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An inter-regional approach to intraspecific variation in habitat association: Rock Buntings *Emberiza cia* as a case study

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The habitat association approach has been increasingly used in ecology to resolve problems in wildlife conservation and management. One problem related to habitat association studies is that they are restricted to small geographical areas within a species' range, and thus they are applicable to only a limited set of environmental conditions utilized by the species. In addition, very few studies address why the preference for specific habitat components may be adaptive for the species in question. The objective of this study was to examine how consideration of populations of a species from two dramatically different environments affects the results of habitat association modelling for a ground-nesting passerine, the Rock Bunting *Emberiza cia*. At a regional scale, a trend to defending breeding habitat patches with relatively higher stone cover was confined to birds from a temperate region in Slovakia. In contrast, in a semi-arid region in southeastern Spain, Rock Buntings preferred to use breeding habitat patches that had relatively higher grass cover. Combining data from both regions, breeding Rock Buntings showed a general pattern of using habitat patches close to hedges, with low bush cover, high ditch density and a steep slope. Whereas regional habitat association models appear to be sensitive to the particularities of the breeding environment, our study suggests that Rock Bunting breeding habitat association is constrained by the adults' tactics to protect themselves against predators. Although the birds prefer to nest in patches of low vegetation, the better to see nearby predators, these patches are ideally close to taller vegetation that can be used to provide cover when evading predators, and they are also of a rugged profile that helps the birds to approach and leave the nest stealthily.

Keywords: generalized linear model, habitat management, habitat selection, predation, vegetation cover.

Habitat selection is a complex process involving responses to physical and biotic resources (Hildén 1965, Cody 1985, Mills *et al.* 1991), competition with conspecifics (Fretwell & Lucas 1970, Wiens 1989, Rosenzweig 1991) and predator pressure (Ricklefs 1969, Lima 1998). Due to its bearing on fitness, habitat selection theory is increasingly applied in an attempt to resolve problems in wildlife management (see Morris 2003).

One of the problems related to the applicability of habitat association studies in species management is that they are often confounded by the quality and quantity of resources, or by the density of con- and hetero-specific competitors occurring in a particular geographical area (Whittingham *et al.* 2007). For example, if an environment consists of only a few habitat types, an infrequent use of one habitat type may be wrongly perceived as selection for the other (Aebischer *et al.* 1993). Another important shortcoming of many habitat association studies occurs as a consequence of a focus on single populations, which can be insufficient to explain why the preference for some habitat types may be adaptive for the species as a whole (Jones 2001). One way to overcome these problems is to examine the habitat use of a species living in dramatically different environments (Morris 2003) or alternatively to examine habitat use of several populations spread over a wide geographical area (Whittingham *et al.* 2007).

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Knowledge of habitat preferences in open-habitat birds associated with farmland ecosystems is one of the key targets in European conservation strategies because farming and agro-grazing activities represent major land-use activities throughout Europe (e.g. Pain & Dixon 1997), and open-habitat-associated birds have experienced a rapid decline over the last few decades (Siriwardena *et al.* 1998, Pärt & Söderström 1999, Donald *et al.* 2001, Evans 2004). The management of vegetation is one of the conservation priorities for open-habitat birds (Whittingham *et al.* 2005, 2007). Therefore, the understanding of the species' habitat use in sites characterized by contrasting vegetation types might prove fruitful for broad-scale management plans.

We examined habitat use in an open-habitat, ground-nesting passerine associated with upland agro-systems, the Rock Bunting *Emberiza cia*. Our aim was to reveal the common attributes of habitat selection at the scale of the territory in populations from two contrasting environments within the species' range. We focused at the scale of a territory because territory choice reflects decisions on such critical parameters as nest safety and the proximity to food resources (Whittingham *et al.* 2007). Moreover, a recent study on a shrub-steppe songbird (Chalfoun & Martin 2007) has shown that territory choice includes habitat attributes that reflect preferences and fitness benefits at both the scale of the landscape and the nest-site selection. We conducted a 4-year study in a semi-arid region in southeast Spain and in a temperate region in southeast Slovakia. These two sites represent the southern and northern limits of the Rock Bunting's distribution and provide contrasting conditions in terms of climate, vegetation density and structure.

METHODS

Study sites and species

We studied habitat association in Rock Buntings in the Slovenský Karst National Park, Slovakia (48°57′N, 20°44′E, 450–580 m asl) and within the Sierra Alhamilla Natural Park, Spain (36°97′N, 02°40′W, 620–870 m asl). The Slovak study site was situated on south-facing rocky slopes and had a xerothermic flora dominated by tussock grasses *Festuca* spp. and broad-leaved scrub vegetation: *Quercus petraea*, *Carpinus betulus*, *Cornus mas*, *Acer campestre*, *Crataegus monogyna*, *Cerasus mahaleb* and *Rosa canina*. The study area consists of fragments of scrubland patches created inside the forest by cattle grazing. This site has a cool temperate climate with warm and wet summer months and a mean annual precipitation of 600 mm and a mean temperature of 9 °C (Slovak Hydrometeorological Institute). The vegetation within the Spanish study site was dominated by low bushes, *Stipa tenacissima* and *Anthyllis cytisoides*, with sparsely scattered scrubs: *Ephedra fragilis*, *Rhamnus oleoides*, *Prunus dulcis*, *Retama sphaerocarpa* and *Opuntia ficus-indica*. Aleppo pines *Pinus halepensis* were distributed at the border of the study site. This site represents degraded bushland as a consequence of deforestation, grazing and prickly-pear plantation. The climate of the Spanish site is semi-arid with wet winter months, a typical period of summer drought (June to September), and a mean annual precipitation of 285 mm and temperature of 18 °C (Junta de Andalucía, Spain).

