

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

Myles H. M. Menz^{1,*}, Paul Mosimann-Kampe² & Raphaël Arlettaz^{1,3,4}

Menz M.H.M., Mosimann-Kampe P. & Arlettaz R. 2009. Foraging habitat selection in the last Ortolan Bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction. *Ardea* 97(3): 323–333.

The Ortolan Bunting *Emberiza hortulana* has suffered a general decline across much of Western Europe in recent decades. In Switzerland, only one population remains in sub-Mediterranean shrub-steppe on the south-facing slopes of the Rhône Valley (Valais). We aimed to collect data on foraging ecology of the last Swiss Ortolan Buntings during reproduction. However, this population underwent a considerable decline, with no breeding confirmed in Switzerland in 2007. We investigated foraging habitat selection of four unpaired males at the habitat and microhabitat scales, and compared patterns of foraging habitat use with patterns of terrestrial invertebrate abundance. 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 disproportionate use of conventional maize fields that had been treated with herbicides, while also exhibiting an avoidance of meadows and riparian vegetation. These observed patterns of habitat use may be driven by unavailability of optimal foraging habitat, with birds being forced to use the best of a poor set of options. Structurally, it was shown that birds foraged in areas with a high proportion of bare ground, as well as moderately dense overhead vegetation. These areas did not support higher arthropod abundance, suggesting that food accessibility (and/or cover) rather than food abundance dictated habitat selection. It remains to be seen whether these patterns of microhabitat use 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. Additionally, effort needs to be focused on identifying factors affecting the species on the wintering grounds, which may assist in explaining the observed declines in the breeding areas.

Key words: Habitat selection, generalised linear mixed models, prey availability, population decline, species conservation

¹Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland;

²Breiten 37, CH-3232 Ins, Switzerland; ³Swiss Ornithological Institute, Valais Field Station, Nature Centre, CH–3970 Salgesch, Switzerland; ⁴The Ecology Centre, University of Queensland, St Lucia, QLD 4072, Australia;

*corresponding author (myles.menz@bgpa.wa.gov.au); current address: Kings Park and Botanic Gardens, The Botanic Gardens and Parks Authority, West Perth, WA 6005, Australia; School of Plant Biology, The University of Western Australia, Crawley, WA 6009, Australia



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 *et al.* 2001). Loss of habitat heterogeneity, changes in culture types and farming regimes, and widespread herbicide and pesticide application has led to massive declines in food abundance and diversity, especially invertebrates, during the breeding season (Stoate *et al.* 1998, Moreby & Stoate 2001, Robinson *et al.* 2001, Newton 2004, Britschgi *et al.* 2006). In bird breeding areas, declines in invertebrate populations can have severe adverse effects on survival of nestlings, which rely on a diet rich in proteins. 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 *et al.* 2001, Fournier & Arlettaz 2001).

The Ortolan Bunting *Emberiza hortulana* 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). In addition to potential issues associated with habitat degradation on the breeding grounds, it is also likely that other factors in the wintering areas and stopover sites, such as hunting (Claessens 1992) and rainfall (Zwarts *et al.* 2009), may be responsible for the observed population declines (von Bülow 1990, Stolt 1993, Cramp & Perrins 1994, Tucker & Heath 1994, Vepsäläinen *et al.* 2005), though little is known about the wintering areas of this species (Cramp & Perrins 1994, Yosef & Tryjanowski 2002, Vepsäläinen *et al.* 2005).

In the early 1980s, the Ortolan Bunting still bred near Geneva and in the canton Graubünden, but since then has ceased to do so (Revaz *et al.* 2005, see also G eroudet 1954). The only remaining breeding population of the Ortolan Bunting in Switzerland occupies the south-exposed slopes of the Rh one Valley in the canton Valais, between 600 and 1400 m a.s.l. (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, exclusively from the canton Valais (Revaz *et al.* 2005).

Farmland has been determined as an important foraging habitat for Ortolan Buntings during the breeding season (Dale 2000, Dale & Olsen 2002, Dale & Manceau 2003), and it is suggested that maintenance of traditional, small parcel farming and high crop variety are important for breeding Ortolan Buntings (Claessens 1992, Dale 2000). In Switzerland, it is said that the species requires the availability of patchy, structurally diverse habitats, with solitary trees, bushes and rocks, which are used as song posts (Lang *et al.* 1990, Veps al ainen *et al.* 2005), as well as warm, dry areas with small parcel farming (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. Oat is considered an important resource for Ortolan Buntings upon arrival and before departure on migration (Keusch 1991). Not much more is known about the foraging habitat requirements of the Ortolan Bunting in Switzerland.

Initially, our aim was to identify the preferred diet and foraging habitats of Ortolan Buntings when adults are provisioning nestlings. However, there was an unforeseen population crash, and to our knowledge, the remaining population consisted essentially of unpaired males, with no confirmed 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 at the habitat and microhabitat scales. At the habitat scale, we aimed to identify which habitat types are favoured by foraging Ortolan Buntings, and on the microhabitat scale, the main structural features at sites visited by foraging Ortolan Buntings. At the habitat scale, we also aimed to determine if oat fields were used during the breeding season. Finally, we investigated if there is a link between 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-breeding status of the population, but think that some of our results could still shed more light on the ecology of this declining species.



