nager 2000). Although the Ortolan bunting is primarily known as a ground-forager, it might benefit from these food reservoirs by temporarily feeding in foliage, or simply exploiting low shrub branches from the ground. Only detailed studies of foraging, e.g. through radiotracking, could help to further interpret these patterns of habitat selection in the context of food resource exploitation.

We also show evidence of a positive relationship between the predicted abundance of Ortolan buntings and bare ground cover. The availability of bare ground has previously been shown to be an important variable regarding habitat selection of the species (M.H.M. Menz, P. Mosimann-Kampe & R. Arlettaz unpublished data). Santos, Tellería & Carbonell (2002) described a negative relationship between occurrence of the Ortolan Bunting and cover of herbaceous plants, which, given the habitat configuration at their study plot in Spain, infers a preference for bare ground. Contrastingly, Fonderflick, Thévenot & Guillaume (2005) found that bare ground was not an important variable regarding occurrence of the species, though this has been interpreted as a result of availability of bare ground not being a limiting factor in their study area. As in several terrestrially foraging insectivorous

birds (Moorcroft *et al.* 2002; Butler & Gillings 2004), bare ground may be an essential habitat feature for the Ortolan bunting. Actually, the species is likely to be affected by reduced food accessibility in areas with dense ground-level vegetation (M.H.M. Menz, P. Mosimann-Kampe & R. Arlettaz unpublished data). In the end, availability of bare ground may well be the principal drive of the Ortolan bunting's habitat selection pattern, with the other factors discussed above (southern aspect, shallow slopes, shrubland regrowth) being simply subordinate to that principal factor.

A first important question arises then what is the optimal stage in postfire regeneration of oaks that offers the most suitable habitat to the Ortolan buntings? This is crucial in the context of habitat management for conservation. Unfortunately, our static approach, with all forest fragments investigated burnt in the same year, only allows speculation. Secondly, although post-fire vegetation regeneration may prove imperative to the persistence of the Ortolan bunting, it is impossible, based on our data to recognize the ideal spatial mosaic offering patches of burnt vegetation at different regeneration stages. We can merely guess that in a 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. What is certain at this stage, is that in many European breeding areas outside the Mediterranean, such a juxtaposition of burnt areas in different rejuvenation stages does not occur anymore. This is because the traditional practice of farmland management through vegetation burning has been banned or abandoned in most of Western and Central Europe. Even where this habit has

persisted, mostly illegally (Revaz, Schaub & Arlettaz 2008), the extremely simplified agricultural matrix following agricultural rationalisation and the expansion of monocultures has totally eradicated the ancestral fine-grained habitat structure, thus anyway eliminating chances to obtain a local mosaic of burnt and unburnt parcels. Progressive land-use changes may hence explain why the last north European populations of the Ortolan bunting now mostly persist in late-stage regenerating burnt areas, where they apparently do not thrive at all, to say the least (Dale 2005; Revaz *et al.* 2005; M.H.M. Menz, P. Mosimann-Kampe & R. Arlettaz unpublished data).

Actually, these birds have been shown to exhibit an unusual strategy among terrestrial birds (see Alexander & Cresswell 1990; Rothstein, Verner & Stevens 1984), by occupying separate breeding and foraging areas, with birds moving to nearby farmland to forage (Dale 2000; Dale & Olsen 2002; Dale & Manceau 2003; M.H.M. Menz, P. Mosimann-Kampe & R. Arlettaz unpublished data). This may be an indication that the species is currently occupying sub-optimal habitats in these areas, due for instance to a lack of open foraging grounds close to breeding sites, as suggested by Fonderflick, Thévenot & Guillaume (2005). Whether or not this strategy is inherent in the Ortolan bunting as a species, or just a response of declining populations to a lack of suitable foraging habitat close to breeding sites, still requires further clarification. Studies in the Mediterranean may provide decisive insights here. Yet, the fact that proximity to farmland was not considered an important variable governing Ortolan bunting territory occupancy in a Mediterranean habitat in France (Fonderflick, Thévenot & Guillaume 2005) and did not

determine occurrence in the present study, suggests that long commuting flights between breeding and foraging grounds are detrimental, as shown for other insectivorous birds (e.g. Fournier & Arlettaz 2001).

