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Coexistence in Mediterranean warblers: ecological differences or interspecific territoriality?

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Abstract. We studied the coexistence of four species of *Sylvia* warblers living in Mediterranean matorral in order to identify the respective role of ecological segregation and of interspecific territoriality in explaining the local distribution of these four species. Data on habitat use, foraging behaviour and interspecific spacial segregation were collected on Corsica and on Spargi (Sardinia) islands. Despite large overlap in patch selection and in foraging behaviour the four species did segregate ecologically and behaviourally while foraging (differences in the choice of plant species used for foraging, in the height of the plant selected, in the selection of the portion of the plant volume used and in the selection of the plant structure explored). Complementarity in foraging behaviour was observed in the morphologically and ecologically closest species: the Dartford (*Sylvia undata*) and the Marmora's (*Sylvia sarda*) warblers. We did not observe any evidence of direct interspecific interactions in song, alarm, or aggressive behaviour. Nor did we observe patterns of spatial distribution that would support the idea of coexistence by interspecific territorial exclusion. These results contrast with the results of Cody & Walter (1976) suggesting interspecific territoriality in Mediterranean *Sylvia* warblers. They are consistent with other published results emphasizing ecological differences as explanation for species coexistence.

Key words. Mediterranean warblers, ecological segregation, habitat selection, interspecific territoriality.

Résumé. Nous avons confronté le rôle de la ségrégation écologique et de la territorialité interspécifique pour expliquer la coexistence de quatre espèces de fauvettes dans les maquis en Corse et en Sardaigne. Nous avons collecté des données sur l'utilisation de l'espace et sur la recherche alimentaire par ces espèces. Malgré un important chevauchement dans la sélection de l'habitat et les comportements de recherche de nourriture les espèces étudiées se ségrègent par leur écologie (choix de l'habitat) et par leur comportement (différences dans le choix des plantes, de leur hauteur et des parties utilisées pour l'alimentation). Les différences de comportement alimentaire les plus marquées sont observées entre les deux espèces les plus semblables dans leur morphologie et leur sélection d'habitat (la Fauvette sarde *Sylvia sarda* et la F. pitchou *S. undata*). Nos résultats ne confirment pas les interactions directes entre ces espèces par le chant, les alarmes, les comportements agressifs ou la territorialité interspécifique qui avaient été suggérées par Cody et Walter (1976).

Mots clés. Fauvettes méditerranéennes, ségrégation écologique, sélection de l'habitat, territorialité interspécifique.

INTRODUCTION

The local coexistence of species similar in their morphology, usually congeners, has stimulated special interest in the attempts to understand the composition of local species assemblages. In the Western Palearctic habitat selection of several such guilds of congeneric passerines sharing the same habitat has been investigated. Among them are the titmice (genus *Parus*) found in broad leafed and boreal woodlands (Lack, 1971; Perrins, 1979; Alatalo, 1981, 1982; Oksanen, 1987), the reed warbler (genus *Acrocephalus*) found in wetlands (Henry, 1979; Leisler, 1981; Leisler & Winkler, 1985) and the warblers (genus *Sylvia*) that breed in evergreen matorrals of the Western Mediterranean (Cody & Walter, 1976; Diesselhorst, 1971; Cody, 1981; Zbinden & Blondel, 1981; Martin & Thibault, 1983; Walter, 1988).

The presence in the same habitat of morphologically close species is usually explained by two hypotheses. The first one emphasizes competition for space, with interspecific territorial exclusion as an extreme result (individuals of different species therefore spatially segregate within the habitat) (Ferry & Deschaintre, 1974, for the genus *Hippolais*; Lemaire, 1977; Catchpole, 1977, 1978; Svensson, 1978, for the genus *Acrocephalus*; and Cody & Walter, 1976; Cody, 1978, for the genus *Sylvia*). The second hypothesis emphasizes ecological segregation resulting from subtle differences in habitat use made possible by morphological differences in size and shape and/or by behavioural differences (Hartley, 1953; Gibb, 1954; Lack, 1971, for the genus *Parus*; Zbinden & Blondel, 1981; Martin & Thibault, 1983; Blondel, 1985; Glutz von Blotzheim & Bauer, 1991, for the genus *Sylvia*; see Wiens, 1989, for a review). These two hypotheses are not necessarily exclusive (see the literature on the genus *Acrocephalus*, Glutz von Blotzheim & Bauer, 1991).

In the case of *Sylvia* warblers Zbinden & Blondel (1981), Martin & Thibault (1983) and Blondel (1985) suggest that differences in habitat selection explain the co-occurrence of several *Sylvia* warblers within a habitat whereas Cody & Walter (1976) and Cody (1978, 1985) consider interspecific interactions leading to interspecific territoriality as the essential mechanism involved. For North Palearctic *Sylvia* warblers Cody's (1978, 1985) hypothesis was refuted by Haila & Hanski (1987).

In this paper we revisit the spatial and ecological segregation between the four species that breed in Mediterranean matorral (shrublands dominated by evergreen shrubs) on Corsica and Sardinia (Marmora's warbler *S. sarda*, Dartford warbler *S. undata*, Sardinian warbler *S. melanocephala* and Subalpine warbler *S. cantillans*). Three sets of questions are addressed. First, to what extent and at which scale are these species sympatric? How do they differ in their habitat selection for foraging? Second, when the species co-occur within a patch type how much overlap in microhabitat use is there between foraging individuals belonging to different species? Third, is there evidence of interspecific spatial segregation?

STUDY SITES AND METHODS

Study sites

We collected data in two different sites: the island of Spargi in Sardinia and the Scandola Nature Reserve on Corsica. The two study sites were selected because they were representative of the range of matorral conditions typical of this part of the Mediterranean. The grain of patches in the matorral mosaic is finer on Scandola than it is on Spargi (average patch size is smaller on Scandola). The other main differences in habitat features (Table 1) are: a higher maximum vegetation height within each matorral type on Scandola and a few differences in plant species composition. *Arbutus unedo*, *Olea europaea* and *Pistacia lentiscus* are abundant on Scandola, whereas *Juniperus phoenicea* is abundant on Spargi. Vegetation cover tends also to be denser on Scandola especially in the patches of lower matorral. This can have an effect both on the occurrence and on the detectability of ground foraging.

On the island of Spargi, a 420 ha island of the Maddalena archipelago situated between Sardinia and Corsica (41°15′N, 9°22′E, Fig. 1) we delimited three plots in the north eastern part of the island on the basis of their vegetation height and cover. They range in area from 0.6 to 0.7 ha. Each plot was selected so as to be characteristic of one of the three main types of matorral that form the matorral mosaic which covers the island. These three types of matorral patches are defined according to vegetation height: matorral with low canopy height (plot 1), matorral with medium canopy height (plot 2), matorral with higher canopy height (plot 3) (see Table 1). The plots were almost adjacent, the distance between two adjacent plots being less than 200 m. Each plot was mapped with the help of a topothread and its vegetation described (see Fig. 2). All four warbler species had to be observed at least once in each plot. The distribution of land birds in relation to habitat structure was analysed on the entire island by means of point counts in order to make sure that what we observed in the study plots was representative (Martin, Thibault and Guyot, unpubl.).

