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AVIAN-HABITAT RELATIONSHIPS IN A MEDITERRANEAN HIGH MOUNTAIN

Regino ZAMORA*

The study of avian-habitat relationships was traditionally centered on an analysis of the degree of association of birds with certain vegetation features (review in Cody, 1985a). Studies conducted in forest habitats demonstrated strong correlations between bird species diversity and abundance and vertical complexity of the vegetation (e.g. MacArthur and MacArthur, 1961 ; MacArthur *et al.*, 1966 ; Recher, 1969 ; Karr and Roth, 1971 ; Blondel *et al.*, 1973 ; Willson, 1974 ; but see James and Wamer, 1982 ; Erdelen, 1984). Other studies have pointed out the importance of other habitat characteristics such as horizontal heterogeneity (Wiens, 1974 ; Roth, 1976 ; Wiens and Rotenberry, 1981) and floristic composition of the vegetation, especially in structurally simple habitats (Tomoff, 1974 ; Wiens and Rotenberry, 1981 ; Rice *et al.*, 1983, 1984 ; Robinson and Holmes, 1984 ; Ralph, 1985 ; Rotenberry, 1985 ; Sherry and Holmes, 1985). In some terrestrial environments, such as high-mountain habitats, rocks and stones may cover as much area as vegetation, and they may be just as important to birds as shrubs and grass, because they serve as song posts or provide shelters from predators and even nest-sites, therefore acting as proximal and ultimate factors in territorial establishment (Hilden, 1965).

This paper analyzes the habitats of eight species of passeriformes breeding in the pasture-scrubland of the high mountain in the Sierra Nevada, Southeastern Spain : Wheatear (*Oenanthe oenanthe*), Skylark (*Alauda arvensis*), Tawny pipit (*Anthus campestris*), Black redstart (*Phoenicurus ochruros*), Rock bunting (*Emberiza cia*), Ortolan bunting (*Emberiza hortulana*), Wren (*Troglodytes troglodytes*), and Whitethroat (*Sylvia communis*). The aim of this paper is to answer, within the scope of the environment studied, the following questions :

- 1) What is the typical habitat of each species ?
- 2) What are the species-specific distributions along habitat gradients ?
- 3) Which variables are more important in habitat segregation by the species ?

The analysis of such questions in the high-mountain habitats of the Sierra Nevada is especially interesting for two reasons. First, the ecology of high-mountain birds is little known (Cody, 1985c). In this respect, the present study appears to be the first detailed quantification of habitat preferences by birds in high mediterranean mountains. Second, this habitat shows features such as the

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lack of a tree layer, the presence of rocks and stony-ground, and a patchy distribution of the various habitat components (e.g. shrubs, rocks, bare ground). These characteristics provide a good opportunity to test the validity of the generalizations made on avian-habitat relationships.

MATERIAL AND METHODS

STUDY AREA

The study area is located in the pasture-scrubland habitat that extends from about 2 000 m to 2 700 m in the high-mountains of the Sierra Nevada (southeastern Spain). The bushy vegetation consists mainly of *Juniperus communis*, *Genista baetica*, *Cytisus purgans*, *Berberis vulgaris*, *Juniperus sabina* and *Ptilotrichum spinosum*. The height of the shrub layer seldom exceeds 1 m. The shrubs are interspersed with rocks and grasses. The habitat remains covered by snow for 5-7 months each year, usually between November and April. A more detailed description of the habitat can be found in a previous publication (Zamora, 1988).

DATA COLLECTION

Observations were carried out during the breeding season, May to June, in 1984 and 1985, in wide sectors of the northern, southern and western slopes of the Sierra Nevada. The sampling design includes almost all the pasture-scrubland habitats of this high-mountain.

Habitat composition and structure were determined by measuring 15 variables (Table I) in 0.1 ha circular plots centered on the song posts, nest-sites and foraging sites of the breeding pairs (James, 1971 ; Collins *et al.*, 1982). Habitat sampling was carried out in the following manner : four lines, each 18 metres long, were drawn outwards from the song post, nest-site or foraging-site, the first direction being chosen at random and the other three following successively at ninety degree angles. The sample points were taken at 3 m intervals along each line (6 per line), giving a total of 24 sample points. This sample size provided an adequate level of sampling per territory, bearing in mind the simplified structure of these high-altitude habitats. The data were obtained by sticking a round metal rod, 1 cm in diameter and 1.5 m high, vertically into the ground at each sample point and recording the type of substrate that touched the bottom of the rod, and at 5 cm intervals upwards (as described by Wiens and Rotenberry, 1981). The variables measured are listed in table I.