Unfortunately, one cannot be conclusive on this point, due to some methodological limitations inherent in both ours and the study by Fonderflick, Thévenot & Guillaume (2005). The two analyses of habitat use are based primarily on locations obtained from singing males. It is therefore questionable to which extent data collected from singing territorial males yield appropriate information regarding foraging grounds. Again, only fine-grained habitat selection studies at the individual level could allow determination of whether or not birds in the Mediterranean have separate foraging grounds, or forage in close proximity to singing areas. Some of the uncertainty around the results could also stem from the estimation method used when recording the habitat variables. Variables were recorded in the field as an average across the whole transect, which may not fully capture the small-scale variation in the sites where the birds were observed. The best way to increase the accuracy of the estimations and improve the certainty around the effect of different habitat variables would be to conduct the individual-based study of fine-grained habitat suggested above.

Breeding groups have been shown to be particularly important regarding the spatial distribution of the Ortolan bunting in the landscape (Vepsäläinen *et al.* 2007). Additionally, it has also been established that male Ortolan buntings may move great distances during the breeding season in search of habitat patches with available females (Dale, Lunde & Steifetten

2005; Dale *et al.* 2006). Females have been observed to colonise areas with several singing males, while solitary males typically remain unpaired (Guerrieri, Miglio & Santucci 2006). Though males may show increased site fidelity as they get older, younger males may prospect relatively widely in the landscape during the breeding season, searching for suitable territories (Dale, Lunde & Steifetten 2005; Dale *et al.* 2006). As mentioned in Brotons, Pons & Herrando (2005), local breeding groups or populations may in fact be functionally connected, operating hence within a complex meta-population system. Depending on the stage of post-fire vegetation regeneration, areas may be settled and then abandoned as they progressively become unsuitable. We know of no studies focusing on individual movements in the species' southern breeding areas.

### ***Implications for Conservation***

This study demonstrates that the presence of patches of bare ground interspersed with scattered, shrubby oak vegetation is essential to the persistence of the Ortolan bunting in mosaic landscapes affected by fire. We suggest that a similar habitat configuration may also prove crucial to the persistence of the rapidly declining northern European populations.

Management actions should thus be directed towards maintaining open areas representative of early stages in vegetation succession after disturbance.

Increased grazing has been previously proposed as a management measure to promote the persistence of several open habitat species, including the Ortolan bunting (Moreira *et al.* 2001; Herrando, Brotons & Llacuna 2003;

Brotons, Herrando & Pons 2008). We believe, however, that unless over-grazing is achieved, sufficient bare ground areas will hardly be obtained in that way. Another, complementary alternative to retain the desired degree of openness, especially at ground level, is prescribed burning. Already recommended for maintaining biodiversity in Mediterranean biomes, this method has so far, to our knowledge, not been experimented with on a large scale at northern latitudes (Moreira *et al.* 2001; Herrando, Brotons & Llacuna 2003; Brotons, Herrando & Martin 2004; Brotons, Herrando & Pons 2008).

Based on our modelling, we can already provide guidance for concrete habitat management. Measures for obtaining the desired habitat openness must first and foremost be implemented on locations exposed to the South, on gentle slopes. Second, the cover of rejuvenating shrubland must amount to ca. 20-30% and promote oak regrowth. Third, and probably most importantly, areas of bare ground should cover around 20% of the managed area.

We finally propose to launch new studies to define, firstly, what is the most suitable stage in vegetation succession, and, secondly, what is the best spatial scale and most beneficial habitat matrix arrangement for breeding Ortolan buntings. This would certainly enable further refinement of the conservation guidelines provided above.