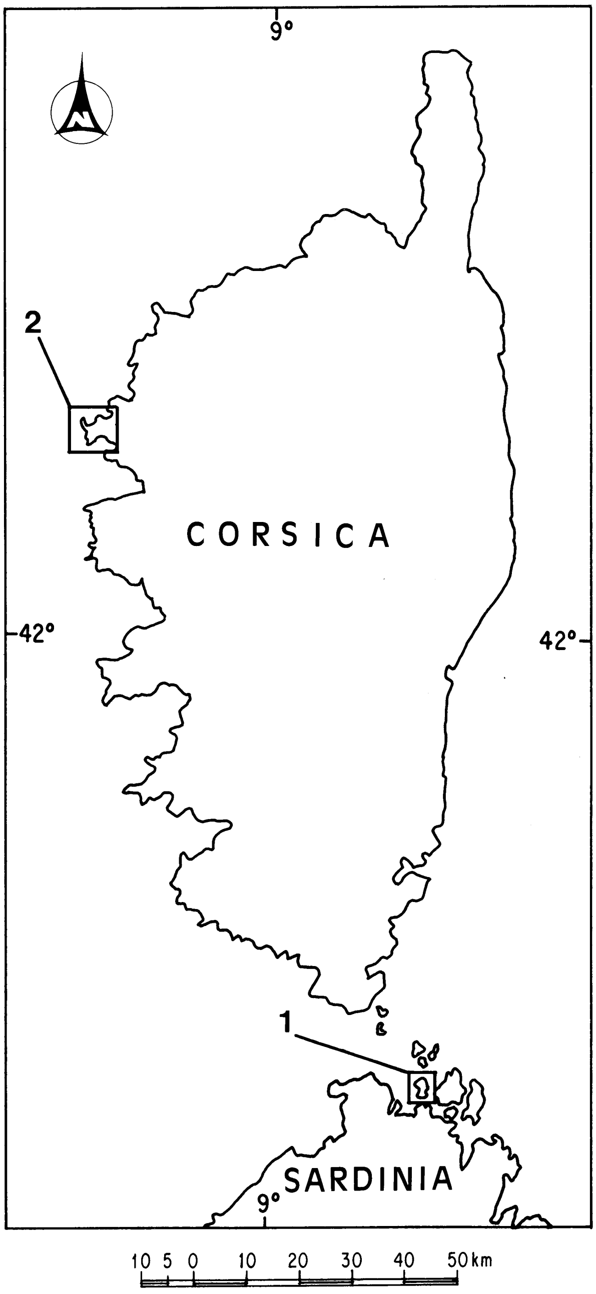

FIG. 1. Position of the two study sites. 1, Spargi island; 2, the Scandola peninsula.

TABLE 1. Characteristics of the vegetation in the three study plots on Spargi and in the matorral types in Scandola. Plot 1 and Matorral Type 1 = low matorral; Plot 2 and Matorral Type 2 = matorral of medium canopy height; Plot 3 and Matorral Type 3 = high matorral. CM = *Cistus monspeliensis*, EA = *Erica arborea*, JP = *Juniperus phoenicea*, AU = *Arbutus unedo*, PL = *Pistacia lentiscus*, PA = *Phyllirea angustifolia*, OE = *Olea europaea*, RA = *Rhamnus alaternus*, PT = *Pittosporum tobira*, CS = *Cistus salviaefolius*. Upper (Spargi): figures between parentheses refer to % of cover. Lower (Scandola): standard deviations for average vegetation heights are indicated between parentheses, % refer to the percent of census points in which the plant species was recorded as first or second dominant. Canopy height ranges between 0.5 and 1 m in matorral patches of type 1, from 1 to 2 m in patches of type 2 and from 2 to 3 m in patches of type 3.

SPARGI	Plot 1	Plot 2	Plot 3
Area	6200 m^2	7200 m^2	6000 m^2
Maximal height	1.9 m	2.3 m	2.9 m
Average height	0.6 m	1.6 m	1.6 m
Bare soil	5%	6%	6%
1st dominant plant	CM (60%)	CM (42%)	CM (61%)
2nd dominant plant	EA (13%)	EA (29%)	JP (12%)
3rd dominant plant	JP (5%)	AU (18%)	EA (6%)
Other plants	PL, PA		OE NO RA PT

SCANDOLA Matorral type	Type 1	Type 2	Type 3
Number of census points	13	12	9
Average max. height	2.8 m (1.0)	3.3 m (1.0)	4.7 m (1.0)
Average canopy height	0.8 m (0.2)	1.5 m (0.4)	2.6 m (0.9)
1st dominant plant	CM (87%) EA (10%)	CM (60%) AU (31%)	CM (49%) AU (41%)
2nd dominant plant	EA (22%) PL (20%) OE (14%) CS (13%)	EA (37%) OE (30%) CM (24%)	AU (49%) EA (40%)

On the island of Corsica we established a study site in the Nature Reserve of Scandola (42°25′N, 8°34′E, Fig. 1). Because of the finer grain of the vegetation mosaic, we could not restrict observations of foraging behaviours to permanent plots and scattered them all over the Elbo Valley (about 250 ha). For each bird observed foraging the matorral patch type in which it was seen was recorded and described. The relation between vegetation and land bird distribution in Scandola has been studied and described in Martin & Thibault (1983).

Sampling of macro habitat selection and of foraging behaviour

On Spargi three observers collected the data in a standardized way between 15 and 24 May 1986 (10 days per person, 120 h of observation in total). Each of the three observers (JLM, JCT and I. Guyot) censused one study plot (see Fig. 2). We used 1 (plot 2) or 2 (plots 1 and 3) observation points chosen so as to give the best overview of the study site (area less visible to the observer is shaded on Fig. 2). We mapped the vegetation for each plot and marked and measured a certain number of reference points. We carried out our observations at the periods of highest foraging activity (from 2 to 5 h after sunrise, and from 6 to 4 h before sunset) except when there was a strong wind. A single observer (JLM) made all foraging observations on Scandola and recorded the structure of the habitat around the observation points, this between 21 May and 3 June 1982 (12 days, 60 h of observation) and between 13 and 25 June 1983 (12 days and 70 h of observation). We therefore have a total of 54 days and of 250 h of standardized observation spread over three breeding seasons and over two localities. The census periods are included in the nesting season. They are similar to the one of Cody & Walter (1976) who made their observations from May to July 1974.