A total of 51 skylarks, 21 tawny pipits, 22 wrens, 22 whitethroats, 78 wheatears, 27 black redstarts, 38 rock buntings and 16 ortolan buntings circular plots were surveyed, each corresponding to a separate territory. The size of these samples allows an analysis of intraspecific variability in habitat selection to be made.

DATA ANALYSIS

The position of species along habitat gradients is commonly analyzed by using one or two multivariate techniques : stepwise discriminant function analysis

TABLE I

Description of the measured and derived variables used in habitat selection analysis.

	VARIABLE	CODE
Coverage		
1)	Percent cover vertical herbaceous layer	GRAS1
2)	Percent cover herbaceous rosettes	GRAS2
3)	Percent cover <i>Genista baetica</i>	GENI
4)	Percent cover <i>Juniperus communis</i>	JUNI
5)	Percent cover <i>Cytisus purgans</i>	CYTI
6)	Percent cover <i>Berberis vulgaris</i>	BERB
7)	Percent cover <i>Ptilotrichum spinosum</i>	PTIL
8)	Total shrub cover	SHCO
9)	Percent cover bare ground	BARE
10)	Percent cover stone (rocks smaller than 30 cm in diameter)	STON
11)	Percent cover rock (rocks larger than 30 cm in diameter)	ROCK
Structural		
12)	Average number of vegetation hits along the rod per sample	HITX
13)	Average maximum interval of the rod recording contacts	MAXH
14)	Diversity index of the vertical profile of the shrub layer	DIVI
15)	Horizontal heterogeneity index of the vegetation	HETI

This heterogeneity index was calculated from the equation :

$$HI = \frac{\Sigma(\text{Max}-\text{Min})}{N} \frac{\Sigma x}{N'}$$
 where Max = maximum number of contacts recorded among the 24 points in a circle, Min = minimum number of hits recorded, N = total number of sample point (24), and x = mean number of contacts within a circle (see Wiens 1974).

(James, 1971 ; Whitmore, 1975 ; Cody, 1978 ; Leisler, 1981 ; James *et al.*, 1984 ; Sedgwick, 1987) or factor analysis (James, 1971 ; Anderson and Shugart, 1974 ; Whitmore, 1977 ; Collins *et al.*, 1982 ; Shy, 1984). These two techniques differ in principle, respectively emphasising classification and ordination. In this paper I first used factor analysis which represents a multivariate approximation to the gradient concept (Whittaker, 1975 ; James and Macculloch, 1985).

Measurements of habitat breadth and overlap in the multivariate space have often been carried out by calculating confidence ellipses (e.g. Cody, 1978 ; Dueser and Shugart, 1979 ; Noon, 1981 ; Sedgwick, 1987). Nevertheless, the use of ellipses entails some difficulties such as, for example, the dependence of the surface size of the ellipse on the sample size (Sokal and Rolf, 1979 ; Van Horne and Ford, 1982 ; James *et al.*, 1984). For these reasons I used a procedure similar to that employed by Rotenberry and Wiens (1980), where each factor is divided into 12 equally spaced intervals, without reference to the number of samples that fall into each interval. A species' niche breadth is calculated by the diversity of distribution along a multivariate axis by means of Levins' index (1968) :

$$B_j = 1 / \sum_{i=1}^m p_{ji}^2$$

where P_{ji} is the proportion of habitats occupied by species j within the interval i . Habitat overlap between two species (Schoener's index, 1968) is calculated by the similarity of their distribution along a multivariate axis :

$$O_{jk} = 1 - 0.5 \sum_{i=1}^m |P_{ji} - P_{ki}|$$

where P_{ji} and P_{ki} represent the proportion of territories corresponding to species j and k .

To determine which variables are important in species separation, all 275 cases (territories) in their corresponding groups (species) were subjected to stepwise discriminant analysis. The classification matrix generated by this analysis was then evaluated according to the Kappa statistics (Titus *et al.*, 1984).