The Rock Bunting breeds in the open habitat on steep rocky hillsides. It is a territorial bird during the breeding season, with adults feeding predominantly on grass seeds and their young on invertebrates. It usually raises two broods per season, usually consisting of four chicks (Cramp 1998, R. Václav unpubl. data). The breeding period of the nominate *E. c. cia* normally lasts from April to July (Cramp 1998), with the Slovak and Spanish study sites representing the northern and southern limits of the distribution. Although the European population of the species is relatively large compared with the population outside Europe, it underwent a large decline during 1970–90 (Birdlife International 2008). In Spain the population of Rock Buntings is widespread but of largely unknown status (Birdlife International 2008). In Slovakia the species' abundance is low, and the population is concentrated in only a few sites in southern Slovakia (Krištín 2002). Despite the distinct landscape features of the study areas (see Fig. 1, Table 2), the species occupies a similar ecological niche in both study areas: the mosaics of low and high vegetation on hillsides consisting of open habitat patches.

Bird surveys

The breeding territories of Rock Buntings in the Slovak study area (16 ha along a 1.4-km transect) were determined by the locations of singing males during 2003–05. Over these 3 years, we conducted censuses with up to 2-week intervals from mid-March until mid-August. In addition to the censuses, we confirmed the position of breeding territories by nest searches in May–June 2003 and 2004. The Spanish study site (15 ha along a 1.5-km transect) was visited on a weekly basis from the beginning of February 2005

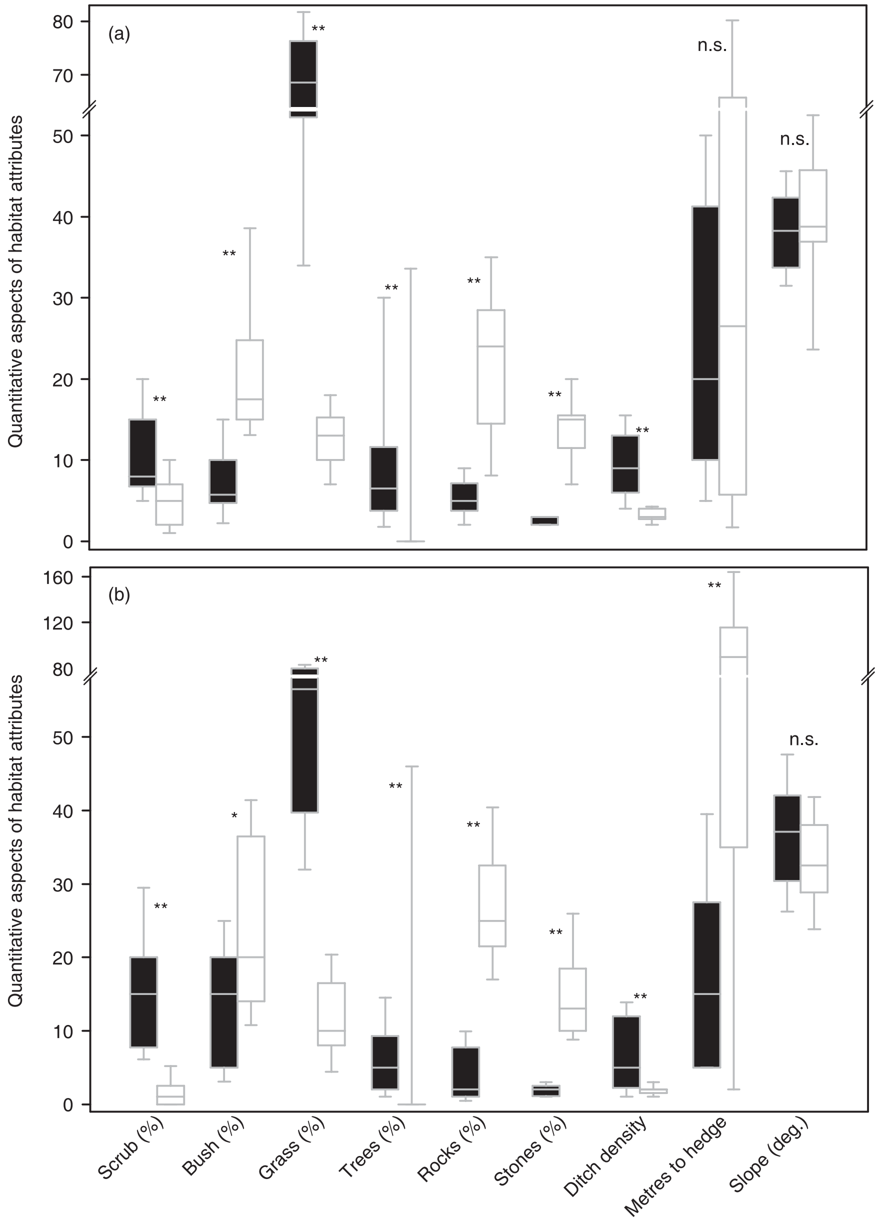

Figure 1. Differences in Rock Bunting habitat attributes between Slovak and Spanish (a) breeding and (b) unused habitat patches. Dark and light grey boxes refer to Slovak and Spanish habitat patches, respectively. The boxes are quartiles, error bars are 95% CI and the lines inside the boxes are medians. One or two asterisks denote *P* values for Mann–Whitney *U*-tests lower than 0.05 or 0.01, respectively.

until the end of July 2006. The surveyed area in each country represented suitable breeding habitat for Rock Buntings and was delineated based on the distribution of singing and calling individuals prior to regular censuses.