Figure 1. Habitat of the last Ortolan Bunting population in Switzerland. The population historically bred on the steppe, which can be seen in the background. Results from this study showed that unpaired males foraged almost exclusively in the Maize fields, which can be seen in the foreground (Photo M. Menz).

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 extends onto the plain at the base of the steppe, which nowadays is primarily occupied by intensive agriculture (Fig. 1). 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 singing male. Males were attracted with playback of the territorial song. 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 in between. 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 harness was 55 mm, using the formula as presented by Naef-Daenzer (2007). Leg loops were constructed from 0.5 mm diameter natural rubber. 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 *et al.* 1993). Locations were marked with a Global Positioning System (GPS, Garmin eTrex Summit, Garmin Ltd., USA).

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 with ArcView v3.3 GIS software (Environmental Systems Research Institute Inc., California) with the Animal Movement extension v2.0 (Hooge *et al.* 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.

Habitat selection

At each location, broad-scale habitat type was recorded. Nine distinct habitat types were present in the foraging areas: Maize fields treated with herbicide, untreated Maize 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 Maize fields (those with and without use of herbicides) were used to a different extent by foraging birds, thus, these are treated as separate habitat types. The habitat type Other was not considered as available foraging habitat for the birds, therefore it was excluded from further analyses. As a result, the remaining area within the MCP was 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 habitat types changing between years, such as crops, were verified by mapping in the field with the use of a GPS.

Microhabitat selection

In addition to habitat type, at each of the recorded foraging and random locations, a number of habitat variables were recorded within a 2×2 m square around the focal location. The habitat variables recorded were: Bare ground cover, Vegetation cover at 0.5–1 m and at 1–2 m (all in %, 5–10% accuracy). Only those males with ≥ 40 foraging locations were included in the analysis.

Prey availability

Availability of ground-dwelling invertebrate prey was sampled by pitfall trapping, as, being a ground-foraging species, ground-dwelling invertebrate fauna feature prominently in the diet of Ortolan Buntings during the breeding season (Cramp & Perrins 1994). 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 of our study, the crops and grasses were still green. This indicated a very low availability of seeds. Thus, it was considered that the birds were still feeding on invertebrates, which could be confirmed by *in situ* observations. Pitfall trapping was employed in the three main habitat types, Maize fields treated with herbicides, untreated Maize fields, and Meadow. Pitfall 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 cm²) placed approximately 3 cm above the trap. Traps were installed in two rows of three, with 2 m between traps and rows. Four trapping grids were placed at random in each habitat type, within the overall area used by the foraging Ortolan Buntings. Traps were emptied three times, at three-day intervals from 4–14 August 2007. Sampling was conducted in August, as there was a need to first determine the foraging area of the males, in which to conduct the invertebrate sampling. Invertebrate samples were stored in 70% ethanol in sealed plastic bags. Invertebrates 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 balance (Mettler Toledo PB303-L Delta Range, Switzerland) to an accuracy of ± 0.001 g. Only invertebrates longer than 2 mm were considered as potential prey.

Statistical analyses

Habitat use was assessed using a randomised contingency table procedure (Estabrook & Estabrook 1989, Arlettaz 1999, Estabrook *et al.* 2002), comparing visited foraging locations and random locations within the MCP of each male.

Microhabitat requirements were assessed using binomial logistic regression, comparing habitat variables of visited locations with random locations. Continuous variables were first tested for pair-wise correlation, using Spearman's Rank Correlation Coefficient (r_s). An $r_s = |0.7|$ was used as the acceptable lower limit of correlation. If a variable pair exceeded this, the

least biologically meaningful variable was excluded from further analysis. Multicollinearity between the variables was tested for using Variance Inflation Factors (VIF, Faraway 2004). 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, Bolker *et al.* 2008) was applied, including the individual bird as a random factor. Eighteen models were defined *a priori* and ranked based on Akaike's Information Criterion, corrected for small samples (AIC_c) (Burnham & Anderson 1998, Johnson & Omland 2004). The models with AIC_c weights (w_i) summing to 0.95 were defined as the most parsimonious set of models, and the model with the highest w_i was selected to make predictions.

Relationships between habitat type and invertebrate abundance and dry biomass were tested using Linear Mixed-effects Models (Crawley 2007). Site and habitat were included as random factors in the models, with site nested within habitat. The effect of habitat was determined by 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. The mean of the three sampling replicates for each pitfall trap was used for the analysis. In order to improve normality, the variables Total abundance, Total biomass, Aranea abundance and Coleoptera abundance were log-transformed, and the variable Aranea biomass was 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 (Broström

2003) was used for Generalised Linear Mixed Models, and the library nlme (Pinheiro *et al.* 2009) for linear mixed-effects models (both available at <http://cran.r-project.org>).