The variables were transformed prior to statistical analysis : the arcsine transformation ($X = \arcsin (\sqrt{X/100})$) was used for variables expressed as percentages (e.g. ground cover), and the logarithmic transformation ($Y = \log (y + 1)$) was applied to the remaining ones. I used multivariate analysis as a tool for data exploration and not for rigorous statistical testing (Williams, 1983 ; James and Macculloch, 1985).

The BMDP statistical package (Dixon, 1983) was used for all analysis.

RESULTS

Univariate analysis of variance showed statistically significant differences between species ($p < 0.05$ or better) for each of the 15 variables that appear in table I. A factor analysis was then carried out on this set of variables. The SHCO variable was not included in these calculations because it was closely correlated to the shrub cover measurement for each of the shrub species. The first 5 factors explained 71.6 % of the variance contained in the original matrix (Table II). The highest absolute values of factor loadings on factor I were for the variables DIVI, GENI, MAXH and HITX, which loaded positively, while 5 variables (of which HETI, STON and ROCK have the highest absolute values) had a negative loading factor. Thus factor I represented a gradient between those territories with thick shrub cover (particularly *Genista baetica*) and those with bare ground, rocks, grass and scarcely any shrub cover. In factor II the GRAS1, GRAS2, HITX and BARE variables were associated positively, while ROCK, HETI and STON loaded negatively. Therefore, factor II described the gradient among territories with a scarcity of shrub cover (those with more soil and grass at the one extreme, and those with more rock and stone components at the other). Factors III, IV and V expressed the variability between the relative importance of the three shrub species *J. communis*, *C. purgans* and *P. spinosum* found in each territory.

The distribution of species with respect to the three first factors is illustrated on figure 1. The habitat of each species was compared to that of the others by testing the differences between centroids in multivariate habitat space. There were significant differences ($P < 0.05$, Kruskal-Wallis test) between 26 of the 28 species pairs. Only Whitethroat-Ortolan Bunting and Skylark-Tawny Pipit pairs did not show statistical differences. These results clearly show interspecific differences in multivariate space and indicate a segregation in the high-mountain habitats.

TABLE II

Factor analysis made with 14 habitat variables.

Only loading higher than 0.200 are shown.

Variables	Factor I	Factor II	Factor III	Factor IV	Factor V
BARE		0.566	- 0.407		- 0.289
STON	- 0.444	- 0.489	- 0.231		
ROCK	- 0.469	- 0.694		- 0.285	
GRAS1		0.498		- 0.276	0.306
GRAS2		0.698		- 0.378	
GENI	0.856		- 0.254		
JUNI	0.205		0.889		
CYTI	- 0.208			0.850	
BERB	0.252		0.348		0.465
PTIL					0.816
HITX	0.800	0.350	0.312		
MAXH	0.815		0.212	- 0.303	
DIVI	0.859		0.243	- 0.232	
HETI	- 0.356	- 0.585	- 0.402	- 0.258	
Cumulative% of variance	34.8	47.8	56.6	64.9	71.6
Eigenvalue	4.18	2.32	1.77	1.33	1.13

Species-specific distribution profiles on factors I and II (Figs. 2 and 3) respectively show that some species have differentially shaped distributions along habitat gradients ; for example, Whitethroat and Skylark on factor I, and Rock Bunting on factor II, show a nearly symmetrical distribution, whereas other species, such as Ortolan Bunting on factors I and II, and Whitethroat on factor II, show discontinuous and/or skewed distributions, with the maximum towards an extreme of its distribution.

There is no real segregation between groups of species on factor I along a gradient of increasing cover and thickness of the shrub layer (from Black Redstart to Whitethroat). Nevertheless, the majority of the territories of black redstarts, wheatears, skylarks and tawny pipits appeared in the negative side of factor I, while wrens, whitethroats, ortolan and rock buntings fell into the positive side. Thus, the former four species preferred a habitat with scarce bushy cover, while the latter four species favoured sectors where shrubs predominate. As far as factor II is concerned (Fig. 3), only those habitats occupied by the Black Redstart were mainly in the negative side of the axis (high proportion of rock and pebble cover) ; the Whitethroat and Ortolan Bunting appeared on the positive side, while the habitats of the other five species fell evenly on both sides.