During the breeding season of 2004, when we examined the phenology of the singing behaviour of male Rock Buntings in the Slovak site, we detected the first singing male on 19 April and the last one on 24 June. At the Spanish field site, during the breeding seasons of 2005 and 2006 we detected the first singing male Rock Buntings on 12 April and 9 April, respectively, and the last singing males on 25 June and 1 July, respectively. We detected 22, 25 and 24 Rock Bunting territories per 16 ha in the Slovak site in 2003–05, respectively, and 20 and 19 territories per 15 ha in the Spanish site in 2005 and 2006, respectively.

Habitat determination and measurement

To avoid the fine- and coarse-scale problem in habitat assessment (see Garshelis 2000), we defined the Rock Bunting breeding habitat patch as an area with a 50-m radius, with a prominent scrub, tree or rock structure used as a post for a singing male representing the centre of the breeding habitat patch. A Rock Bunting breeding territory includes a nest-site, which is located close to a song post. In turn, feeding usually occurs 50–150 m from the nest (Cramp 1998). A 50-m radius around a song post was chosen to represent a breeding habitat patch because we found that the maximum distance from the song post to the nest of the singing male was up to about 50 m (range, 3–46 m, $n = 20$ nests; see also Györgypál 1981). If a male was detected to sing from different adjacent points (e.g. after a territorial dispute with another male), the mid-point between song posts was selected as the territory centre (e.g. Dale & Olsen 2002). In addition, we chose a 50-m radius because we found that two successive nests built by the same, colour-ringed pairs were constructed within 50 m (range: 28–54 m, $n = 8$ pairs; see also Groh 1988). It is unlikely that two Rock Bunting territory centres would be placed less than 30 m from each other (see Cramp 1998). Therefore, if we detected that a distance between two potential territory centres was shorter than 30 m, we considered such cases as single breeding territories, with the mid-point between the song posts representing the territory centre.

To avoid the problem of pseudoreplication, territories from different years were considered as reoccupied if their centres were within 30 m. In such cases, territory centres were determined by taking mid-points ($n = 18$ and $n = 13$ reoccupied territories in the Slovak and Spanish sites, respectively). In total, we detected 34 and 26 distinct territories in the Slovak and Spanish sites, respectively. All of these territories represent habitat patches that were defended by a singing male during at least three different bird surveys per year.

In contrast to breeding habitat, available but unused habitat (hereafter referred to as unused habitat) refers to the patches within the surveyed area that were immediately surrounded by breeding habitat patches and were comparable to them, but where either no activity was observed or where activities such as feeding, calling and only sporadic singing (two or fewer surveys) took place. The area of each unused habitat patch was equivalent to that of the breeding habitat patch (i.e. 50-m radius). In total, we determined 20 and 13 unused habitat patches for the Slovak and Spanish sites, respectively, together with breeding habitat patches covering all suitable habitat in each study area. There was no difference between countries in the proportion of unused to all 'available' habitat patches (20 of 54 and 13 of 39 habitat patches for Slovakia and Spain, respectively; Fisher exact test, $P = 0.84$). For the Spanish site, no activity ($n = 6$), calling ($n = 4$) and sporadic singing ($n = 3$) were recorded in 13 unused habitat patches. For the Slovak site, no activity ($n = 12$), calling ($n = 4$) and sporadic singing ($n = 4$) were recorded in 20 unused habitat patches.

To construct a map with the spatial distribution of all habitat patches (i.e. breeding and unused habitat patches), we first plotted distinct breeding territories (see above) on the map using OziExplorer 3.95.4 GPS mapping software. Based on the spatial distribution of the distinct breeding habitat patches, we determined the location of unused habitat patches. For each patch and study site we used a standardized method to measure habitat attributes. Based on digital photographs (calibrated in OziExplorer) for each patch we estimated the number of ditches and percentage cover for six habitat attributes: scrubs, bushes, trees, grass, rocks and stones. In addition, for each plot we determined in the field the nearest distance to dense woody vegetation (hereafter referred to as hedge) and the mean slope. We selected these variables because they have been suggested in other studies to be important for Rock Buntings (see Table 1).

Data analysis

Generalized linear models and logistic regression were used to calculate statistics for the models including different sets of predictors of Rock Bunting habitat use. Schwarz's Bayesian Information Criterion (BIC) was used to select the models providing the maximum fit for the fewest predictors. The information criteria such as BIC or Akaike Information Criterion (AIC) are superior to stepwise modelling, and we preferred the BIC because it has a harsher penalty than the AIC method for models with a greater number of predictors (Quinn & Keough 2007). We used the Hosmer-Lemeshow $\hat{C}$ statistic to estimate the fit of models. This test is appropriate when models include continuous predictors, with greater P values (i.e. smaller $\hat{C}$ values) indicating better fit, and P values < 0.05 indicating

Table 1. List of habitat attributes recorded as putative explanatory variables for breeding habitat association in Rock Buntings in Spain and Slovakia.