Both on Spargi and in Scandola we used a sequential observation method. Each individual bird was followed as long as possible. This is the only practicable method in dense matorral vegetation, and minimizes the under-representation of less conspicuous behaviours (Morrison, 1984). However, sequential (or continuous) observations of the same individual are not independent (see below).

On Spargi we mapped the movements of each bird observed in the vegetation and we dictated onto a tape recording the following behaviours: foraging, alarming, singing, feeding young, moving from one foraging site to another, the substrata used (ground or rocks, low bushes, bushes, small trees), the position in the plant's volume (top, middle inner part, middle outer part, lower part, trunk), the plant's part explored (leaves, flowers, twigs, leafed branches), small branches (section less than 1 cm, branches and trunk), the plant species explored, the plant's height (converted afterwards into classes) and the bird's height in the plant. Each bird was continuously followed as long as possible. Every transition between different behaviours, positions, or plant parts were recorded. Events between transitions were considered as single observations and the set of continuous observations were defined as a sequence.

Because of the dense vegetation, frequency of bird visits on the ground was probably underestimated, especially on Scandola. The same is certainly true for activity in the inner parts of the plants. But as our main objective was to compare differences in habitat selection these biases are more likely to underestimate differences than to exaggerate them. Our results should therefore be considered as conservative.

In sum habitat selection by warblers was studied in a fine grained way on Spargi, over a limited area, together with informations on interspecific interactions. These observations involved a restricted number of individuals leading to an unknown amount of dependency among observations. On Corsica observations were done at a coarser grain, over a larger area, on a larger number of individuals but with informations only on habitat selection for foraging.

Data analysis

We studied the selection of matorral type and of habitat features by the warblers by testing the distribution of their

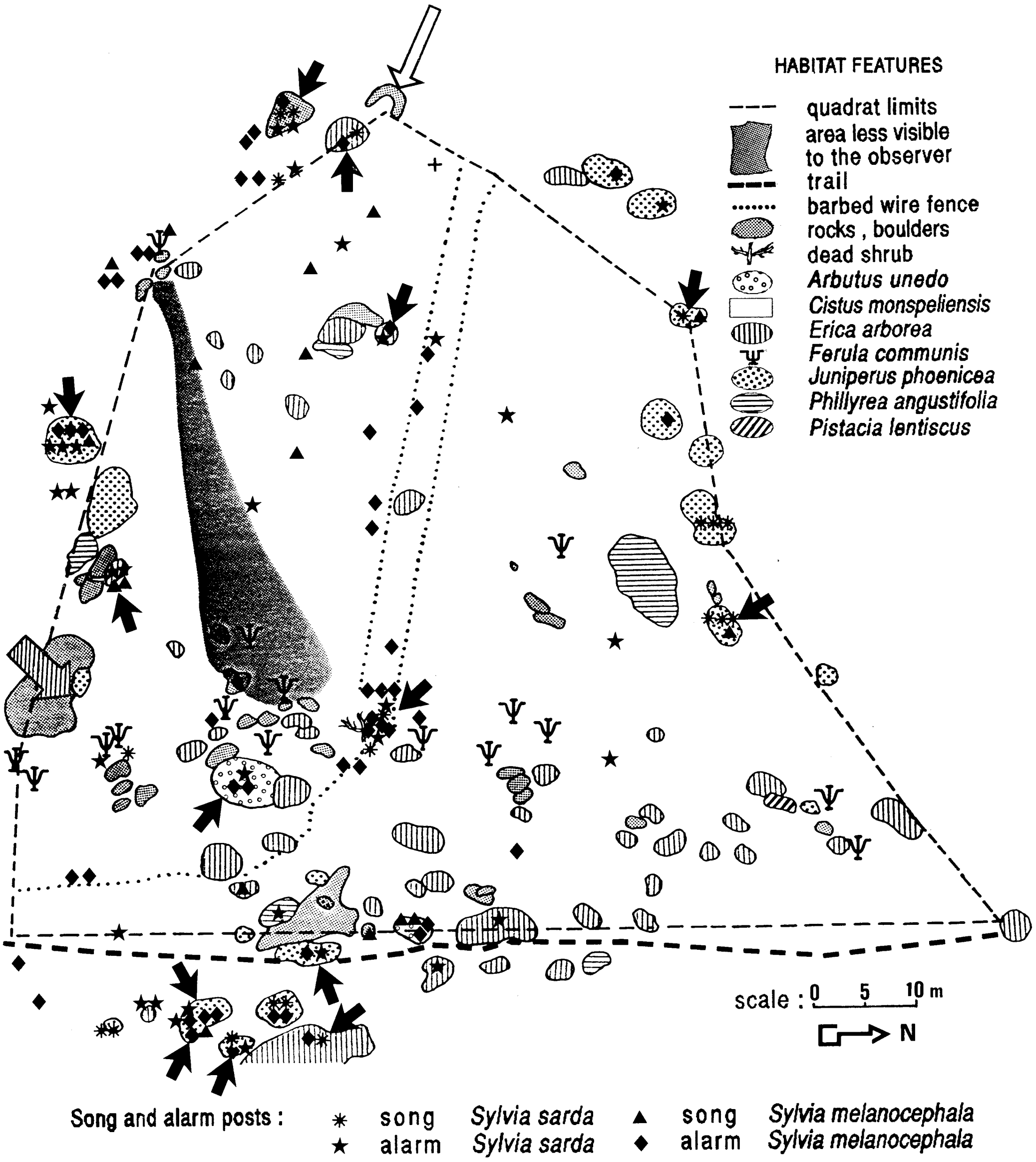

FIG. 2. Sketch map of study plot 1 on Spargi showing the principal vegetation and physical features that occur within a matrix of *Cistus monspeliensis* and the localization of alarming and singing observations of warblers. Large hatched arrow = main observation point used by the observer, large open arrow = other observation point. Asterisks, stars, triangles and lozenges identify observations of song or alarm behaviours by the four species. Song and alarm posts that were occupied by several individuals belonging to different species are identified by small full arrows. +, Occupied nest of Sardinian warblers (top of map).

observation frequencies within contingency tables (Chi-square tests, Everitt, 1977). We did this first for Spargi and Scandola overall and second individually for the three plots on Spargi. In order to identify for each variable the categories responsible for a significant Chi-square value we analysed their adjusted residuals (Haberman, 1973 in Everitt, 1977). Assuming that the variables forming the table are independent these residuals are approximately normally distributed with mean 0 and standard deviation 1. Statistical significance at the 5% level of residual values can then be estimated by comparing their absolute values with the 5% standard normal deviate (1.96). In order to estimate the impact of biases due to non-independent observations within sequential observations the analyses were repeated for data subsets in which only the first foraging observation was kept in each observation sequence.