Only the gradients described by factors I and II were taken into account in the quantification of habitat breadth and overlap, as these two factors accounted for most of the variance. The extreme values of habitat breadth in factor I correspond to the Wren (3.56) and the Wheatear (6.01, Fig. 2), whereas the Whitethroat had the narrowest value for habitat breadth (2.85) and the Wheatear

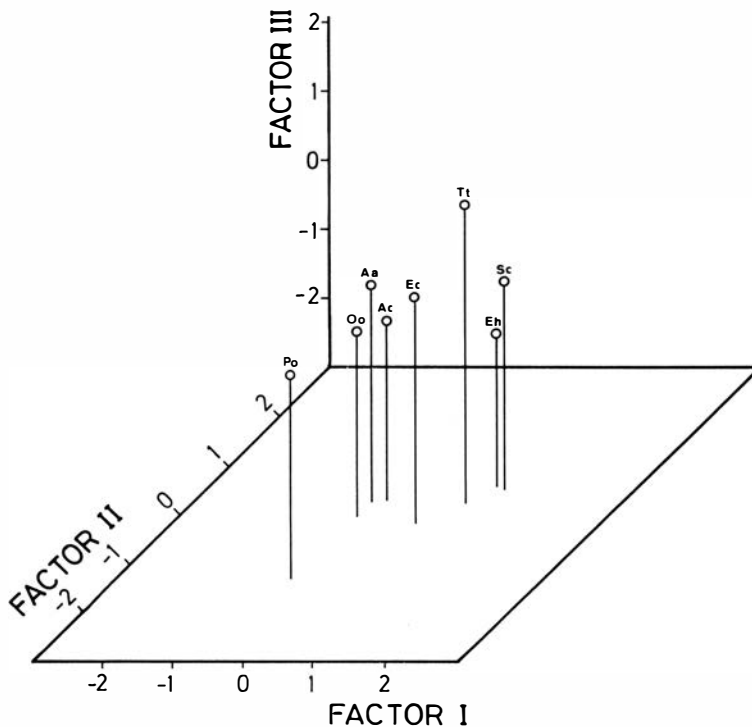


Figure 1. — Ordination of eight species along factors 1, 2 and 3. Aa = *Alauda arvensis*; Ac = *Anthus campestris*; Tt = *Troglodytes troglodytes*; Sc = *Sylvia communis*; Oo = *Oenanthe oenanthe*; Po = *Phoenicurus ochruros*; Ec = *Emberiza cia*; Eh = *Emberiza hortulana*. Points represent species means.

the widest (7.06) in factor II (Fig. 3). Overall niche breadth between factors I and II was calculated by the product of a species' niche breadth on each single axis (May, 1975). The most extreme values corresponded to the Whitethroat (10.6) and Wheatear (42.4, see Fig. 3). On the whole, the three species most closely associated with shrub cover (Whitethroat, Wren and Ortolan Bunting) were those with the narrowest overall habitat range.

The interspecific overlap in habitat characteristics was quantified by means of cluster analysis (average distance method). The corresponding dendrogram produced two groups of species (Fig. 4): the « open areas » group was mainly composed of the Skylark, the Tawny Pipit and the Wheatear. These species tend to establish their territories in sectors with scarce stunted shrubs, where grass and bare ground predominate over rocks. The Black Redstart and the Rock Bunting appeared to be associated with these « open areas » species, whereas the Ortolan Bunting, the Wren and the Whitethroat clustered together, forming a shrubby group. The Ortolan bunting and Whitethroat territories were restricted to some shrub patches with thick *G. baetica* cover, whereas the Wren also extended its range into patches of *J. communis* intermingled with rocks.