Habitat attribute	Description	Reason for inclusion (source)
No. of ditches/patch	No. of surface depressions deeper than 0.5 m and longer than 15 m/patch	Breeds in rugged terrain, rock gullies, ravines, in-between bigger rocks (Groh 1982, Mann *et al.* 1990, Cramp 1998).
Nearest distance to the hedge	Nearest distance (m) to a cluster of woody plants	Occupies open areas containing scrubs, hedge or younger conifers (e.g. Groh 1982, Mann *et al.* 1990, Cramp 1998).
Slope	Mean slope (°) measured with a clinometer in four directions, 90° apart	Occupies steep slopes of hillsides (e.g. Groh 1982, Mann *et al.* 1990, Cramp 1998).
Grass cover	Percentage cover of herbaceous plants	Feeds on grass seeds and invertebrates on ground (e.g. Györgypál 1981, Groh 1982, Cramp 1998).
Bush cover	Percentage cover of low woody plants with multiple stems	Occupies open areas with variable bush cover (e.g. Groh 1982, Cramp 1998).
Scrub cover	Percentage cover of low woody plants with one main stem	Occupies *Quercus* scrub-grassland (Cramp 1998) and other open areas with variable cover of scrub plants such as *Prunus dulcis* or *Prunus mahaleb* (this study).
Tree cover	Percentage cover of tall woody plants with one main stem	Occupies areas above tree line (Cramp 1998), clearings in forests or clearcuts (Groh 1982).
Stone cover	Percentage cover of smaller and fragmented rocky formations	Occupies stony areas and usually nests near bigger stones (e.g. Mann *et al.* 1990, Cramp 1998).
Rock cover	Percentage cover of large and compact rocky formations	Occupies rocky terrain, steep cliffs or quarries (Cramp 1998).

lack of fit. Moreover, McFadden's Rho-squared (r_L^2) was used as an analogue of r^2, with values between 0.2 and 0.4 considered very satisfactory (Hensher & Johnson 1981). A likelihood-ratio score was used to compare the fit (i.e. deviance) of pairs of competing models: likelihood-ratio χ^2 (G statistic) $= -2 *$ (log-likelihood reduced model – log-likelihood saturated model), testing the *G*-statistic significance against the χ^2 distribution (Quinn & Keough 2007). Classification success of a model was based on predicted probabilities for each case and a 0.5 cut-off point. All statistics were obtained with Systat 12 (Systat Software Inc. 2007) and Statistica 7 (StatSoft Inc. 2004). BIC weights, parameter selection probabilities and weighted averages of parameter estimates were calculated by considering models within 2 BIC units (Burnham & Anderson 2002).

Tree cover showed a binomial distribution for the Spanish site but was continuous for the Slovak site. However, tree cover was revealed as an insignificant predictor of habitat use for both study sites. Therefore, we discarded this variable from the analysis of pooled data. It is unlikely that the exclusion of this variable would change our results because Rock Buntings avoid tree habitat (see Cramp 1998). Scrub cover for the Spanish site and stone and tree cover for the Slovak site were rank-transformed (Conover & Iman 1981).

RESULTS

Rock Bunting habitat in two contrasting environments

The Spanish and Slovak study sites differed markedly with respect to vegetation and physical attributes of available Rock Bunting habitat. The habitat in Slovakia was dominated by grass and scrubs and represented a grassland-scrubland ecotone (Fig. 1a & 1b). In Spain the study site represented a bushland habitat (Fig. 1a & 1b), and here unused habitat patches were considerably further from the hedge than those in Slovakia (Fig. 1b); nearest distance to the hedge for breeding habitat patches was roughly the same at both sites (Fig. 1a). With respect to the physical environment, both study sites were similarly steep, but the Spanish site generally had higher stone cover and was rockier than the Slovak site (Fig. 1a & 1b). The Rock Bunting habitat in Slovakia had more ditches per unit area than that in the Spanish site (Fig. 1a). Importantly, the two sites differed not only quantitatively in habitat attributes, but also in terms of within-site relationships (e.g. whereas in Slovakia bush cover was negatively related to distance to hedge, the relationship was reversed for Spain; Table 2).

Table 2. Correlations (Spearman's rank) among vegetation and physical habitat attributes within two populations of the Rock Bunting ($n = 54$ and $n = 39$ habitat patches for Slovakia and Spain, respectively). Correlations in the upper right and lower left corners of the table are for the Slovak and Spanish sites, respectively. Attributes: 1 = ditch density, 2 = mean slope, 3 = scrub cover, 4 = bush cover, 5 = rock cover, 6 = stone cover, 7 = tree cover, 8 = nearest hedge distance, 9 = grass cover. Values in boldface are significant at the 0.01 level.

	Habitat attributes								
Attribute	1	2	3	4	5	6	7	8	9
1		**0.61**	0.25	**0.40**	**0.72**	0.35	0.11	–**0.41**	–**0.40**
2	0.29		0.24	0.34	**0.62**	**0.47**	0.29	–0.33	–**0.47**
3	**0.67**	0.29		**0.77**	0.34	–0.04	–0.03	–**0.64**	–**0.68**
4	0.29	0.29	0.14		**0.41**	0.06	0.05	–**0.69**	–**0.70**
5	–0.21	0.10	0.12	0.03		**0.54**	0.20	–**0.39**	–**0.61**
6	–0.33	–0.19	–0.24	–0.41	0.04		0.28	–0.02	–**0.39**
7	–0.31	–0.14	–**0.47**	–**0.58**	–**0.46**	0.03		–0.30	–**0.50**
8	–0.13	0.02	–0.12	**0.66**	0.32	–0.04	–**0.56**		**0.67**
9	0.03	0.14	0.10	0.37	0.12	0.14	–**0.45**	0.35	

Regional pattern of habitat attributes

Three variables best fit the data of breeding habitat use for the Slovak population of Rock Buntings, with bush and stone cover consistently being included in the best models (Table 3). Ditch density as a predictor is also important because, apart from the inference based on BIC, a direct model comparison suggests that a model including ditch density provides a significantly better fit than the reduced model with only bush and stone cover (likelihood-ratio $\chi^2 = 4.76$, df = 1, $P = 0.029$; see also Table 3 for r_L^2 and $\hat{C}$ indices).