RESULTS

Capture and radio-tracking

Of six males captured, four could be successfully radio-tracked. Only one female was observed during the study period, with no confirmed breeding in Switzerland in 2007. From 25 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 (Fig. 1). For each of Males 3, 5 and 6, 40 foraging locations were recorded from the plain, with only eight locations recorded for Male 1. The most abundant habitat type (disregarding Other) within the foraging ranges of the males was Meadow, followed by Maize fields treated with herbicide, Rye, untreated Maize fields and Riparian vegetation, Lucerne and Oat (Table 1); Oat was only present within the foraging area of Male 3. The most commonly used habitat was Maize fields treated with herbicides, followed by Rye and Meadow and untreated Maize fields (Table 1). The remaining four habitat types were not visited by foraging birds.

Habitat selection

Results from the randomised contingency tables show strong disproportionate use of Maize fields treated with herbicides, for all four birds (Males 5 and 6, $P < 0.001$; Male 3, $P < 0.01$; Male 1, $P < 0.05$; Fig. 2), and avoidance of meadows for three out of the four males (Males 5 and 6, $P < 0.001$; Male 3, $P < 0.01$). Male 6 avoided untreated Maize fields (Fig. 2, $P < 0.05$).

Table 1. Area (ha) and percentage of each habitat type within the foraging range of four radio-tracked male Ortolan Buntings (represented by ring number). Foraging area is expressed as the minimum convex polygon determined from the radio-tracking study. 'Other' includes infrastructure, road works and river. Males 2 and 4 are not included as insufficient data for foraging habitat selection analyses were collected (see text for details).

Bird	Ring number	Maize herbicide		Maize 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 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 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		

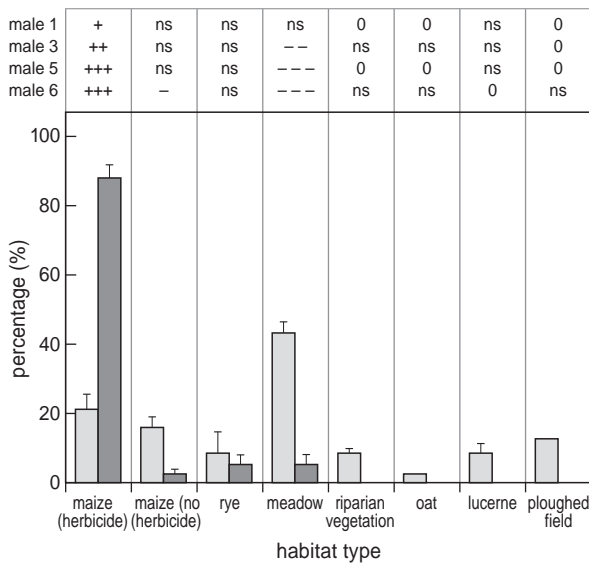


Figure 2. Results of randomised contingency tables for foraging habitat use by four male Ortolan Buntings. Presented are mean values (+ SE). Comparisons were made between absolute frequencies of visited (dark grey bars) vs. random (light grey bars) locations within the foraging minimum convex polygon (MCP) for each male. + or - 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.

Microhabitat selection

None of the microhabitat variables were strongly correlated ($r_s \leq 0.38$; $VIF \leq 1.15$), thus all variables were retained in the modelling. Four models had a combined $w_i = 0.95$ (Table 2). The most parsimonious model contained only the variables Bare ground, Vegetation to 1 m and the square of Vegetation to 1 m (Table 2), thus

these are considered to be important for determining foraging habitat selection of Ortolan Buntings. The inclusion of an interaction between Bare ground and Vegetation to 1 m did not improve the AIC_c of this model. Parameter estimates for the variables included in this model showed an increasing probability of occurrence, with increasing percentage cover of Bare ground (Fig. 3A). Bare ground cover above 70% exceeded the 0.5 level of probability, indicating positive selection (Fig. 3A). The quadratic function of Vegetation to 1 m exceeded the 0.5 level of occurrence probability at a cover between 20–70% with an optimum occurrence probability of 0.8 at 50% cover (Fig. 3B).

Prey availability

A total of 5404 invertebrates were collected from 14 orders, totaling 52.48 g dry biomass. 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%).

The total abundance of invertebrates differed significantly between habitat types (Table 3, $P = 0.004$). The highest abundance was recorded from Meadow (Fig. 4). Total dry biomass did not differ significantly between habitat types (Table 3, $P = 0.34$). 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 3, $P < 0.001$); with Meadow providing the highest value (Fig. 4). Dry biomass of Coleoptera did not differ significantly between habitats (Table 3, $P = 0.64$), conversely, abundance showed a significant difference (Table 3, $P = 0.018$), with the highest abundance occurring in Meadow (Fig. 4).

Table 2. Summary of Generalised Linear Mixed Model results for microhabitat variables modelled for three male Ortolan Buntings. Shown are models with total $w_i = 0.95$. B = Coefficient; Veg1m = Vegetation cover between 0.5–1 m; Veg2m = Vegetation cover between 1–2 m; Δ_i = change in AIC_c ; w_i = Akaike weight; Dev = Residual Deviance; NP = number of parameters.