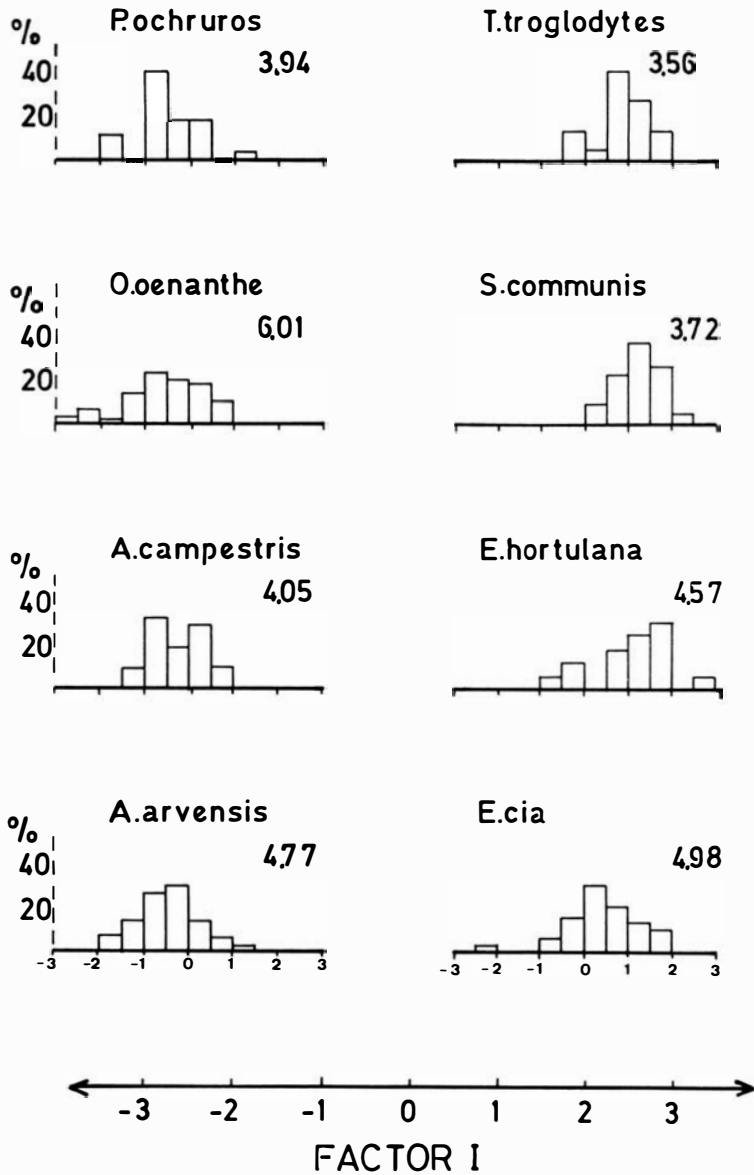


Figure 2. — The relative number of circular plots (expressed as % of total) of bird species in each twelve equally spaced intervals along the factor I. The figure beside each graph refers to the habitat breadth of that species along the axis (see Methods). Factor I represents a gradient from territories with thick shrub cover (positive sector) to bare territories with stones and grass (negative sector).