For the Spanish population of Rock Buntings, the best models consistently include three predictors: ditch density, grass cover and distance to the hedge (Table 3). Yet, slope steepness also plays a significant role because the inclusion of this predictor makes the model a better fit than the reduced model with only ditch density, grass cover and distance to the hedge (likelihood-ratio $\chi^2 = 5.68$, df = 1, $P = 0.017$). In contrast, the further inclusion of rock or bush cover in the model does not significantly improve the fit of the model (rock cover, likelihood-ratio $\chi^2 = 0.82$, df = 1, $P = 0.37$; bush cover, likelihood-ratio $\chi^2 = 0.36$, df = 1, $P = 0.55$; see Table 3).

Inter-regional pattern of habitat attributes

Logistic regression modelling based on the pooled data for Spain and Slovakia and BIC suggests that, after including region as a dummy variable, the best predictors of breeding habitat use are bush cover and slope steepness (Table 3). However, the additional inclusion of ditch density as a predictor significantly improves the fit of the model (likelihood-ratio $\chi^2 = 4.5$, df = 1, $P = 0.034$). In addition, $\hat{C}$ and r_L^2 statistics also suggest that the model with ditch density fits the data better than the reduced model (see Table 3). Therefore, different complementary model selection criteria suggest that breeding habitat use for Slovak and Spanish Rock Bunting populations is best predicted by slope steepness, bush cover and ditch density (Fig. 2).

Whereas the frequency of correctly classified unused patches is lower using the inter-regional approach than with the intra-regional one (Fisher exact test, Spain vs. pooled data: $P = 0.035$; Slovakia vs. pooled data: $P = 0.25$), the frequency of correctly classified breeding patches is similar for the two approaches (Spain vs. pooled data: $P = 0.72$; Slovakia vs. pooled data: $P = 1.00$).

DISCUSSION

The success of species management schemes depends on how well the schemes can be applied in different geographical locations (Morris *et al.* 2001, Whittingham *et al.* 2007). Our study suggests that the comparison of populations from drastically different environments allows us to identify key ecological variables for a species' breeding habitat management and unravel underlying mechanisms behind habitat selection processes. Both used and unused breeding habitats of Rock Buntings differed considerably in terms of vegetation and physical habitat attributes in two

Table 3. Results of Rock Bunting breeding habitat use based on the data from two distinct populations (*n* = 20/54 and *n* = 13/39 breeding/all habitat patches for Slovakia and Spain, respectively). LL, Log-likelihood; r^2_L, MacFadden's Rho-squared; BIC, Schwarz's Bayesian Information Criterion; AIC, Akaike Information Criterion; w_i, BIC weight; $\hat{C}$, Hosmer-Lemeshow statistic; CSR, classification success rate for all (breeding/unused) habitat patches. Selection probabilities for each parameter refer to the sum of BIC weights for all models in which the predictor was included. Parameter estimates (β) for each predictor were obtained by summing parameter estimates weighted by model selection probabilities for all models including the predictor. Scrub and tree cover did not enter into the model (although they were predictor variables) and as a consequence are omitted from the Table. The models shown represent all models within 2 BIC units of the best model. The effects of variables were tested with a likelihood-ratio type-III test; ✓ = positive effect, ✗ = negative effect, ~ = variable in the model but without significant effect. The models with the best fit as determined by multiple indices are shown in boldface.

	Habitat attributes														
Model	Region	Slope	Ditches	% Bush	% Grass	% Stone	% Rock	D-Hedge	LL	r^2_L	BIC	AIC	w_i	$\hat{C}$	CSR
Slovakia (SK)															
1			✓*	✗**		✓**			**–17.68**	**0.50**	**51.32**	**43.37**	**0.31**	**5.45**	**0.83 (0.88/0.75)**
2				✗**		✓**			–20.06	0.44	52.08	46.12	0.21	10.70	0.87 (0.91/0.80)
3		~	✓**	✗**		✓**			–16.07	0.55	52.09	42.15	0.21	5.54	0.89 (0.91/0.85)
4				✗**	~	✓**			–18.40	0.48	52.76	44.80	0.15	2.79	0.87 (0.94/0.75)
5		~	✓*	✗**	~	✓**			–35.59	0.59	53.32	41.39	0.11	3.20	0.89 (0.94/0.80)
Selection probability		0.32	0.63	1.00	0.26	1.00									
β		–0.08	0.21	–0.39	–0.03	0.12									
Spain (E)															
1		✓*	✓**		✓**			✗**	**–5.60**	**0.78**	**29.51**	**21.19**	**0.73**	**2.82**	**0.92 (0.92/0.92)**
2			✓**		✓*			✗**	–8.43	0.66	31.52	24.86	0.27	3.68	0.92 (0.96/0.95)
Selection probability		0.73	1.00		1.00			1.00							
β		0.18	3.44		0.74			–0.12							
SK + E															
1	**	✓**		✗**					–50.12	0.17	118.37	108.24	0.27	9.26	0.74 (0.87/0.52)
2	**	✓*	✓*	✗**					**–47.87**	**0.21**	**118.4**	**105.73**	**0.26**	**7.97**	**0.77 (0.88/0.58)**
3	**	✓**	✓*	✗**			✗*		–45.77	0.24	118.74	103.54	0.22	19.28*	0.82 (0.90/0.67)
4	**		✓**	✗**					–50.79	0.16	119.71	109.58	0.14	9.86	0.77 (0.90/0.55)
5	**	✓**		✗**			~		–60.49	0.20	120.04	107.37	0.12	7.72	0.75 (0.85/0.58)
Selection probability	1.00	0.86	0.61	1.00			0.34								
β		0.10	0.12	–0.13			–0.03								