Model	Parameters														Δ_i	w_i	Dev	NP
	Intercept		Bare ground		Bare ground ²		Veg1m		Veg1m ²		Veg2m		Veg2m ²					
	B	SE	B	SE	B	SE	B	SE	B	SE	B	SE	B	SE				
6	-2.764	0.426	0.025	0.005	-	-	0.096	0.027	-0.001	0.000	-	-	-	-	0.00	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	-	-	-	-	1.50	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

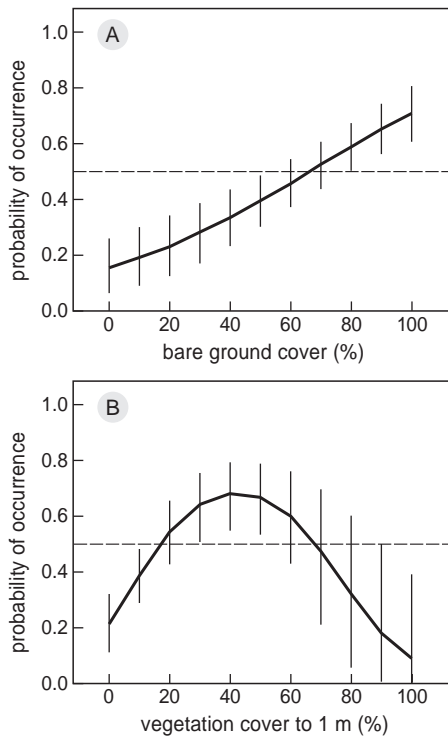


Figure 3. Parameter estimates of microhabitat variables included in the most parsimonious model, derived from a Generalised Linear Mixed Model (GLMM) procedure: (A) estimates of occurrence probability in relation to percentage cover of Bare ground; (B) estimates of occurrence probability in based on 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.

Table 3. Linear Mixed-effects Model results for the effect of Habitat on biomass and abundance of invertebrates. NP = Number of parameters; Δ_1 = Change in AIC_c; LogLik = Log Likelihood; LR = Log ratio. Transformations applied are shown in brackets.

Source of variation	NP	Δ_1	LogLik	LR	P
Total biomass (log)					
Null model	7	1.11	-59.74		
Habitat effect	8	0.00	-60.19	0.90	0.344
Coleoptera biomass (log)					
Null model	7	0.00	58.49		
Habitat effect	8	2.78	58.38	0.22	0.638
Aranaea biomass (log)					
Null model	7	0.00	-132.30		
Habitat effect	8	11.92	-138.75	12.91	<0.001
Total abundance (log)					
Null model	7	0.00	-31.61		
Habitat effect	8	6.37	-38.79	8.36	0.004
Coleoptera abundance (square root)					
Null model	7	0.00	-48.33		
Habitat effect	8	4.56	-51.01	5.55	0.018

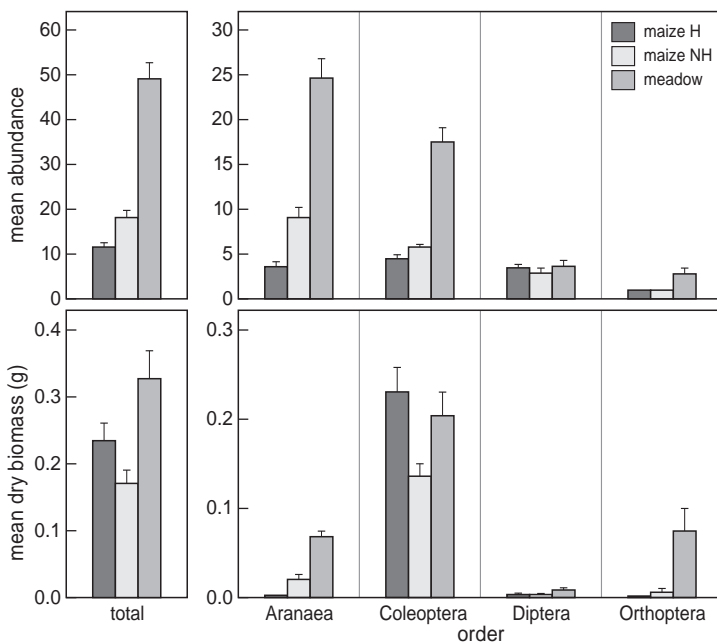


Figure 4. Mean (+ SE) abundance and biomass (g) of invertebrates sampled from the three main habitat types, Maize fields treated with herbicide (Maize H), untreated Maize fields (Maize NH) and Meadow. Each habitat was sampled in a standard way (see Methods). Also presented are mean (+ SE) abundance and biomass (g) of the four dominant invertebrate orders. Results are from untransformed data.