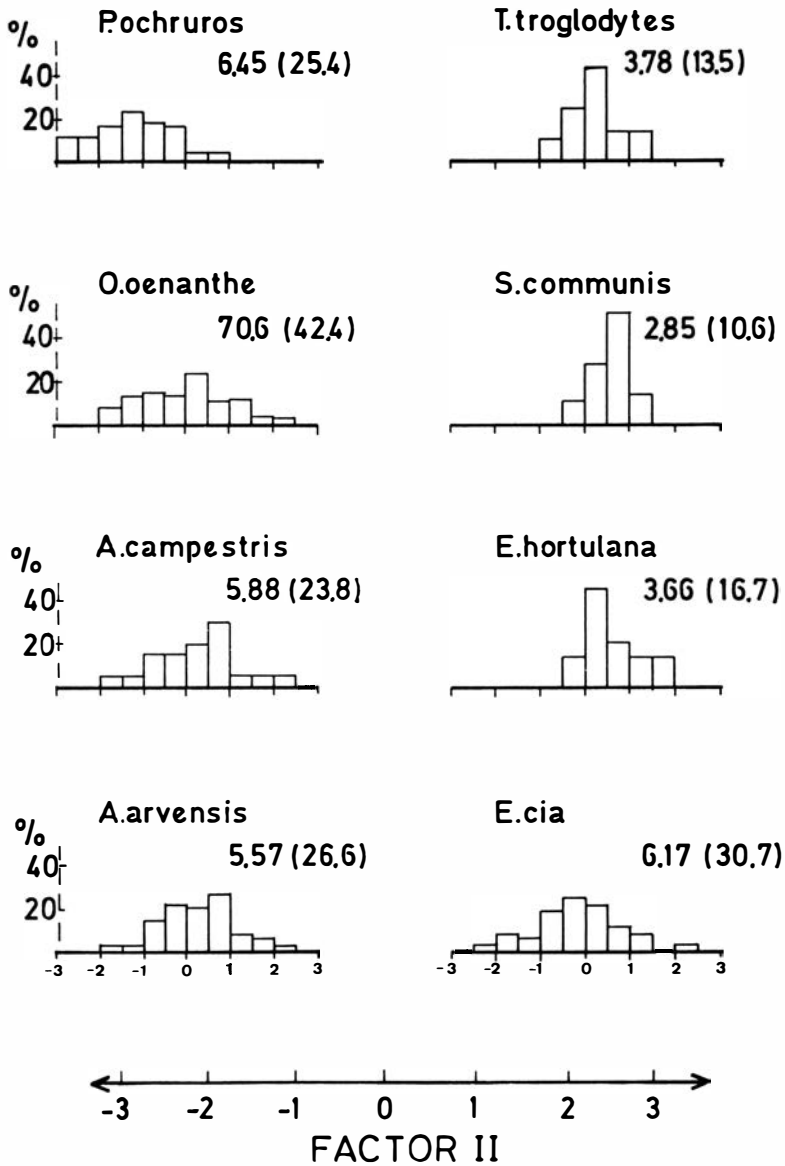


Figure 3. — The relative number of circular plots (expressed as % of total) of bird species in each twelve equally spaced intervals along the factor II. The figure beside each graph refers to the habitat breadth of that species along the axis, and the number in brackets refers to the overall habitat breadth in the factorial plane. Factor II represents a gradient from territories with bare ground and grass (positive sector) to territories with a greater rock and stone component (negative sector).

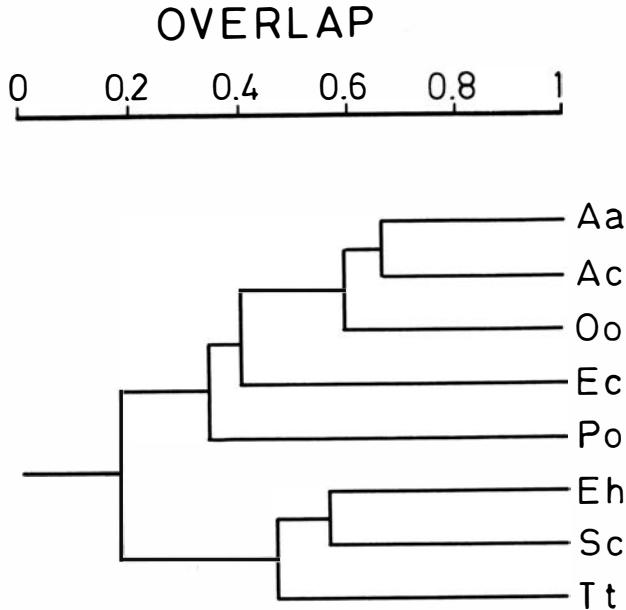


Figure 4. — Dendrogram of the interspecific habitat overlap measured by the co-occurrence of two species (see Methods) in the intervals defined along factors I and II.

DISCRIMINANT ANALYSIS OF HABITAT

Six of the original 14 variables were selected by Discriminant Function Analysis (DFA) for discriminating among the species: HITX, ROCK, JUNI, DIVI, STON and CYTI. All these variables presented statistically significant intergroup differences ($p < 0.001$). The canonical variables I and II explained 82.7 % of the variation and evidenced habitat gradients of similar significance to factors I and II.

A direct way to test the power of the discriminant variables is to determine their accuracy in correctly predicting group membership. The discriminant function correctly classified 48.6 % of the cases to their corresponding groups (Table III), which was 38.3 % better than what would have been obtained by chance classification (Cohen's Kappa statistics, Titus *et al.*, 1984), and was significantly better than what could have occurred by random sampling (Z statistic for Kappa, $p < 0.005$). Four species had less than 50 % of their territories correctly classified (Tawny Pipit, Rock Bunting, Wheatear and Whitethroat), while the habitats of the Black Redstart, the Wren, the Skylark and the Ortolan Bunting were clearly distinguishable from the rest on more than 50 % of occasions. Correct classifications varied between 72.7 % for the Wren and 22.7 % for the Whitethroat. The Wheatear was the only species whose habitats were analytically predicted as possibly belonging to any one of the other seven species.