RESULTS

Tables 2 and 3 summarize the data. There are no significant differences between plots on Spargi or between matorral classes in Scandola in the average number of single behaviour observation per sequence for a given species (i.e. no detectable plot or observer effect). Neither are there significant differences in the average number of observations per sequence and per species between the two sites censused

TABLE 2. Number of observation sequences (NSEQ), number of single observations within the sequences (NOBS, which includes all the behaviour types including foraging), number of foraging observations (NFOR) and average number of single observations per sequence (NOBS/SEQ) in each of the 3 plots studied on Spargi for Marmora's (SSAR), Dartford (SUND), Sardinian (SMEL) and Subalpine (SCAN) warblers. Figures between parentheses refer to % within a plot. For Plot 1 to Plot 3 see Table 1.

Species	Plot 1	Plot 2	Plot 3	Total
SSAR				
NSEQ	116 (40)	27 (13)	2 (1)	145
NOBS	555 (46)	111 (14)	3 (1)	669
NFOR	368	36	1	405
NOBS/NSEQ	4.78	4.11	1.50	
SUND				
NSEQ	26 (10)	46 (22)	25 (19)	97
NOBS	115 (13)	213 (27)	97 (20)	463
NFOR	127	67	38	232
NOBS/NSEQ	5.88	4.63	3.88	
SMEL				
NSEQ	146 (49)	93 (44)	67 (51)	307
NOBS	468 (39)	309 (40)	216 (45)	993
NFOR	204	22	92	318
NOBS/NSEQ	3.20	3.32	3.22	
SCAN				
NSEQ	3 (1)	45 (21)	36 (29)	84
NOBS	25 (2)	145 (19)	164 (34)	334
NFOR	20	50	112	182
NOBS/NSEQ	8.33	3.22	4.55	
Total				
NSEQ	291	211	130	632
NOBS	1201	778	480	2459
NFOR	719	175	243	1137

TABLE 3. Number of observations of foraging behaviours on Scandola (for bird species names see Table 2). For the number of foraging observations per species within each matorral type see Table 4.

	SSAR	SUND	SMEL	SCAN	Total
NSEQ	30	20	11	28	89
NOBS	89	74	33	71	267
NFOR	79	69	31	61	240
NOBS/NSEQ	3.0	3.7	3.0	2.5	

(plot 2 on Spargi, observations on Corsica) by the same observer (JLM) (Chi-square test).

Selection of matorral patch type

TABLE 4. Number of observations of foraging events observed for the four warblers in the three matorral types on Spargi (respectively plots 1 to 3) and in Scandola (for bird species names see Table 2). Differences between plots and between classes are statistically significant (Spargi: $\text{Chi}^2_6=433.9$, $P<0.001$; Scandola: $\text{Chi}^2_6=55.8$, $P<0.001$). +, Significant positive residual at the 5% level; −, significant negative residual at the 5% level. For Plot 1 to Plot 3 and Type 1 to Type 3 see Table 1. The two data sets (Spargi and Scandola) were analysed separately.

	SSAR	SUND	SMEL	SCAN	Total
Plot 1 Spargi	368+	127−	204	20−	719
Plot 2 Spargi	36−	67+	22−	50+	175
Plot 3 Spargi	1−	38−	92+	112+	243
Type 1 Scandola	45+	21	12	7−	85
Type 2 Scandola	33	21−	15	31	100
Type 3 Scandola	1−	27+	4	23+	55

The number of observations per species varies significantly among matorral patch types on Spargi as well as on Scandola (Table 4). Each species tends to be more often observed in one type of matorral. In the lower matorral patches (plot 1 on Spargi, matorral type 1 on Scandola) Marmora's warblers were the most often observed (significant positive residual) whereas Subalpine warblers were missing or rare (significant negative residual). Dartford and Sardinian warblers showed either negative or non-significant residuals for the lower matorral. In the medium height matorral patches, where vegetation structure was most heterogeneous, all four species were commonly observed in both study sites. In the higher matorral type, Marmora's warblers were rare (significant negative residuals) and Subalpine warblers had positive residuals.

Ecological segregation in foraging behaviour

On Spargi all four species were most often observed feeding on the dominant plant species *Cistus monspeliensis* (absolute number of observations; Table 5). However, only Marmora's warblers showed a significant positive residual for *C. monspeliensis*. Subalpine warblers showed a significant negative residual. For plant species choice and for the height of the plant explored while foraging all four species exhibit some level of complementary selection within the ecological space. But complementarity is most remarkable for the Marmora's and Dartford warbler species pair, the two species that occur in the lower matorral and that are morphologically similar (see Géroudet, 1954; Glutz von Blotzheim & Bauer, 1991). In seven out of eight plant species for which at least ten observations were made the residuals of the Marmora's and Dartford warblers are of opposite sign. In six out of seven cases one at least of the two residuals is significant, in four out of these seven cases both residuals are significant. In plant height selection residuals are of opposite sign in four out of five classes and at least one is significant in each pair (Table 5).

On Scandola the predominance of *Cistus monspeliensis* is less marked (Table 6, absolute number of observations). But when we compare the residuals between bird species, the Marmora's warbler was still the only species with a significant positive residual for foraging on *C. monspeliensis* and the Dartford warbler was the only species with a significant positive residual for foraging on *Erica arborea*.

On Spargi significant differences in habitat selection for foraging also appear for each plot when studied separately showing that the overall pattern reflects the pattern observed in each plot (Table 7). Between plot variation exists however. Dartford warblers for instance are most often observed on *C. monspeliensis* and *E. arborea* in plots 1 and 2 but are almost exclusively observed on *J. phoenicea* in plot 3 (our unpubl. results).

All these results are not affected if we only use the first foraging observation within each observation sequence, i.e. if we correct for non-independence of successive foraging events within a foraging sequence (our unpubl. results).

TABLE 5. Number of observations and Chi-square residuals for the overall use of the micro-habitat features on Spargi (for bird species names see legend of Table 2. MV = missing values. MV and categories with less than ten observations have been excluded from Chi-square test. Numbers between parentheses are residuals of Chi-square test. Residuals are significant at the 5% level if their absolute value is higher than 1.96. CMON, *Cistus monspeliensis*; JPHO, *Juniperus phoenicea*; EARB, *Erica arborea*; DSHR, Dead shrub; AUNE, *Arbutus unedo*; GROU, Ground; GCOR, *Genista corsica*; PHIL, *Phillyrea* sp.; PLEN, *Pistacia lentiscus*; MCOM, *Myrtus communis*; PTOB, *Pittosporum tobira*; HERB, grasses; FERU, *Ferula communis*; OLEA, *Olea europaea*; CALI, *Calycotoma villosa*; NOLE, *Nerium oleander*; COBL, *Cydonia oblonga.*