DISCUSSION

The Swiss Ortolan Bunting population has experienced a significant crash in recent years. In 2004, 32 singing males remained in Switzerland, including around 20 males recorded from our study site (Revaz *et al.* 2005); 20 territories were recorded again in 2006 (E. Revaz, pers. comm.). Based on these results, it was assumed that the population was still functioning as a breeding population, though declining and in need of conservation. The present study shows the population is much smaller than previously thought (8–9 singing males, 1 female), and is possibly now functionally extinct as a breeding population. A high proportion of unpaired males has been observed in declining Ortolan Bunting populations elsewhere (Dale 2001, Dale *et al.* 2005, Steifetten & Dale 2006), as well as in other passerine species (Donald 2007).

Male Ortolan Buntings showed a clear disproportionate use of Maize fields treated with herbicides, and an avoidance of Meadows. Additionally, there was an avoidance of Riparian vegetation, and one male avoided untreated Maize fields. An increase in Maize farming, at the expense of cereals, has been mentioned as one of the factors potentially affecting the Ortolan Bunting (Ikemeyer & von Bülow 1995, Steifetten & Dale 2006, Berg 2008). Maize fields are often considered unsuitable for nesting or foraging (Ikemeyer & von Bülow 1995, Hänel 2004), but Bellenhaus (2007) mentioned that Ortolan Buntings of unknown breeding status used Maize fields.

Bare ground is known to be an important habitat characteristic for Ortolan Buntings (Nævra 2002, Berg 2008, Menz *et al.* 2009), as well as for a number of other terrestrially foraging bird species (Moorcroft *et al.* 2002, Butler & Gillings 2004, Maurer 2006, Ioset 2007, Weisshaupt 2007). At our study site, Maize fields treated with herbicides differed from untreated Maize fields by the high proportion of bare ground, contrasting with a dense cover of herbaceous plants in the latter. The use of Maize fields treated with herbicides may be the result of birds being driven to use impoverished habitat when faced with this as the least unfavourable option. Habitats treated with herbicide are not considered favourable habitat, as herbicide has been identified as a major factor involved in the degradation of European farmland habitats (Newton 2004).

The 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, Aranea and Coleoptera) occurred in meadows, this habitat was avoided by foraging Ortolan Buntings. Conversely, Maize fields were shown to harbour a comparatively lower abundance of potential invertebrate prey. This suggests that prey accessibility, here in open terrain created by herbicide application, may be a more important habitat feature than prey abundance itself, at least for unpaired males. Breeding Ortolan Buntings may show different patterns of habitat use (Bellenhaus 2007), to cope with the high protein demand of rapidly growing nestlings. 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 *et al.* 2001, Vickery *et al.* 2001, Benton *et al.* 2003, McCracken & Tallwin 2004, Atkinson *et al.* 2005).

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 opened up the area 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 recorded in older male Ortolan Buntings (Keusch & Mosimann 1984, Dale *et al.* 2005), could explain the persistence of a population consisting primarily of unpaired males. Foraging in agricultural land could thus result simply from the unavailability of crucial foraging habitat (Fonderflick *et al.* 2005). Ortolan Buntings breeding in northern Europe do so in quite different habitat types compared with 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 and central/western Europe (i.e. Lang *et al.* 1990, Ikemeyer & von Bülow 1995, Dale 2000, Dale & Olsen 2002, Deutsch 2007, Lang 2007). The habitats that Ortolan Buntings occupy in these areas, i.e. primarily farmland, 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 Swiss population, which inhabits a sub-Mediterranean landscape. Additionally, there is a pressing need to understand the nature of processes that may be affecting the Ortolan Bunting in its wintering grounds, and at stopover sites.

These may provide explanation for the observed declines in breeding areas, not only of the Ortolan Bunting, but also of a considerable number of other long-distance migrants (Sanderson *et al.* 2006, Heldbjerg & Fox 2008, Zwarts *et al.* 2009).

ACKNOWLEDGEMENTS

Sincere thanks go to M. Schaub, F. Abadi Gebreselassie and A. Aebischer who were of great help regarding statistical advice. P. Keusch, A. Sierro and E. Revaz provided valuable information on the focal Ortolan Bunting population. R. Spaar from the Swiss Ornithological Institute provided financial support for the study. M. Güntert kindly provided the stuffed Ortolan Bunting. B.-O. Stolt, V. Vepsäläinen & M. Berman provided constructive comments on the manuscript. O. Roth assisted in tracking down difficult-to-source literature. Thanks also go to all those who helped with the fieldwork and provided valuable discussion: N. Weisshaupt, U. Kormann, C. Rösti, N. Signorell, M. Mermod and L. Dafond.