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## Tables

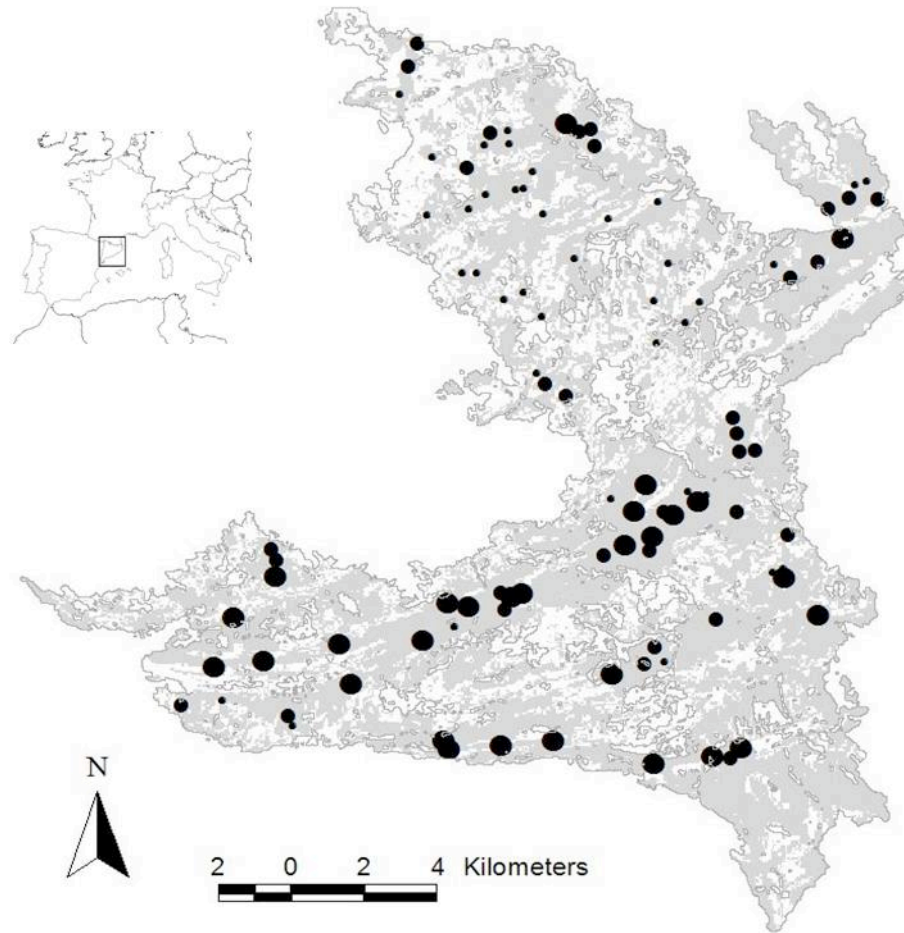
**Table 1.** Zero-inflated Poisson (ZIP) model results and parameter estimates ( $\pm$  se) for the most parsimonious set of landscape-scale models describing the abundance of Ortolan Buntings.  $Z$  = Intercept of the ZIP zero distribution; AICc = Akaike’s Information Criterion corrected for small samples;  $\Delta_i$  = change in AICc;  $w_i$  = Akaike weight; Dev. = Residual Deviance;  $K$  = number of parameters.

Model	Variables												$\Delta_i$	$w_i$	Dev	$K$
	Intercept		Slope		Slope <sup>2</sup>		Southern pixels		Farmland		Z					
	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.				
23	-3.345	1.205	0.422	0.158	-0.012	0.005	0.010	0.004	-	-	-1.649	0.539	0.00	0.767	314.6	5
12	-0.835	0.407	0.066	0.025	-	-	0.010	0.003	-	-	-1.657	0.576	3.39	0.141	320.2	4
11	0.127	0.210	-	-	-	-	0.015	0.003	-0.021	0.011	-1.729	0.652	6.49	0.030	323.3	4
21	-3.875	1.397	0.522	0.176	-0.014	0.005	-	-	0.006	0.012	-1.208	0.338	7.00	0.023	321.6	5