	SSAR	SUND	SMEL	SCAN
Plant species selection (Chi$^2_{36}$ = 489.09, P<0.001)				
CMON	180 (+3.0)	80 (−1.5)	129 (+1.6)	49 (−3.6)
JPHO	19 (−6.6)	40 (+1.7)	71 (+5.4)	26 (+0.2)
EARB	35 (−2.3)	62 (+8.1)	26 (−2.1)	8 (−3.3)
DSHR	53 (+4.9)	9 (−2.5)	19 (−1.4)	8 (−1.9)
AUNE	0 (−5.2)	6 (−1.3)	14 (+0.3)	27 (+7.9)
GROU	44 (+8.5)	0 (−3.5)	3 (−3.3)	0 (−3.0)
GCOR	24 (+2.4	15 (+2.1)	6 (−2.3)	1 (−2.6)
PHIL	18 (+1.8)	7 (−0.1)	8 (−0.7)	3 (−1.3)
PLEN	9 (−0.3)	3 (−1.2)	8 (+0.2)	7 (+1.4)
MCOM	1 (−3.5)	4 (−0.7)	3 (−1.9)	19 (+7.7)
PTOB	0 (−3.7)	0 (−2.5)	3 (−1.7)	21 (+9.6)
HERB	13 (+2.5)	1 (−1.8)	7 (+0.6)	0 (−2.0)
FERU	0 (−3.4)	0 (−2.3)	10 (+2.2)	10 (+4.1)
OLEA	0	0	8	1
CALI	0	3	0	0
NOLE	0	0	0	1
COBL	0	0	0	1
MV	8	2	3	0
Plant height selected (Chi$^2_{12}$ = 331.90, P<0.001)				
0 to 0.5 m	207 (+11.8)	33 (−5.8)	95 (+0.1)	2 (−9.2)
0.5 to 1 m	143 (+2.4)	86 (+2.3)	82 (−2.3)	40 (−2.8)
1 to 1.5 m	35 (−3.4)	42 (+2.5)	45 (+0.6)	28 (+0.9)
1.5 to 2 m	9 (−6.0)	31 (+2.5)	35 (+1.4)	28 (+3.2)
Over 2 m	10 (−9.7)	40 (+0.0)	61 (+1.1)	84 (+11.3)
Position in the plant (Chi$^2_9$ = 57.7, P<0.001)				
Top	94 (+3.0)	65 (+3.0)	43 (−3.7)	25 (−2.6)
Outer	124 (−2.4)	100 (+1.2)	114 (−1.3)	92 (+3.2)
Inner	126 (−0.2)	61 (−3.1)	129 (+2.9)	61 (−0.4)
Basal	13 (−0.7)	5 (−1.8)	24 (+3.6)	4 (−1.5)
Trunk	0	0	3	0
Ground	44	0	3	0
MV	3	1	2	0
Structure explored (Chi$^2_9$ = 69.15, P<0.001)				
MV, Ground	82	12	18	8
Leaf	78 (+2.5)	44 (+0.2)	44 (−2.3)	31 (−0.6)
Twig	180 (−0.0)	146 (+3.6)	158 (−0.5)	76 (−3.3)
S. branch	64 (−0.8)	24 (−4.3)	79 (+2.9)	48 (+2.3)
Branch	0	1	7	3
Trunk	0	0	4	0
Flower	0 (−3.8)	5 (−0.6)	8 (−0.2)	16 (+5.5)
Total	404	232	318	182

TABLE 6. Number of observations and Chi^2 residuals for the overall use of micro-habitat features on Scandola. MV, missing values. For bird species names see legend of Table 2 and for plant species names see legend of Table 5. CSAL, *Cistus salviaefolius*; ASPH, *Asphodelus* sp.; JOXY, *Juniperus oxycedrus*; DVIS, *Dittrichia viscosa*; ROFF, *Rosmarinus officinalis.*

	SSAR	SUND	SMEL	SCAN
Plant species selection (Chi$^2_{15}$ = 88.90, P<0.001)				
AUNE	5 (−5.2)	33 (+4.0)	6 (−1.3)	24 (+2.4)
CMON	32 (+4.6)	11 (−2.0)	4 (−1.6)	10 (−1.4)
EARB	5 (−2.1)	17 (+3.1)	0 (−2.4)	10 (+0.9)
OLEA	13 (+1.9)	2 (−2.7)	10 (+3.8)	2 (−2.2)
PHIL	8 (+0.6)	2 (−2.2)	4 (+0.8)	7 (+1.0)
PLEN	8 (+1.2)	2 (−1.8)	6 (+2.6)	2 (−1.4)
CINC	2	1	0	0
CSAL	1	0	1	0
QILE	0	0	0	2
CVIL	2	0	0	0
JOXY	0	0	0	1
ASPH	1	0	0	0
LVIS	0	0	0	1
ROFF	0	1	0	0
MV	2	0	0	2
Plant height selected (Chi$^2_9$ = 38.87, P<0.001)				
0 to 0.5 m	4	6	0	2
0.5 to 1 m	38 (+4.2)	19 (−0.4)	5 (−2.0)	11 (−2.6)
1 to 1.5 m	19 (+1.1)	12 (−0.5)	5 (−0.7)	12 (−0.2)
1.5 to 2 m	10 (−0.2)	12 (+1.3)	3 (−0.7)	7 (−0.6)
Over 2 m	8 (−5.0)	20 (−0.2)	18 (+3.2)	29 (+3.1)
Position in the plant (Chi$^2_9$ = 9.90, N.S.)				
Top	14 (+1.3)	11 (+0.7)	2 (−1.2)	5 (−1.2)
Outer	40 (−0.2)	40 (+1.2)	15 (−0.4)	27 (−0.7)
Inner	21 (+0.1)	12 (−2.0)	10 (+0.8)	19 (+1.4)
Basal	4 (−1.3)	6 (+0.1)	4 (+0.9)	6 (+0.6)
MV	0	0	0	4
Structure explored (Chi$^2_9$ = 16.45, N.S.)				
MV, Ground	6 (−0.0)	6 (+0.2)	0 (−1.7)	7 (+1.1)
Leaf	17 (−0.3)	22 (+1.8)	4 (−1.5)	13 (−0.5)
Twig	44 (+1.1)	36 (−0.4)	19 (+1.1)	27 (−1.6)
S. branch	7 (−1.3)	5 (−1.9)	7 (+1.6)	13 (+2.1)
Branch	3	0	1	1
Flower	2	0	0	0
Total	79	69	31	61

TABLE 7. Statistical significance for Chi^2 tests on contingency tables for each habitat features used for foraging by the four warblers in the three matorral types studied on Spargi (Plots 1 to 3), on Spargi overall and in Scandola overall. *** = P<0.001; * = P<0.5; N.S. = non-significant. Numbers between parentheses refer to sample size. For Plot 1 to Plot 3 see Table 1. SSAR, Marmora's warbler; SCAN, Subalpine warbler.