TABLE III

Classification matrix from multiple discriminant analysis of habitat characteristics.

Actual Group	Predicted Group Membership								Cases Correctly classified (%)
	<i>P. och</i>	<i>T. tro</i>	<i>A. arv</i>	<i>E. hor</i>	<i>S. com</i>	<i>A. cam</i>	<i>E. cia</i>	<i>O. oen</i>	
<i>P. ochruros</i>	16	0	1	0	0	1	3	6	59.3
<i>T. troglodytes</i>	0	16	0	1	3	0	2	0	72.7
<i>A. arvensis</i>	1	3	28	1	0	4	4	10	54.9
<i>E. hortulana</i>	0	0	1	11	1	1	2	0	68.8
<i>S. communis</i>	0	9	0	8	5	0	0	0	22.7
<i>A. campestris</i>	3	0	5	2	0	6	3	2	28.6
<i>E. cia</i>	4	10	0	5	1	3	15	0	39.5
<i>O. oenanthe</i>	16	5	5	2	2	18	8	22	28.2

DISCUSSION

Passerines that breed at high altitudes in the Sierra Nevada have (on average) different preferences in their habitat choice. Nevertheless, multivariate analysis reveal considerable territorial overlaps as a consequence of intraspecific variation in habitat choice. Some species, especially the Wheatear and the Rock Bunting, establish their territories in a relatively wide range of micro-habitats (at least as far as the spatial scale used in this study is concerned), with different combinations of substrates (scrub, bare ground, rocks, etc...) and varying degrees of vertical and horizontal vegetation cover. These results reflect real intraspecific differences at a local scale in the pasture-scrubland of Sierra Nevada. Nevertheless, at a regional scale, the extent of variability in habitat selection depends on the relationships between the size of the area sampled and the real distribution of the breeding species throughout the Sierra Nevada. At the scale of the entire altitudinal gradient (Zamora, 1987a), the Wheatear, a generalist species in the high mountains (this study and Zamora, 1988), would nevertheless appear as a specialist. The Tawny Pipit and Skylark, like the Wheatear, choose exclusively the high-mountain pasture with some stunted shrubs to breed. The Black Redstart breeds primarily in rocky terrain along the altitudinal gradient, although foraging in all available high-mountain habitats (Zamora, 1990b). The Ortolan Bunting and the Whitethroat exclusively occupy certain sectors of well-developed high mountain shrub (especially *Genistra baetica*). On the other hand, the Rock Bunting and the Wren nest in patches of shrubs intermingled with rocks; their highest densities are reached in the open forest areas between 1 200-1 700 m a.s.l. The high-mountain shrubland, therefore, represents the upper altitudinal limit of the distribution of the latter two species in the Sierra Nevada (Zamora, 1987a). At a continental scale, the majority of the species breeding in high-mountain areas of the Sierra Nevada (with the exception of the Black Redstart) show a wide distributional range on the European Continent, where they inhabit open-country areas such as grassland and low-scrubland (Zamora, 1988). Any recognition of intraspecific variability largely depends on scale (Wiens, 1986; Wiens and Rotenberry, 1981;

Wiens *et al.*, 1987). This becomes obvious when a study is carried out at the scale of individual territories, with habitat samples taken within wide distributional ranges (cf. Cody, 1978 and 1985b ; Leisler, 1981 ; Collins, 1983a and b ; James *et al.*, 1984 ; Shy, 1984).