**P* < 0.05; ***P* < 0.01.

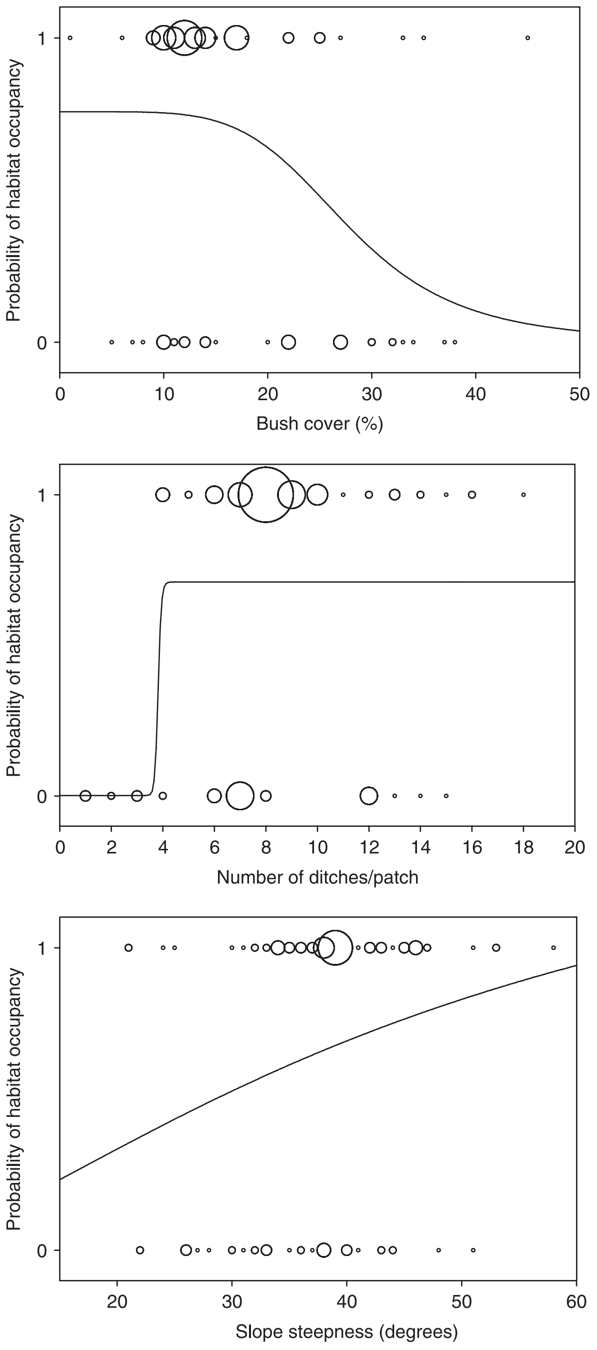

Figure 2. Probability that habitat patches for both Slovak and Spanish sites will be occupied by Rock Buntings as a function of bush cover, ditch density and slope steepness. The size of circles refers to the number of cases. The data are fitted using logistic regression. For illustration purposes, habitat attribute data are not corrected for site differences.

geographically distant populations. Inter-regional differences existed also in the patterns of breeding habitat use. Specifically, whereas a trend to use habitat patches with relatively higher stone cover was confined to Rock Buntings in Slovakia, the characteristic feature of the species in Spain was the use of patches with relatively higher grass cover. In contrast, despite regional differences in distance to the hedge in unused breeding habitat, birds from both sites were conservative in terms of the distance of the breeding habitat patch to the hedge. After controlling for regional effects, Rock Bunting had a general trend towards selecting breeding habitat patches with relatively lower bush cover, steeper slope and higher ditch density.

The risk of predation is considered to be one of the main causes driving habitat selection in ground-nesting birds (see Martin 1993) and increased predation has been suggested to be a cause of the decline of birds inhabiting human altered habitats such as farmland (see Whittingham & Evans 2004). The nest position relative to substrate and the height of surrounding vegetation can affect a bird's view from the nest (Götmark *et al.* 1995). Importantly, because birds need to both increase visual nest concealment and also be able to quickly detect predators (Burhans & Thompson 1998), vegetation height around ground nests might significantly affect the fate of the adult as well as the nest (Götmark *et al.* 1995). Unlike congeneric Yellowhammers *Emberiza citrinella*, which build their nest on the ground or low in scrubs (Bradbury *et al.* 2000), Rock Buntings nearly always place their nest on the ground (Cramp 1998). Thus, the nesting habits of Rock Buntings might impose important constraints on breeding habitat selection with respect to habitat openness. Accordingly, in contrast to Yellowhammers, which can nest in areas with both sparser and denser vegetation (Dale & Manceau 2003), we found that Rock Buntings avoid breeding in dense tall cover. A trend by the Spanish population of Rock Buntings to associate with higher grass cover is consistent with greater visual obstruction in bushland habitat in Spain compared to grassland habitat in Slovakia.

Availability of foraging habitats may also affect breeding habitat selection in birds (e.g. Blomqvist & Johansson 1995). However, Rock Bunting parents collect food for their nestlings well outside of the breeding habitat patch (Cramp 1998, R. Václav pers. obs.). Therefore, it appears that Rock Bunting breeding habitat selection at the scale of a territory is related to nest-site rather than foraging suitability (e.g. Steele 1993). This is similar to the findings of

Chalfoun and Martin (2007), who found that habitat selection in Brewer's Sparrow *Spizella breweri* is related to nest safety at the scale of the territory and food availability at the landscape scale.