Plot	Plant	Height	Position	Structure
Plot 1 Spargi	***	***	***	***
(SCAN excluded)	(659)	(699)	(678)	(614)
Plot 2 Spargi	***	N.S.	*	N.S.
	(130)	(175)	(171)	(134)
Plot 3 Spargi	***	***	N.S.	N.S.
(SSAR excluded)	(242)	(242)	(238)	(229)
All plots Spargi	***	***	***	***
	(1082)	(1137)	(1134)	(1002)
Scandola	***	***	N.S.	*
	(223)	(240)	(236)	(214)

Evidence of direct interspecific interaction and of spatial segregation

Direct interspecific interactions

We recorded 132 songs and 437 alarm calls in the quadrats. Only forty-four of these behaviours were followed by an answer from a nearby individual; twenty of those forty-four events involved two different species with the Sardinian warbler always being one of the two.

We observed only nine direct antagonistic interactions between individuals. In all cases the Sardinian warbler was the aggressor. The Sardinian was the attacked species in two instances, the Marmora's in another two, the Dartford in three and the Subalpine in two.

Interspecific spatial segregation

Interspecific interactions in the control of space can be investigated by mapping song and alarm perching sites in order to look for possible patterns of spatial segregation between species (Fig. 2). Perching sites used for singing and alarming by the two species commonly observed in plot 1 overlapped spacially. These sites usually correspond to prominent shrubs on top of which the birds perch. In fourteen instances the same vantage points were used by the different species (Fig. 2). We did not observe any aggressive reactions from the other users of these perches. This result can be generalized to plots 2 and 3.

There was a large interspecific overlap in the spatial use of the habitat patches while foraging. In plot 1 (Fig. 3) Dartford warblers, less common, were only observed in the southern half of the plot (left half on Fig. 3). Marmora's and Sardinian warblers overlapped extensively. No pattern of spatial segregation seemed to take place. In plot 2 the greatest overlap was observed in the areas where vegetation heterogeneity was highest. Overlap was lowest where the vegetation was homogeneous. For instance, Marmora's warblers were most common in areas uniformly covered with *Cistus monspeliensis.*

DISCUSSION

The vegetation landscape in Mediterranean shrublands is often a mosaic of matorral patches. These patches, which we define as portions of the landscape with uniform canopy height, differ in vegetation structure and in plant species composition. Patches can be of various size. In our two study sites, for instance, we estimate the average patch size to be 0.5 ha on the island of Spargi (Sardinia) and 0.25 ha in the Scandola Nature Reserve (Corsica). The home range of foraging Sylvia warblers certainly exceeds one or two hectares (see Glutz von Blotzheim & Bauer, 1991 for a review of territory size in Sylvia warblers). As a consequence each individual bird has theoretically access, within its home range, to all the types of matorral patches present in the landscape.

As suggested by Haila & Hanski (1987) the choice of the proper scale in studies of habitat segregation by congeners is primordial. Sympatry at a coarse habitat scale, such as the matorral, does not necessarily mean sympatry at the patch scale. Similarly, spatial overlap at the patch scale does not necessarily mean that the habitat is exploited in the same way by different species. Nor does interspecific spatial segregation necessarily warrant that direct interaction is the mechanism involved (contrary to the assumption of Cody & Walter, 1976, see below).

Patch selection, overlap, ecological segregation and island-mainland niche shifts

At the scale of the matorral mosaic the four warblers appeared sympatric. But each species forages more frequently in certain matorral patches than in others, independently of the grain of the landscape (coarser on Spargi, finer on Scandola).

The interspecific differences we observed in patch selection are generally consistent with previous documentations of the ecological preferences of Mediterranean warblers (Cody & Walter, 1976; Martin & Thibault, 1983 for the same species assemblage; Zbinden & Blondel, 1981 for a slightly different assemblage; see also Prodon & Lebreton, 1981; Blondel, 1985; Lebreton *et al.*, 1988; Walter, 1988; Glutz von Blotzheim & Bauer, 1991; and Bibby & Tubbs, 1975 for the Dartford warbler outside the Mediterranean). Marmora's and Subalpine warblers show a marked preference for the lower and higher extremes respectively of the matorral vegetation height. Patch selection is less strict for Dartford warblers and Sardinian warblers (Table 6). The Sardinian warbler seems to be the most generalist species in terms of matorral patch selection whereas the Dartford warbler tends to be most abundant in matorral patches of medium height or above (significant residuals in Table 5).

Differences in patch selection appear, however, for the Dartford and Sardinian warblers when our results are compared to those obtained on the Mediterranean mainland by Zbinden & Blondel (1981), Martin (1982) and Blondel (1985). On the mainland the Marmora's warbler is missing and the Dartford warbler is most abundant in the lower matorral in a way similar to the distribution of the Marmora's warblers on Corsica (Berthold & Berthold, 1973; Zbinden & Blondel, 1981; Martin & Thibault, 1983). Difference in habitat selection between the islands and the mainland also occurs for the Sardinian warbler. On the mainland the Sardinian warbler selects vegetation heights which are intermediate between those selected by Dartford and Subalpine warblers (see Zbinden & Blondel, 1981; Martin, 1982; Blondel, 1985; Walter, 1988; and Glutz von Blotzheim & Bauer, 1991 for a general discussion on Sylvia warbler comparison). On Corsica and on Sardinia the Sardinian warbler uses lower habitats than it does on the mainland, but in these lower habitats it forages on the few shrubs that stick out of the vegetation's canopy (*Juniperus phoenicea* in plots 1 and 3, *Arbutus unedo* in plot 2 on Spargi, *Olea europaea* and *Pistacia lentiscus* in Scandola).

Whether the habitat shifts of the Dartford and the Sardinian warbler between the islands and the mainland have to be analysed as the result of released diffuse competition or as reflecting ecological differences between mainland and insular matorral (such as differences in plant

