Habitat and territory overlap of breeding passerines in the mosaic environment of small islands in the Baltic

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We studied habitat relationships of the 17 most abundant breeding passerines on three different islands (7, 14, 38 ha) and a study plot (16 ha) on a 580 ha island in the Vargskär archipelago on the Åland Islands, SW Finland. Habitats of the plots were described by the 0.04 ha circle areal method, and birds were censused by territory mapping. Habitat space was analyzed by the principal component analysis, and habitat spectra of individual species were assessed using circles that coincided with their territories. The latter were highly variable because of the extreme horizontal mosaic-likeness of habitats, and the spectra of different species showed a great extent of overlap. However, coarse "niche-gestalts" of individual species could be identified, presumably as basic responses to environmental configuration by the species. A group of scrubland birds (*Sylvia* warblers) was thus largely segregated from birds of wooded habitats. On a two-dimensional map, territories of most of the species overlap because of the mosaic-like heterogeneity of habitat configurations. We particularly followed territory structure and movements of *Sylvia* warblers and found considerable overlap among their territories. In our area they are not interspecifically territorial. The high degree of spatial overlap observed on the islands is due to the exceptional mosaic-likeness of the environment. We suggest that in such an area birds actually establish territories that comprise spatially discrete patches. This may be true, but difficult to observe, in more continuous habitats as well.

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Introduction

Habitat selection is a major factor influencing the success of land birds in colonizing small islands in northern conditions. Census data from the Åland archipelago and from similar habitats on the mainland of Åland show that population sizes of most species on these islands match expectations derived from mainland data (see Haila 1983, Haila & Järvinen 1983, Haila et al. 1983, Järvinen & Haila 1984). This demonstrates the overriding importance of habitat structure in the composition of local bird assemblages — the pattern was documented on the mainland of Åland by Palmgren (1930).

However, there are differences in habitat microstructure on the islands and the mainland of Åland that affect bird communities as well. For instance, Haila & Järvinen (1983) and Järvinen & Haila (1984) analyzed causes of faunal impoverishment on Ulversö, a 6 km^2 island, compared with the mainland of Åland. 53 species occurring on the mainland are absent from Ulversö. Most absences are attributable to rarity and the authors concluded that 26 (48%) of the species would be unable to breed on Ulversö because of the lack of suitable habitats.

In this paper we investigate habitat relationships of forest passerines on small islands in the Åland archipelago. A conspicuous characteristic of the island landscapes is their small-scale, mosaic-like variation (Haila 1983, Haila & Järvinen 1983). A major problem in studying bird-habitat relationships in such an environment is collecting the data in an adequate scale. Habitat variation consists of two main components: (1) *Within-site* structural complexity in the characteristics of a given habitat, and (2) *between-site* heterogeneity that is due to varying proportions and configurations of different habitats. The second component is pronounced in our study area.

The prevailing method of analyzing bird-habitat relationships is to relate the presence or absence of bird species to various habitat measurements (see James 1971, Smith 1977, Capen 1981, Collins et al. 1982, James & Wamer 1982, Rice et al. 1983, Verner et al. 1986). Habitat characteristics that are quantified usually describe only within-site variation (for an important exception, see Roth 1976). Consequently, such studies implicitly assume that habitat types are distributed in homogeneous, continuous patches, relative to bird territories. On small islands in the Åland archipelago this is certainly not true. The area of a typical habitat patch is from 0.02 to 0.05 ha. This contrasts with the average territory size of a breeding passerine, which is about one ha.

Assessing bird-habitat realtionships in the mosaic landscape of the Åland islands presents two interesting problems. First, how selective are different species in their territory acquisition relative to the habitat space of the islands as a whole? Second, to what extent are different species spatially segregated from each other in this mosaic environment?

Materials and methods

The study was made in the Vargskär archipelago, northern Föglö (ca. 60°N, 20°E), described in detail by Haila (1983). Four study plots, three of them comprising whole islands, were established and marked with coordinates: (1) Foderholmen, 7 ha; (2) Gåsholmen, 14 ha; (3) Bockholm, 38 ha; and (4) a study plot of 16 ha on Ulversö, the largest island (580 ha) in the archipelago. Bockholm in the following analyses is divided into two, Bockholm-W — 22 ha, and Bockholm-E — 16 ha, because of the pronounced difference in habitat structure on the two halves of the island.

We censused the breeding birds of the study plots using the territory mapping method (Anon. 1970) between 23 May and 1 July, 1983, with 5–7 mapping visits to each of the areas. We directed particular attention to following the movements of individual singing males in order to ascertain the location of their territories. Most parts of the study plots were thus visited several times during each census. We also made additional observations on the foraging behaviour and territory use of warblers (both *Phylloscopus* and *Sylvia*) in order to assess their interspecific relationships. Approximately 40 hours were spent in following the behaviour of individual males.

Consequently we gained a more detailed picture of the location of individual Sylviid territories in the study plots than the number of census visits would suggest. Each territory was outlined on maps of the study plots by drawing lines between observation points lying furthest from each other.