REFERENCES

- Aebischer N.J., Robertson P.A. & Kenward R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Arletta R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* 68: 460–471.
- Atkinson P.W., Fuller R.J., Vickery J.A., Conway G.J., Tallowin J.R.B., Smith R.E.N., Haysom K.A., Ings T.C., Asteraki E.J. & Brown V.K. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *J. Appl. Ecol.* 42: 932–942.
- Bellenhaus V. 2007. Die Habitatpräferenzen des Ortolans (*Emberiza hortulana*) in der Prignitz. Diploma thesis, Westfälische Wilhelms-Universität Münster.
- Benton T.G., Vickery J.A. & Wilson J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18: 182–188.
- Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. & White J.-S.S. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24: 127–135.
- Berg Å. 2008. Habitat selection and reproductive success of Ortolan Buntings *Emberiza hortulana* on farmland in central Sweden – the importance of habitat heterogeneity. *Ibis* 150: 565–573.
- Britschgi A., Spaar R. & Arletta R. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. *Biol. Conserv.* 130: 193–205.
- Broström G. 2003. Generalized linear models with random intercepts. Department of Statistics. Umeå University, Umeå. Available from: <http://www.stat.umu.se/forskning/reports/glmmML.pdf> [accessed 28th February, 2008].
- Burnham K.P. & Anderson D.R. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.
- Butler S.J. & Gillings S. 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis* 146 (Suppl. 2): 123–130.
- Claessens O. 1992. La situation du Bruant ortolan *Emberiza hortulana* en France et en Europe. *Alauda* 60: 65–76.
- Cramp S. & Perrins C.M. (eds) 1994. The Birds of the Western Palearctic, Vol. 9. Oxford University Press, Oxford.
- Crawley M.J. 2007. The R Book. John Wiley and Sons Ltd., Chichester.
- Dale S. & Hagen Ø. 1997. Population size, distribution and habitat selection of the Ortolan Bunting *Emberiza hortulana* in Norway. *Fauna norv. Ser. C, Cinclus* 20: 93–103.
- Dale S. 2000. The importance of farmland for Ortolan Buntings nesting on raised peat bogs. *Ornis Fenn.* 77: 17–25.
- Dale S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* 92: 344–356.
- Dale S. & Olsen B.F.G. 2002. Use of farmland by Ortolan Buntings (*Emberiza hortulana*) nesting on a burned forest area. *J. Ornithol.* 143: 133–144.
- Dale S. & Manceau N. 2003. Habitat selection of two locally sympatric species of Emberiza Buntings (*E. citrinella* and *E. hortulana*). *J. Ornithol.* 144: 58–68.
- Dale S., Lunde A. & Steifetten Ø. 2005. Longer breeding dispersal than natal dispersal in the Ortolan Bunting. *Behav. Ecol.* 16: 20–24.
- Deutsch M. 2007. Der Ortolan *Emberiza hortulana* im Wendland (Niedersachsen) – Bestandszunahme durch Grünlandumbbruch und Melioration? *Vogelwelt* 128: 105–115.
- Di Giulio M., Edwards P.J. & Meister E. 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *J. Appl. Ecol.* 38: 310–319.
- Donald P.F. 2007. Adult sex ratios in wild bird populations. *Ibis* 149: 671–692.
- Donald P.F., Green R.E. & Heath M.F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* 268: 25–29.
- Estabrook C.B. & Estabrook G.F. 1989. ACTUS: A solution to the problem of small samples in the analysis of two-way contingency tables. *Historical Methods* 22: 5–8.
- Estabrook G.F., Almada V.C., Almada F.J. & Robalo J.I. 2002. Analysis of conditional contingency using ACTUS2 with examples from studies of animal behavior. *Acta Ethol.* 4: 73–80.
- Faraway J.J. 2005. Linear models with R. Chapman and Hall/CRC, Boca Raton, Florida.
- Fonderflick, J., Thévenot, M. & Guillaume, C.-P. 2005. Habitat of the Ortolan Bunting *Emberiza hortulana* on the Causse Méjean (Lozère, southern France). *Vie et Milieu* 55: 109–120.
- Fournier J. & Arletta R. 2001. Food provision to nestlings in the Hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps. *Ibis* 143: 2–10.
- Géroutet P. 1954. La distribution du Bruant ortolan en Suisse. *Nos Oiseaux* 22: 217–225.
- Glutz von Blotzheim U.N. & Bauer K.M. 1997. *Emberiza hortulana* Linnaeus 1758 - Ortolan (Gartenammer). In: Glutz von Blotzheim U.N. (ed.) *Handbuch der Vögel Mitteleuropas*, Bd. 14/III: 1565–1625. Aula-Verlag, Wiesbaden.