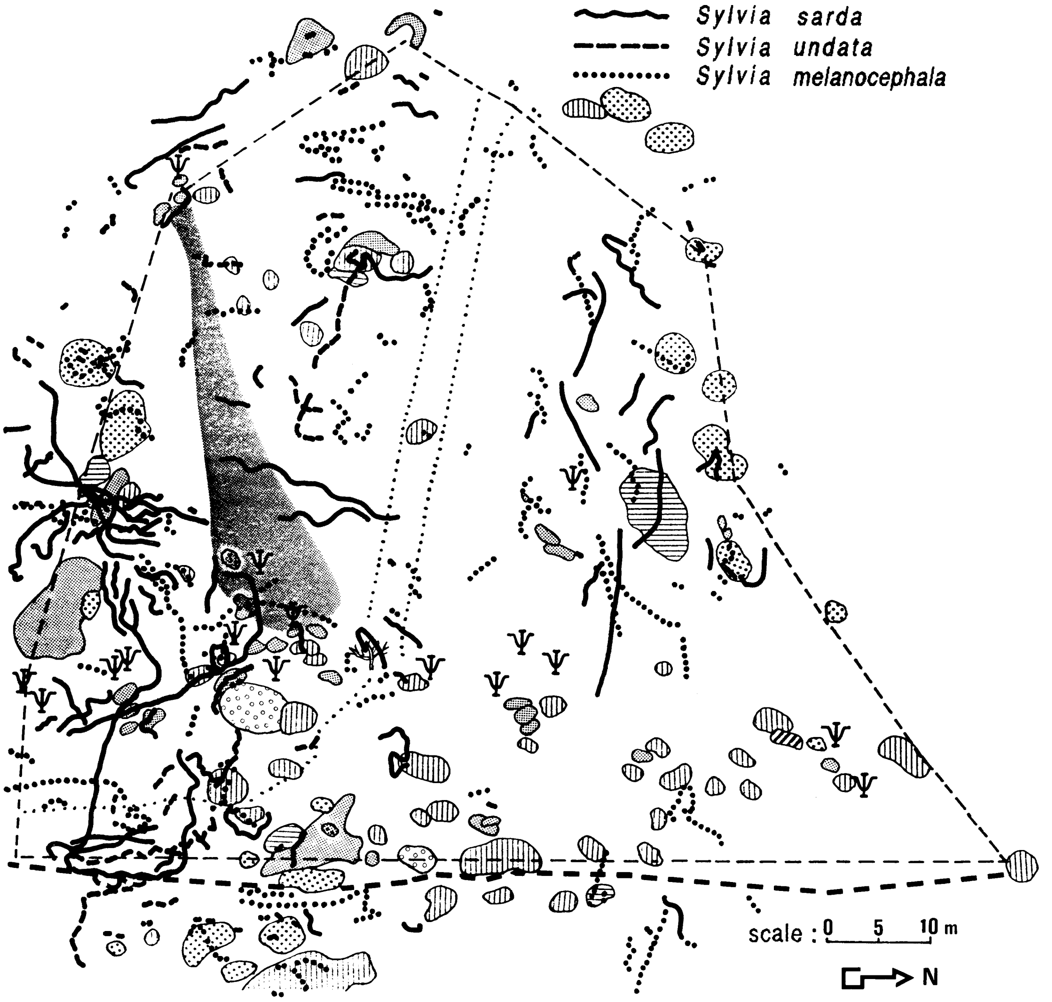

FIG. 3. Sketch map showing the segments of foraging movements that could be recorded during the period of study within plot 1 on Spargi (see Fig. 2 for description of the vegetation). Movements for each of the three main species are shown by a different symbol (see Fig. 2). The figure illustrates the extent of overlap of the three species and the difficulty to use such data to document home ranges and territories with unmarked birds (compare to Fig. 5 in Cody & Walter, 1976).

species composition in the lower vegetation layers) remains an open question.

Similarly to what we observe for patch selection, overlap exists, at first sight, in the use of micro-habitat features by the four warblers. For some micro-habitat features all four species have their highest absolute observation value for the same category (such as plant species used for foraging, position in the plant or structure explored). But the species differ in their relative use of the categories (differences in residuals on Tables 5 and 6). These differences are statistically significant and are most remarkable between the two species that are morphologically and ecologically closest the Marmora's and the Dartford warbler.

Evidence of interspecific territoriality?

In opposition to Cody & Walter's (1976) results neither the spatial distribution of the birds we observed in the plots on Spargi nor their song or alarm interactions support the idea of interspecific territoriality in Mediterranean warblers. Direct interspecific conflicts were rare events and all involved the larger and more generalist Sardinian warbler. Gomendy (1990) also could not find any evidence of interspecific territoriality in the study of a 7 ha matorral plot situated in northern Corsica. The four warblers we studied did occur within this plot. The Subalpine warbler was restricted to the section of the plot with highest vegetation but the three other species did overlap extensively. The Sardinian warbler used the small portion of the plot used by the Subalpine warbler whereas the Marmora's warbler was the only species found in the portions of the plot where vegetation was lowest. Similar results were obtained by Lovaty (1992) who monitored during an entire breeding season a 2.8 ha quadrat of matorral on Corsica. Three pairs of Marmora's warbler coexisted in the plot together with two pairs of Sardinian warbler and one pair plus a single male of Dartford warbler. Lovaty did not observe direct interspecific conflict. He found, as we did, that males of different species used the same perches for singing even when these perches were situated near another species' nest. Interspecific territory overlap was inconsistent with the hypothesis of interspecific territoriality. Zbinden & Blondel (1981) also found no evidence of interspecific territoriality in their study of habitat selection in a slightly different warbler species assemblage on the French mainland. Their assemblage included Dartford, Sardinian, Subalpine and Orphean warbler *S. hortensis*. They monitored song activity year round and did not find any evidence in the sedentary species (Dartford and Sardinian warblers) for mechanisms of interspecific interactions that would take place outside the breeding season.

The conclusions of Cody & Walter (1976) were based on complex numerical analysis of overlap between 'territories'. They should be treated with caution (see Wiens, 1989, p. 349). Indeed, their statistically significant 'non-random spatial overlap' may result from differences in the responses to the micro-habitat (micro-habitat selection) rather than from active interspecific avoidance. Their approach cannot discriminate between the two interpretations. Moreover they gave only scant information on the validity of the territory maps they drew in their Fig. 5 (Cody & Walter, 1976). These maps were based on the movements of birds that were not individually marked. From our own experience it seems difficult to distinguish between different individuals within a species over a period of weeks without marking the birds individually.

Interspecific segregation among Mediterranean warblers living in the same habitat, therefore, seems to be ecological rather than territorial (competition for space). It can be defined as the addition, at different scales, of slight differences in habitat patch selection and in foraging behaviour.

Such patterns of habitat selection and the shifts in habitat selection observed for two of the three species that use the lower matorral patches (Dartford and Sardinian warblers) when a third species, the Marmora's warbler, is missing, recall the patterns of habitat selection and niche shifts that have been documented for congeners of the genus *Parus* in the woodlands of the Western Palearctic (Gibb, 1954; Lack, 1971; Perrins, 1979). Both direct and exploitation competition have been proposed as the mechanism explaining species coexistence or niche shifts in tits when assemblage composition changed (Herrera, 1978, 1981; Alatalo, 1981, 1982; Alatalo *et al.*, 1987; Alatalo & Gustavsson, 1988; Laurent, 1986; Oksanen, 1987), whereas interspecific territoriality has not been documented for these species.

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REFERENCES

Alatalo, R.V. (1981) Interspecific competition in tits *Parus* spp and the goldcrest *Regulus regulus*: foraging shifts in multispecific flocks. *Oikos*, **37**, 335–344.

Alatalo, R.V. (1982) Evidence for interspecific competition among European tits *Parus* spp: a review. *Ann. Zool. Fennici*, **19**, 309–317.