The presence of ditches has been shown to be an important attribute of breeding habitat association of Yellowhammers (Bradbury *et al.* 2000, Morris *et al.* 2001, Whittingham *et al.* 2005). However, even though Bradbury *et al.* (2000) reported that Yellowhammers nesting in ditches face higher predation rates than those nesting in scrubs, neither Bradbury *et al.* (2000) nor Whittingham *et al.* (2005) suggested why birds prefer to breed in habitat with higher ditch density. Boundary habitat features such as ditches provide higher diversity and abundance of invertebrates (e.g. lepidopterans, Feber *et al.* 1996). Therefore, birds could favour breeding patches which include ditches as a consequence of having access to better food resources. Though Yellowhammers, a species consistently preferring boundary features in its breeding habitat patches, select foraging sites non-randomly within 400 m of the nest, their nests are not located close to preferred foraging sites (Morris *et al.* 2001). The main risk of nest predation for ground-nesting birds is from snake and mammalian predators (see Söderström *et al.* 1998). Yet, it is unlikely that Rock Buntings would seek to nest in rugged terrain as protection against snakes or rodent predators, which use olfactory cues, because in this case the fate of the nest is unrelated to bird or nest concealment tactics (Weidinger 2002). Also, the use of ditches is unlikely to prevent predation by avian predators, which use the activity of adults in locating nests (Whittingham & Evans 2004). Instead, more complex terrain creates corridors that could provide better concealment of the bird's foraging and parental activity around the nest from mammalian predators such as weasels, stouts or foxes, which use the combination of visual and olfactory cues to catch prey. This is plausible for ground-nesting birds such as Rock Buntings because these mammalian species are important nest predators (Cramp 1998, see also Suarez *et al.* 1993).

Many ground-nesting birds breed on flat ground as well as on the slopes of hillsides (e.g. Evans *et al.* 2005). Nesting in a flat, open landscape has been suggested to facilitate predator detection through improving the field of view from the nest (Götmark *et al.* 1995, Whittingham *et al.* 2002). In addition, nesting on steep slopes may improve adult survival through higher initial acceleration when escaping predators (Huey & Hertz 1984). We propose that nesting on steeper slopes could be a strategy to improve the prospects of the nest, and also to enhance adult survival of birds nesting on the ground in less open habitats. Our results suggest that predation risk is more important in Spain where slope steepness was highlighted in our regional model, although breeding on steep slopes is common to both populations because stone cover, a breeding habitat attribute typical for the Slovak population, was significantly positively related to slope steepness.

Implications for habitat management

Changing habitat quality due to alterations of vegetation density and structure may negatively affect habitat occupancy by open-habitat birds associated with agro-systems (Pons *et al.* 2003). Our inter-regional study suggests that Rock Buntings, a species associated with upland agro-systems, are particularly sensitive to bush cover and the spatial extent and configuration of low (i.e. grass) and tall (i.e. bush and scrub) vegetation. Hence, the abandonment of traditional farming practices, which occurred at both study sites in the last few decades, and resulting vegetation succession are likely to have negative consequences for this and other open-habitat birds that require mosaics of herbaceous vegetation and clusters of woody plants at various stages of succession. Different habitat management plans appear to be optimal to prevent habitat degradation and the species' decline in the two countries. In Spain, management plans proposed to restore the *Stipa tenacissima* pseudosteppe to scrubland with native Mediterranean scrubs such as Mastic Tree *Pistacia lentiscus* or Kermes Oak *Quercus coccifera* (e.g. Maestre & Cortina 2004) appear to be compatible with the management of open-habitat birds such as Rock Buntings. Controlled grazing could aid to prevent expansion of woody plants into the grassland-scrubland ecotone in Slovakia.

Our study further suggests that the lack of suitable breeding habitat can raise a potential problem for the generalization of local habitat association studies. Whereas suitable Rock Bunting breeding habitat in the Spanish site was available over an extensive area, suitable habitat in the Slovak site was restricted to the fragments of scrubland patches created through cattle grazing inside forested habitat. In line with this, Rock Bunting breeding density was about 20% higher in Slovakia, where distribution of territories within the breeding area was patchier compared with the rather homogeneously distributed territories in the Spanish site. Classification success results also indicate that many pairs bred in suboptimal habitat in Slovakia because for this population it was more difficult than for the Spanish population to discern unused patches. Therefore, caution should be exercised when inferring management plans from populations where a large proportion of birds are forced to breed in suboptimal habitat. This suggestion is not trivial because many studies focused on species management are based on data collected from human-altered environments and declining populations (Morris *et al.* 2001).

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REFERENCES

Aebischer, N.J., Marcström, V., Kenward, R.E. & Karlbom, M. 1993. Survival and habitat utilisation: A case for compositional analysis. In Lebreton, J.D. & North, P.M. (eds) *Marked Individuals in the Study of Bird Populations*: 343–353. Basel: Birkhauser Verlag.

BirdLife International 2008. Species factsheet: *Emberiza cia*. <www.birdlife.org> [accessed on 11 September 2008].

Blomqvist, D. & Johansson, O.C. 1995. Trade-offs in nest-site selection in coastal populations of Lapwings *Vanellus vanellus*. *Ibis* **137**: 550–558.

Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J. & Wilson, J.D. 2000. Habitat associations and breeding success of Yellowhammers on lowland farmland. *J. Appl. Ecol.* **37**: 789–805.