HABITAT VARIABLES DETERMINING SPATIAL DISTRIBUTION OF THE SPECIES

Despite the structural simplicity of the high-mountain habitats, all the breeding species occupy a specific position in the habitat gradients generated by multivariate analysis. This interspecific segregation appears both with respect to the vertical complexity of the shrub layer (factor I), as well as the patchy distribution of habitat components (Horizontal heterogeneity, factor II). A major question is to understand the importance of habitat composition and structure in the species-specific responses to characteristics of the high-mountain habitats. Cody (1985c) concludes, among many others, that the structure of the vegetation is the determining factor in interspecific segregation of open-country birds. Nevertheless, out of the six variables that make the discriminant function, four concern the composition of the habitat and only two its structure, emphasizing the importance of the former factor in territorial segregation in this kind of habitat (see also Zamora, 1988). These results indicate that the floristic composition of the shrub cover, and the presence of rocks and stones, are just as important to high-mountain passerines in their habitat choice as are the vertical and horizontal heterogeneity of the vegetation. Thus, in such high-mountain habitats, some species breed, forage and sing in the shrub layer (the Whitethroat, the Wren), whereas others use a rocky substrate for nest concealment, feeding-perches and song-posts (the Black Redstart, the Wheatear, see Zamora, 1990a, d). Still other species use both shrub and rock substrates (e.g. the Rock Bunting), while the Skylark and Tawny Pipit nest and forage at ground level (see Zamora, 1987b, 1990b and c). Accordingly, species ordination along habitat gradients based on samples of territorial habitats is very similar to that based exclusively on feeding-substrates (Zamora, 1990b) and song-posts (Zamora, 1990d). These habitat preferences fit in with recent observations on habitat selection at the population distributional level (Zamora, 1988).

Bearing in mind the importance just discussed, of a rocky and stony substrate in interspecific avian segregation, I suggest that abiotic components of bird habitats should also be quantified in studies on habitat selection in birds. This suggestion should also apply to every high-mountain area, and to terrestrial environments such as tundras, deserts and all open habitats in general.

SUMMARY

The characteristics of the habitats of eight breeding species of birds in the pasture-scrubland of the high-mountain areas of the Sierra Nevada (S. Spain) were studied. Habitat composition and structure were determined by measuring 15 variables in 0.1 ha circular plots within the territories of breeding pairs. The passerines that nest in the high-mountain areas of the Sierra Nevada show

different preferences in their choice of habitat. This interspecific segregation appears both with respect to the vertical complexity of the shrub layer (factor I), and to the patchy distribution of habitat components (factor II). Cluster analysis identified two groups of species: those preferring scrubland (*Sylvia communis*, *Emberiza hortulana* and *Troglodytes troglodytes*), and those favouring open ground (mainly *Alauda arvensis*, *Anthus campestris* and *Oenanthe oenanthe*). *Emberiza cia* shared characteristics common to both groups, while *Phoenicurus ochruros* bred in rocky terrain. Discriminant function analysis showed the importance of habitat composition (both shrubs and rocks) and structural variables in species segregation. According to these results, I recommend that studies about avian habitat use include quantitative estimates of rocky substrates, especially in high-mountain areas, tundras and deserts.

RÉSUMÉ

L'auteur a étudié les caractéristiques de l'habitat de reproduction de huit espèces de passereaux nichant dans les prairies et broussailles d'altitude (2 000-2 700 m) de la Sierra Nevada, en Espagne méridionale. La nature et la structure du milieu ont été déterminées par mesure de 15 variables sur des placettes circulaires de 0,1 ha, situées dans le territoire de reproduction des couples. Les passereaux étudiés choisissent des habitats différents pour se reproduire. Cette ségrégation spécifique des emplacements de reproduction prend en compte la complexité structurelle verticale de l'étage des buissons (facteur I), et la distribution par taches des composantes de l'habitat (facteur II). L'analyse hiérarchique permet d'identifier deux groupes d'espèces: (1) celles qui préfèrent les broussailles (*Sylvia communis*, *Emberiza hortulana* et *Troglodytes troglodytes*), et (2) celles qui préfèrent les milieux ouverts (principalement *Alauda arvensis*, *Anthus campestris* et *Oenanthe oenanthe*). *Emberiza cia* se situe en position intermédiaire, alors que *Phoenicurus ochruros* préfère les terrains rocheux. Dans ce choix de l'habitat de nidification, l'analyse discriminante met en évidence à la fois l'importance de la nature de l'habitat de reproduction (des buissons comme des rochers) et celle des variables structurelles. S'appuyant sur les résultats de cette étude, l'auteur recommande d'inclure dans toute analyse de l'habitat chez les oiseaux, des mesures quantitatives des substrats rocheux, en particulier en haute altitude, dans les toundras, et en milieux désertiques.

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