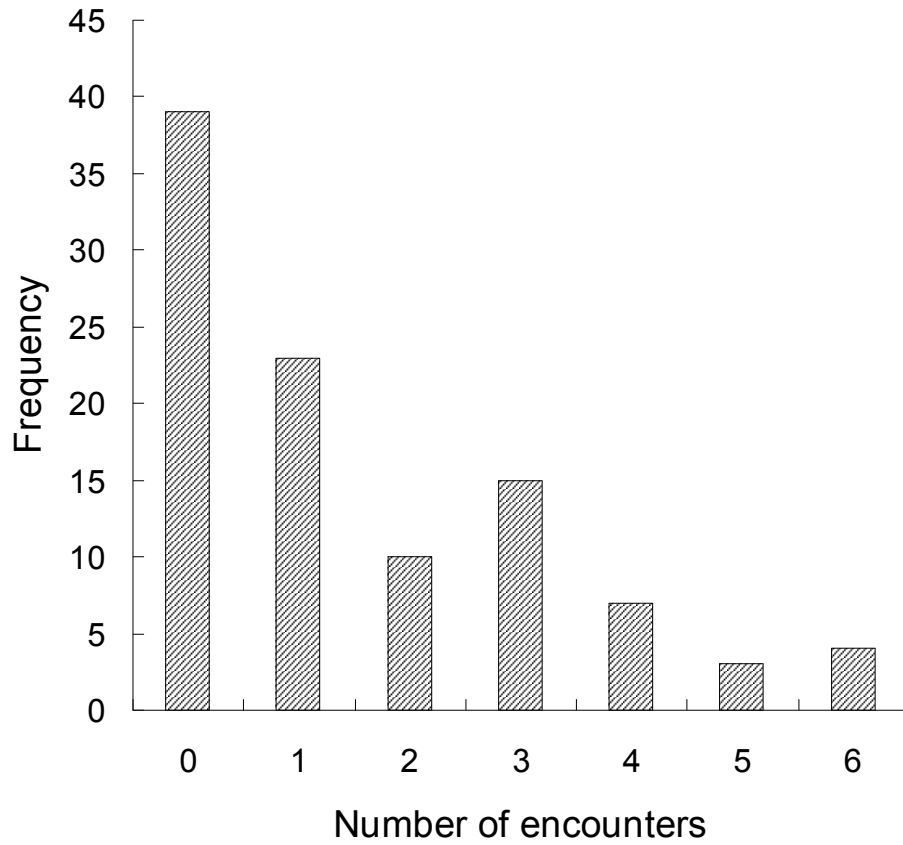
**Table 2.** Zero-inflated Poisson (ZIP) model results and parameter coefficients ( $\pm$  se) for the most parsimonious set of microhabitat models describing the abundance of Ortolan Buntings. Regen. = Regenerating;  $Z$  = Intercept of the ZIP zero distribution;  $AIC_C$  = Akaike's Information Criterion corrected for small samples;  $\Delta_i$  = change in  $AIC_C$ ;  $w_i$  = Akaike weight; Dev. = Residual Deviance;  $K$  = number of parameters.

Model	Variables												$\Delta_i$	$w_i$	Dev	$K$
	Intercept		Bare ground		Bare ground <sup>2</sup>		Regen. Oaks		Regen. Oaks <sup>2</sup>		$Z$					
	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.	Coef.	s.e.				
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	0.00	0.638	293.6	6
16	-0.143	-0.636	0.045	0.012	-	-	0.040	0.036	-0.001	0.000	-2.104	0.959	2.84	0.154	298.7	5
18	0.026	0.455	0.127	0.037	-0.002	0.001	-0.018	0.008	-	-	-2.282	0.906	3.34	0.120	299.2	5
20	-0.747	0.312	0.159	0.036	-0.003	0.001	-	-	-	-	-1.796	0.593	6.02	0.031	304.1	4
3	0.643	0.341	0.045	0.011	-	-	-0.022	0.008	-	-	-2.272	1.016	6.62	0.023	304.7	4