Burhans, D.E. & Thompson, F.R. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. *Condor* **100**: 663–672.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Chalfoun, A.D. & Martin, T.E. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *J. Appl. Ecol.* **44**: 983–992.

Cody, M.L. 1985. *Habitat Selection in Birds*. New York: Academic Press.

Conover, W.J. & Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* **35**: 124–129.

Cramp, S. 1998. *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford: Oxford University Press.

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. & Olsen, B.F.G. 2002. Use of farmland by Ortolan Buntings (*Emberiza hortulana*) nesting on a burned forest area. *J. Ornithol.* **143**: 133–144.

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.

Evans, K.L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146**: 1–13.

Evans, D.M., Redpath, S.M., Evans, S.A., Elston, D.A. & Dennis, P. 2005. Livestock grazing affects the egg size of an insectivorous passerine. *Biol. Lett.* **1**: 322–325.

Feber, R.E., Smith, H. & MacDonald, D.W. 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields *J. Appl. Ecol.* **33**: 1191–1205.

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical developments. *Acta Biotheor.* **19**: 16–36.

Garshelis, D.L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In Boitani, L. & Fuller, T.K. (eds) *Research Techniques in Animal Ecology: Controversies and Consequences*: 111–164. New York: Columbia University Press.

Götmark, F., Blomqvist, D., Johansson, O.C. & Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *J. Avian Biol.* **26**: 305–312.

Groh, G. 1982. Zur Ökologie, Biometrie und zum jahreszeitlichen Vorkommen der Zippammer (*Emberiza c. cia*) in der Pfalz. *Mitt. Pollichia* **70**: 217–234.

Groh, G. 1988. Zur Biologie der Zippammer (*Emberiza c. cia*) im Pfälzerwald. *Mitt. Pollichia* **75**: 261–287.

Györgypál, Z. 1981. Contributions to the ethology of the Rock Bunting (*Emberiza cia*). *Aquila* **87**: 71–78.

Hensher, D.A. & Johnson, L.W. 1981. *Applied Discrete Choice Modeling*. London: Croom Helm.

Hildén, O. 1965. Habitat selection in birds. A review. *Ann. Zool. Fenn.* **2**: 53–75.

Huey, R.B. & Hertz, P.E. 1984. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* **110**: 113–123.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* **118**: 557–562.

Krištín, A. 2002. Strnádka cia/Strnádka ciavá (*Emberiza cia*). In Danko, Š., Darolová, A. & Krištín, A. (eds) *Rozšírenie Vtákov na Slovensku*: 632–633. Bratislava: Veda.

Lima, S.L. 1998. Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* **48**: 25–34.

Maestre, F.T. & Cortina, J. 2004. Insights into ecosystem composition and function in a sequence of degraded semiarid steppes. *Restor. Ecol.* **12**: 494–502.

Mann, P., Herlyn, H. & Untheim, H. 1990. Bestandigung und Habitat der Zippammer *Emberiza cia* im Südschwarzwald. *Vogelwelt* **111**: 142–155.

Martin, T.E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* **141**: 897–913.

Mills, G.S., Dunning, J.B. & Bates, J.M. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bull.* **103**: 468–479.

Morris, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Kyrkos, A., Buckingham, D.L. & Evans, A.D. 2001. Foraging habitat selection by Yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. *Biol. Conserv.* **101**: 197–210.

Morris, D.W. 2003. How can we apply theories of habitat selection to wildlife conservation and management? *Wildl. Res.* **30**: 303–319.

Pain, D. & Dixon, J. 1997. Why farming and birds in Europe? In Pain, D. & Pienkowski, M.W. (eds): *Farming and Birds in Europe*: 1–24. London: Academic Press.

Pärt, T. & Söderström, B. 1999. The effects of management regimes and location in landscape on the conservation of farmland birds breeding in semi-natural pastures. *Biol. Conserv.* **90**: 113–123.

Pons, P., Lambert, B., Rigolot, E. & Prodon, R. 2003. The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. *Biodiv. Conserv.* **12**: 1843–1860.

Quinn, G.P. & Keough, M.J. 2007. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* **9**: 1–48.

Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. *Am. Nat.* **137**: S5–S28.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *J. Appl. Ecol.* **35**: 24–43.

Söderström, B., Pärt, T. & Rydén, J. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia* **117**: 108–118.

Statsoft Inc. 2004. *Statistica 7.0*. Tulsa: Statsoft.

Steele, B.B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers – their relative influence on habitat choice. *Condor* **95**: 568–579.

Suarez, F., Yanes, M., Herranz, J. & Manrique, J. 1993. Nature-reserves and the conservation of Iberian shrubsteppe passerines – the paradox of nest predation. *Biol. Conserv.* **64**: 77–81.

Systat Software Inc. 2007. *Systat 12.0.* San Jose: Systat.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *J. Anim. Ecol.* **71**: 424–437.

Whittingham, M.J. & Evans, K.L. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146**: 210–220.

Whittingham, M.J., Percival, S.M. & Brown, A.F. 2002. Nest site selection by Golden Plover: why do shorebirds avoid nesting on slopes? *J. Avian Biol.* **33**: 184–190.

Whittingham, M.J., Swetnam, R.D., Wilson, J.D., Chamberlain, D.E. & Freckleton, R.P. 2005. Habitat selection by Yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management. *J. Appl. Ecol.* **42**: 270–280.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D. & Freckleton, R.P. 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol. Lett.* **10**: 25–35.

Wiens, J.A. 1989. *The Ecology of Bird Communities. Processes and Variation*. Cambridge: Cambridge University Press.

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