- Golawski A. & Dombrowski A. 2002. Habitat use of Yellowhammers *Emberiza citrinella*, Ortolan Buntings *E. hortulana*, and Corn Buntings *Miliaria calandra* in farmland of east-central Poland. *Ornis Fenn.* 79: 164–172.
- Hänel K. 2004. Zur Populationsstruktur und Habitatpräferenz des Ortolans (*Emberiza hortulana*). *Mitteilungen des Vereins Sächsischer Ornithologen* 9: 317–357.
- Heldbjerg H. & Fox A.D. 2008. Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study* 55: 267–279.
- Hooge P.N., Eichenlaub W. & Solomon E. 1999. The animal movement program, v2.0 beta. USGS, Alaska Biological Science Center, Anchorage, USA.
- Ikemeyer D. & von Bülow B. 1995. Zum Rückgang der Ortolan-Population (*Emberiza hortulana*, L. 1758) am Rande der Hohen Mark bei Haltern/Westfalen. *Charadrius* 31: 137–146.
- Ioset A. 2007. The importance of bare ground for terrestrially foraging insectivorous farmland birds: a case study of the endangered Hoopoes (*Upupa epops*). Diploma thesis. University of Bern.
- Johnson J.B. & Omland K.S. 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19: 101–108.
- Keusch P. 1991. Vergleichende Studie zu Brutbiologie, Jungentwicklung, Bruterfolg und Populationsökologie von Ortolan *Emberiza hortulana* und Zippammer *E. cia* im Alpenraum, mit besonderer Berücksichtigung des unterschiedlichen Zugverhaltens. PhD thesis. University of Bern.
- Keusch P. & Mosimann P. 1984. Vergleichende ökologische Untersuchungen an Ortolan (*Emberiza hortulana*) und Zippammer (*E. cia*) in der Walliser Felsensteppe. Diploma thesis. University of Bern.
- Lang M. 2007. Niedergang der süddeutschen Ortolan-Population *Emberiza hortulana* – liegen die Ursachen außerhalb des Brutgebiets? *Vogelwelt* 128: 179–196.
- Lang M., Bandorf H., Dornberger W., Klein H. & Mattern U. 1990. Verbreitung, Bestandsentwicklung und Ökologie des Ortolans (*Emberiza hortulana*) in Franken. *Ökol. Vögel* 12: 97–126.
- Mason C.F. & Macdonald S.M. 2000. Corn Bunting *Miliaria calandra* populations, landscape and land-use in an arable district of eastern England. *Bird Conserv. Int.* 10: 169–186.
- Maurer M.L. 2006. Emergence of new cultivation practices in vineyards: any benefit for the endangered Woodlark *Lullula arborea*. Diploma thesis. University of Bern.
- McCracken D.I. & Tallowin J.R. 2004. Swards and structure: the interactions between farming practices and bird food in lowland grasslands. *Ibis* 146 (Suppl. 2): 108–114.
- Menz M.H.M., Brotons L. & Arlettaz R. in press. Habitat selection by Ortolan Buntings *Emberiza hortulana* in post-fire succession in Catalonia: implications for the conservation of farmland populations. *Ibis* 151: 752–761.
- Mohr C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37: 223–249.
- Moorcroft D., Whittingham M.J., Bradbury R.B. & Wilson J.D. 2002. The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J. Appl. Ecol.* 39: 535–547.
- Moreby S.J. & Stoate C. 2000. A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. *Bird Study* 47: 320–331.
- Moreby S.J. & Stoate C. 2001. Relative abundance of invertebrate taxa in the nestling diet of three farmland passerine species, Dunnock *Prunella modularis*, Whitethroat *Sylvia communis* and Yellowhammer *Emberiza citrinella* in Leicestershire, England. *Agricult. Ecosys. Environ.* 86: 125–134.
- Naef-Daenzer B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *J. Avian Biol.* 38: 404–407.
- Nævra A. 2002. Hortulanens skjebnetime. *Vår Fuglefauna* 25: 62–81.
- Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579–600.
- Pinheiro J., Bates, D., DebRoy S. & Sarkar D. 2009. nml: Linear and Nonlinear Mixed Effects Models. Available at <http://cran.r-project.org>.
- Pons P. 2004. Hortolà *Emberiza hortulana*. In: Estrada J., Pedrocchi V., Brotons L. & Herrando S. (eds) *Atles dels ocells nidificants de Catalunya 1999–2002*. Institut Català d'Ornitologia (ICO) and Lynx Edicions, Barcelona, pp. 544–545.
- Rappole J.H. & Tipton A.R. 1991. New harness design for attachment of radio transmitters to small passerines. *J. Field Ornithol.* 62: 335–337.
- Rehsteiner U., Spaar R. & Zbinden N. 2004. Elemente für Artenförderungsprogramme Vögel Schweiz. Koordinationsstelle des Rahmenprogramms Artenförderung Vögel Schweiz. Schweizer Vogelschutz SVS/Birdlife Schweiz and Schweizerische Vogelwarte, Zürich and Sempach.
- Revaz E., Posse B., Gerber A., Sierro A. & Arlettaz R. 2005. Quel avenir pour le Bruant ortolan *Emberiza hortulana* en Suisse? *Nos Oiseaux* 52: 67–82.
- Robinson R.A., Wilson J.D. & Crick H.Q.P. 2001. The importance of arable habitat for farmland birds in grassland landscapes. *J. Appl. Ecol.* 38: 1059–1069.
- Sanderson F.J., Donald P.F., Pain D.J., Burfield I.J. & van Bommel F.P.J. 2006. Long-term population declines in Afro-Palaearctic migrant birds. *Biol. Conserv.* 131: 93–105.
- Small B. 1992. Ageing and sexing Ortolan and Cretzschmar's Buntings in the field. *Birding World* 5: 223–228.
- Steifetten Ø. & Dale S. 2006. Viability of an endangered population of Ortolan Buntings: The effect of a skewed operational sex ratio. *Biol. Conserv.* 132: 88–97.
- Stoate C., Moreby S.J. & Szczyr J. 1998. Breeding ecology of farmland Yellowhammers *Emberiza citrinella*. *Bird Study* 45: 109–121.
- Stolt B.-O. 1993. Notes on reproduction in a declining population of the Ortolan Bunting *Emberiza hortulana*. *J. Ornithol.* 134: 59–68.
- Tucker G.M. & Heath M.F. 1994. *Birds in Europe: their conservation status*. BirdLife International, Cambridge (BirdLife Conservation Series no. 3).
- Vepsäläinen V., Pakkala T., Piha M. & Tiainen J. 2005. Population crash of the Ortolan Bunting *Emberiza hortulana* in agricultural landscapes of southern Finland. *Ann. Zool. Fenn.* 42: 91–107.
- Vickery J.A., Tallowin J.R., Feber R.E., Asteraki E.J., Atkinson P.W., Fuller R.J. & Brown V.K. 2001. The management of lowland neutral grasslands in Britain: Effects of agricultural practices on birds and their food resources. *J. Appl. Ecol.* 38: 647–664.