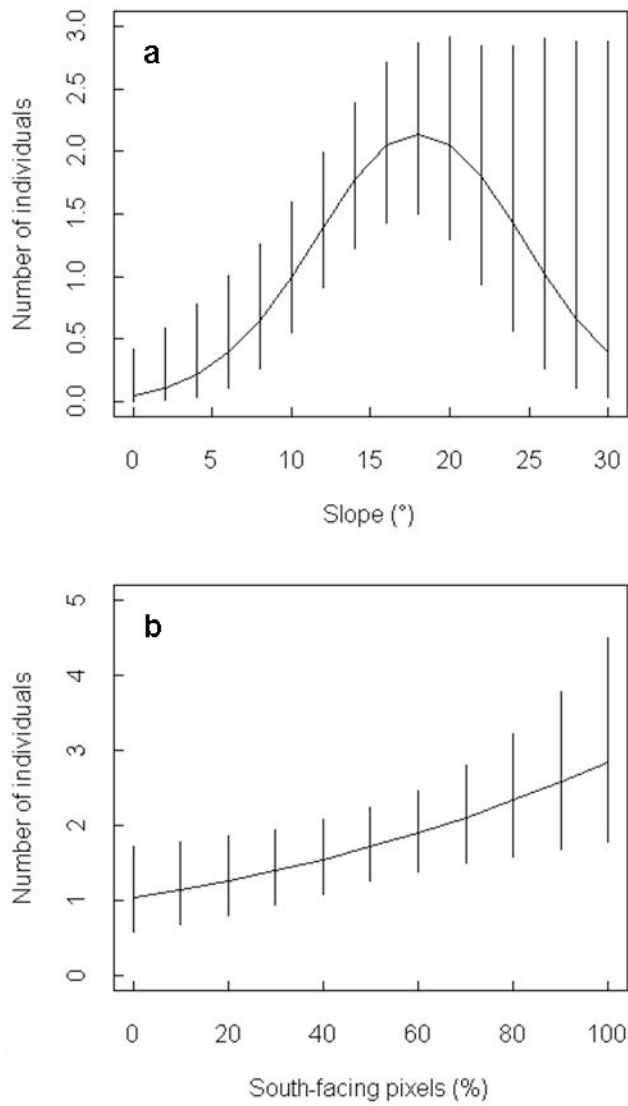
## Figures



**Fig. 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 wildfire 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).

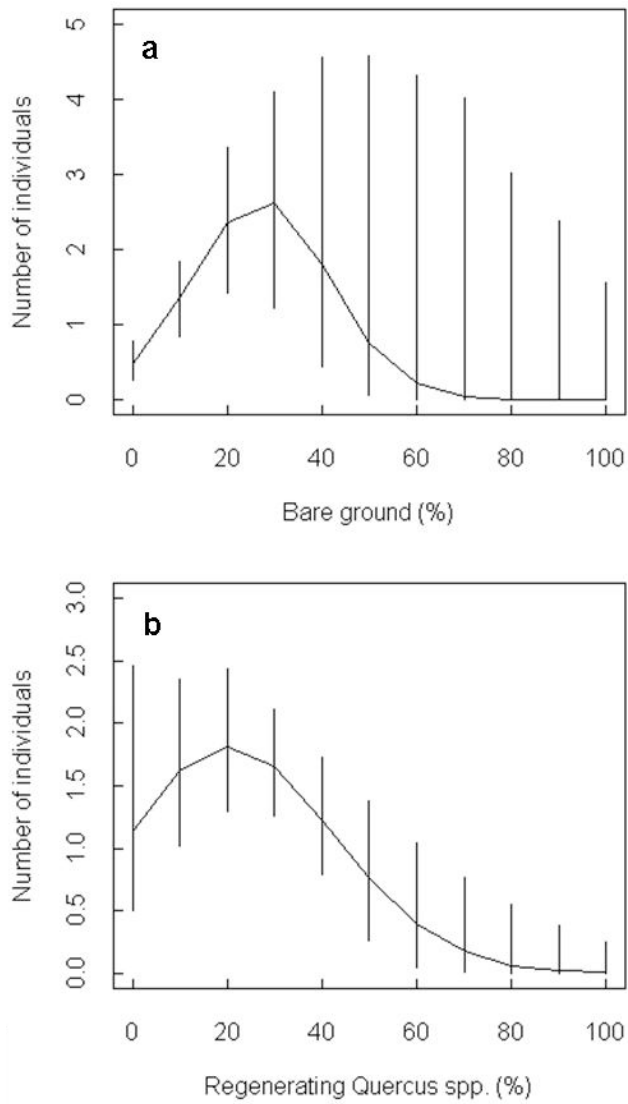


**Fig. 2.** Frequency of encounters of Ortolan buntings from 101 survey transects, showing excess zero observations.



**Fig. 3.** Estimates of abundance of Ortolan buntings in relation to landscape-scale habitat variables from the most parsimonious Zero-inflated Poisson model: (a) estimate of abundance in relation to Slope; (b) estimate of abundance in relation to percentage of South-facing pixels.





**Fig. 4.** Estimates of abundance of Ortolan buntings in relation to microhabitat variables from the most parsimonious Zero-inflated Poisson model: (a) estimate of abundance in relation to percentage cover of Bare ground; (b) estimate of abundance in relation to percentage cover of regenerating *Quercus* spp.