Alatalo, R.V., Eriksson, D., Gustavsson, L. & Larsson, K. (1987) Exploitation competition influences the use of foraging sites by tits: experimental evidence. *Ecology*, **68**, 284–290.

Alatalo, R.V. & Gustafsson, L. (1988) Genetic component of morphological differentiation in coal tits under competitive release. *Evolution*, **42**, 200–203.

Berthold, P. & Berthold, H. (1973) Zur Biologie von *Sylvia sarda balearica* und *Sylvia melanocephala*. *J. Ornithol.* **114**, 79–95.

Blondel, J. (1985) Habitat selection in island birds. *Habitat selection in birds* (ed. by M.L. Cody), pp. 477–511. Academic Press, New York.

Bibby, C.J. & Tubbs, C.R. (1975) Status, habitats and conservation of the Dartford Warbler in England. *Brit. Birds*, **68**, 177–195.

Catchpole, C. (1977) Aggressive responses of male sedge Warbler to play-back of species song and sympatric species song, before and after pairing. *Anim. Behav.* **25**, 489–496.

Catchpole, C. (1978) Interspecific territorialism and competition in *Acrocephalus* Warblers as revealed by play-back experiments in areas of sympatry and allopatry. *Anim. Behav.* **26**, 1072–1080.

Cody, M.L. (1978) Habitat selection and interspecific territoriality among the sylviid Warblers of England and Sweden. *Ecol. Monogr.* **48**, 351–396.

Cody, M.L. (1981) Habitat selection in birds: the role of vegetation structure, competitors and productivity. *Bioscience*, **31**, 107–113.

Cody, M.L. (1985) *Habitat selection in birds*. Academic Press, London.

Cody, M.L. & Walter, H. (1976) Habitat selection and interspecific interactions among Mediterranean sylviid Warblers. *Oikos*, **27**, 210–238.

Diesselhorst, G. (1971) Zur Ökologie von Samtkopfgrasmücke (*Sylvia melanocephala*) und Sardengrasmücke (*Sylvia sarda*) im September in Sardinien. *J. Ornithol.* **112**, 131–137.

Everitt, B.S. (1977) *The analysis of contingency tables*. Chapman and Hall, London.

Ferry, C. & Deschaintre, A. (1974) Le chant signal interspecifique chez *Hippolais icterina* et *polyglotta*. *Alauda*, **42**, 289–311.

Géroudet, P. (1954) *Les passereaux*, vol. II. Delachaux and Niestlé, Neuchatel, Paris.

Gibb, J. (1954) Feeding ecology of tits, with notes on Treecreeper and Goldcrest. *Ibis*, **96**, 513–543.

Glutz von Blotzheim, U.N. & Bauer, K.M. (1991) *Handbuch der Vögel Mitteleuropas*, vol. 12/II. Aula Verlag, Wiesbaden.

Gomendy, V. (1990) *Etude de la recolonisation d'un maquis brûlé par l'avifaune nicheuse en Corse*. Mémoire MST, Université P. Paoli, Corté.

Haberman, S.J. (1973) The analysis of residuals in cross classified tables. *Biometrics*, **29**, 205–220.

Haila, Y. & Hanski, I.K. (1987) Habitat and territory overlap of breeding passerines in the mosaic environment of small islands in the Baltic. *Ornis Fennica*, **64**, 37–49.

Hartley, P.H. (1953) An ecological study of the feeding habits of the English titmice. *J. anim. Ecol.* **22**, 263–288.

Henry, C. (1979) Le concept de niche écologique illustré par le cas de populations congénériques sympatriques du genre Acrocephalus. *Revue d'Ecol. (Terre et Vie)* **33**, 457–492.

Herrera, C.M. (1978) Niche shifts in the genus Parus in southern Spain. *Ibis*, **120**, 236–240.

Herrera, C.M. (1981) Combination rules among western European Parus species. *Ornis Scand.* **12**, 140–147.

Lack, D. (1971) *Ecological isolation in birds.* Blackwell Scientific Publications, Oxford.

Laurent, J.-L. (1986) Winter foraging behaviour and resource availability for a guild of insectivorous gleaning birds in a southern alpine larch forest. *Ornis Scand.* **17**, 347–355.

Lebreton, J.-D., Chessel, D., Prodon, R. & Yoccoz, N. (1988) L'analyse des relations espèces-milieu par l'analyse canonique des correspondances. *Acta Oecol. Oecol. Generalis*, **9**, 53–67.

Leisler, B. (1981) Die Ökologische Einnischung der mitteleuropäischen Rohrsänger. I. Habitattrennung. *Vogelwarte*, **31**, 45–74.

Leisler, B. & Winkler, H. (1985) Ecomorphology. *Current ornithology*, **2**, 155–186.

Lemaire, F. (1977) Mixed song, interspecific competition and hybridation in the Reed and Marsh Warblers. *Behaviour*, **63**, 215–240.

Lovaty, F. (1992) Observations sur le comportement territorial et vocal de la Fauvette sarde (*Sylvia sarda*) durant le cycle de reproduction. *Nos oiseaux*, **41**, 463–487.

Martin, J.-L. (1982) Insularité: l'infiltration des oiseaux forestiers dans les milieux buissonnants de Corse. *Revue d'Ecol. (Terre et Vie)* **36**, 397–419.

Martin, J.-L. & Thibault, J.-C. (1983) Les oiseaux de la Réserve Naturelle de Scandola (Corse). Inventaire et Structure des Peuplements. *Bull. Ecol.* **14**, 279–296.

Morrison, M.L. (1984) Influence of sample size and sampling design on analysis of avian foraging behaviour. *The Condor*, **86**, 146–150.

Oksanen, L. (1987) Interspecific competition and the structure of bird guilds in boreal Europe: the importance of doing fieldwork in the right season. *TREE*, **2**, 376–379.

Perrins, C. (1979) *British tits.* Collins, London.

Prodon, R. & Lebreton, J.-D. (1981) Breeding avifauna of a Mediterranean succession: the holm oak series in the eastern Pyrénées; I. Analysis and modelling of the structure gradient. *Oikos*, **37**, 21–38.

Svensson, S.E. (1978) Territorial exclusion of *Acrocephalus schoenobaenus* by *A. scirpaceus* in reed-beds. *Oikos*, **30**, 467–474.

Walter, H. (1988) Temporal and spatial dynamics of Sylvia Warblers in the Tyrrhenis. *Bull. Ecol.* **19**, 375–402.

Wiens, J.A. (1989) *The ecology of bird communities*, vol. 1. Cambridge University Press, Cambridge.

Zbinden, N. & Blondel, J. (1981) Zu Raumnutzung, Territorialität und Legebeginn mediterraner Grasmücken (*Sylvia melanocephala*, *S. sarda*, *S. cantillans*, *S. hortensis*) in Südfrankreich. *Der Ornithol. Beobach.* **78**, 217–231.