- von Bülow B. 1990. Verbreitung und Habitate des Ortolans (*Emberiza hortulana*, L. 1758) am Rande der Hohen Mark bei Haltern/Westfalen. *Charadrius* 26: 151–189.
- Weisshaupt N. 2007. Habitat selection by foraging wrynecks *Jynx torquilla* during the breeding season: identifying optimal species habitat. Diploma thesis. University of Bern.
- White G.C. & Garrott R.A. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego.
- Wilson J.D., Morris A.J., Arroyo B.E., Clark S.C. & Bradbury R.B. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agricult. Ecosys. Environ.* 75: 13–30.
- Yosef R. & Tryjanowski P. 2002. Differential spring migration of Ortolan Bunting *Emberiza hortulana* by sex and age at Eilat, Israel. *Ornis Fenn.* 79: 173–180.
- Zwarts L., Bijlsma R.G., van der Kamp J. & Wymenga E. 2009. Living on the edge: Wetlands and birds in a changing Sahel. KNNV Publishing, Zeist.

SAMENVATTING

De Ortolaan heeft in Zwitserland een zelfde ontwikkeling te zien gegeven als elders in West- en Midden-Europa. Stond de teller in 1978–79 hier nog op 243 zingende mannetjes, in 2004 was dat gezakt naar 32. De soort bewoont in Zwitserland voornamelijk droge, rotsachtige submediterrane habitats, afgewisseld met kleinschalige landbouw. De precaire stand was aanleiding om in 2007 een onderzoek te starten naar de habitat- en voedselkeus van broedvogels met jongen, factoren waarvan verwacht mag worden dat ze bepalend zijn voor de reproductie. Al snel werd duidelijk dat de werkelijkheid het onderzoek had ingehaald: in de vallei van de Rhône in het kanton Valais waren de 20 mannetjes van 2006 geslonken naar 8–9 ongepaarde

mannetjes en 1 vrouwtje in 2007. Er werd niet meer gebroed, zodat de populatie functioneel als uitgestorven kan worden beschouwd. Het onderhavige onderzoek is een poging de laatste stuip trekking van de Zwitserse Ortolanen vast te leggen, in de hoop lessen te trekken die van pas kunnen komen bij andere in aantal afnemende broedvogelsoorten. Van de zes gevangen mannetjes werden er vier succesvol van een zender voorzien en gevolgd. Vanaf 25 juni verlieten de mannetjes hun zangposten in de bergsteppe ten faveure van het boerenland in de lager gelegen vlakke. De meest voorkomende habitat was hier grasland, gevolgd door met herbiciden bespoten maïs, rogge, onbespoten maïs, rivieroevers, luzerne en haver. Als foerageergebied werd bespoten maïs het vaakst gebruikt, gevolgd door rogge en grasland, en vervolgens onbespoten maïs. De overige habitats werden niet door Ortolanen bezocht. Binnen de bezochte habitats hadden foeragerende vogels een voorkeur voor kale grond, wat de keuze voor met herbiciden bespoten maïs verklaart (hoewel de graslanden een groter aanbod van ongewervelde dieren hadden). Of dit voedselaanbod ook voldoende zou zijn geweest voor Ortolanen die jongen te voeden hebben, blijft ongewis bij gebrek aan nestelende paren. De oorspronkelijke habitat van deze kleine populatie Zwitserse Ortolanen, namelijk de submediterrane bergsteppe, is na een brand in 1979 geleidelijk gevolgen met vegetatie, waardoor de vogels bij gebrek aan foeragegelegenheid moesten uitwijken naar het lager gelegen cultuurland. De keuze voor bespoten maïs moet daarom worden gezien als de minst ongunstige optie binnen een sterk verarmd leefgebied. Waardoor de Zwitserse Ortolanen zijn afgenomen, is onbekend. Onderzoek naar Ortolanen in (sub)mediterrane habitats is dringend gewenst, omdat de soort het daar nog goed doet, in tegenstelling tot de bewoners van cultuurland in de rest van Europa. (RGB)

Corresponding editor: Rob G. Bijlsma

Received 26 September 2008; accepted 10 September 2009