General features of the island habitats are described by Haila (1983) and Haila & Järvinen (1983). For making habitat measurements in the study plots we used the 0.04 ha circle areal method, suggested by James & Shugart (1970). The variables measured in each circle were (1) number of trees (two size categories, three groups of species); (2) number of saplings along two 1.5 m wide diagonals of the circle (coniferous and deciduous distinguished); (3) the coverage of main vegetation elements in the field layer, estimated on a logarithmic scale running from 0 to 5 (six vegetation types); (4) foliage height in meters; (5) foliage cover (%), estimated by 20 vertical point-sightings within each circle; (6) horizontal denseness, by recording the visibility of a three-meter stick (logarithmic scale from 0 to 5), erected in the middle of the circle, from four points on the circumference, and (7) the number of major habitat types (see Haila 1983) within the circle. The latter typically numbered two or three which gives an indication of the small "grain-size" of pure habitat patches on the islands. All percentage measurements were transformed to $\log_{10}((x+1)/(101-x))$ (James & Warner 1982).

We placed randomly the circles in the study plots as follows: Foderholmen, 28 circles; Gåsholmen, 35 circles; Bockholm-E, 40 circles; Bockholm-W, 63 circles; and the Ulversö plot, 40 circles. Descriptions are from late June to early August, 1983.

Table 1. The 17 species included in the analysis, the number of pairs of the species in the study plots, and the number of habitat circles within their territories. Included, also, is the total number of pairs (all species) in the plots. Abbreviations of the plot names: Fh=Foderholmen, Gh=Gåsholmen, Bh-E=Bockholm-E, Bh-W=Bockholm-W, Ulv=Ulversö.

	Fh	Gh	Bh-E	Bh-W	Ulv	circle
Area (ha)	(7)	(14)	(16)	(22)	(16)	
Anthus trivialis	1	2	2	1	5	12
Prunella modularis	3	1	3	2	0	17
Erithacus rubecula	1	0	3	2	5	14
Luscinia luscinia	2	1	1	7	1	14
Turdus merula	2	3	1	3	3	21
T. iliacus	1	3	1	5	3	20
Sylvia nisoria	0	0	1	4	0	11
S. curruca	2	3	2	4	3	24
S. communis	2	1	0	9	5	30
S. borin	3	1	4	9	9	34
Phyllosc. trochilus	2	5	3	4	10	53
Regulus regulus	0	1	3	1	0	15
Muscicapa striata	2	2	3	2	3	26
Parus montanus	2	1	2	3	3	31
P. major	1	1	1	3	4	11
Fringilla coelebs	15	19	23	25	21	117
Emberiza citrinella	1	0	1	8	10	16
All species	44	55	66	106	117	

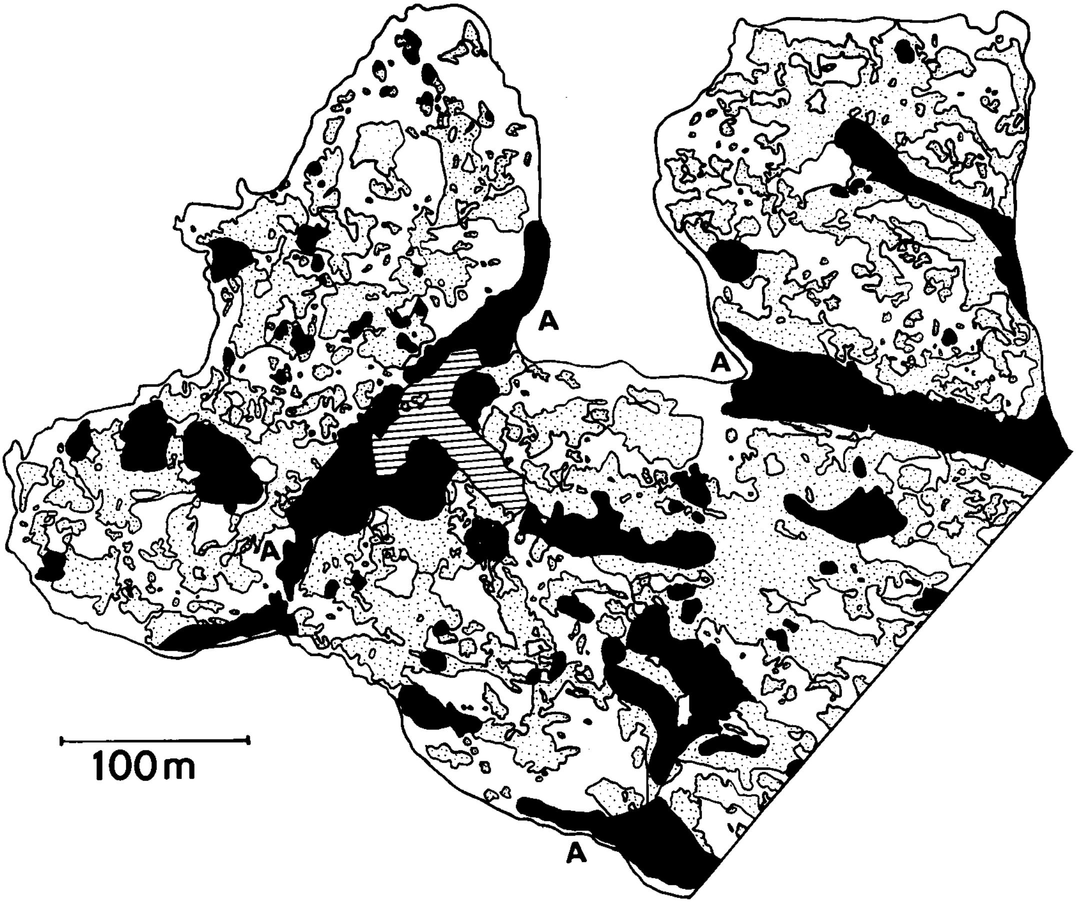

Fig. 1. A map of Bockholm-W, showing the configuration of patches of different habitats and open cliffs (indicated by the white areas). Low scrublands (shaded areas), mainly of *Juniperus* but mixed with deciduous bushes such as *Rosa, Crategus* and *Prunus*, dominate. The blackened areas refer to high (>10 m) vegetation, the four A's indicating continuous *Alnus glutinosa* stands, the rest being heterogeneous pine, birch and alder stands. The hatched area is a meadow.

The average number of circles was 2.5/ha, but on Foderholmen and Bockholm-W the number was increased. Thus the efficiency of the method in providing a satisfactory picture of the overall habitat variation on the islands could be evaluated. In Fig. 1 we show the location of different habitat types on Bockholm-W.

For assessing bird-habitat relationships in the study plots we determined the coincidence of individual territories and habitat description circles. Primary data used in the analysis thus comprises a matrix with 206 habitat description circles as rows and 17 bird species with at least ten description circles in their territories as columns, and each entry in the matrix indicates whether a circle fell within a territory of a species. The species, the number of pairs of the species in the study plots, and the number of habitat description circles within their territories are given in Table 1.

We investigated the structure of the study plots' "habitat space" using the principal component analysis (PCA) of the BMDP statistical package. By using the PCA it is possible (1) to reduce the number of variables that characterize overall variation to a smaller number of linear-combination variables; and (2) to ordinate original data points in the new PCA-space. We used the PCA in an explorative fashion, namely in trying to summarize main gradients in habitat space by the PCA-axes. Therefore, no significance levels will be attached to principal components. Components are used only as a descriptive aid. We excluded from the models variables showing a very pronounced deviation from normal or which were strongly correlated with each other. Several combinations of the original variables gave qualitatively similar results.

We analyzed interspecific differences in habitat selection patterns by making comparisons pairwise between habitat spectra of individual species, using the stepwise discriminant analysis in an exploratory manner to investigate the degree of separation in different species and to identify which environmental factors most consistently differ in their pairwise comparisons (see Williams 1981, Rice et al. 1983). The stepwise version of the discriminant analysis directly indicates the relative importance of different original variables by the order in which they are incorporated into the discriminant model. Statistical significance can be evaluated by conducting one-way analysis of variance at each step, and by evaluating the proportion of correct classifications of single observation points among the groups. In most of the comparisons the species co-occurred in some habitat circles. These "common circles" were used as a third group in the comparisons.

The habitat space

The PCA-model (with axis rotation) used in the following analyses is presented in Table 2. The three first axes of the PCA-ordination can be interpreted as follows:

1) PC I indicates a trend toward dense undergrowth and has a high positive correlation with the number of saplings and horizontal denseness, and a negative correlation with bare bedrock.

2) PC II has a high positive correlation with the number of large trees and foliage cover, and a negative correlation with bare bedrock.

3) PC III is related to the proportion of conifers (pine in the tree layer and juniper in the bush layer) among trees and saplings.

Table 2. The principal component model (with axis rotation) of the habitat space of the study plots used in the analyses. The model is based on a correlation matrix.

Variable included in the model	Correlation with principal component I	II	III
Coverage of open cliff on the ground	–0.68	–0.44	0.30
Coverage of herbs in the ground layer	0.48	0.11	–0.62
Canopy height (m)	0.33	0.82	–0.08
Number of large trees	0.11	0.90	0.08
Number of saplings	0.84	0.12	–0.08
Prop. of junipers among the bushes	0.21	–0.05	0.85
Prop. of pine among trees and saplings	–0.43	0.28	0.54
Horizontal denseness of the habitat	0.84	0.30	0.13
Eigenvalue of the factor	2.45	1.87	1.51

The habitat structure of each study plot is characterized by mosaic-like horizontal heterogeneity (see Fig. 1), but they nevertheless differ from each other. The plots are compared with each other in Table 3 using factor scores of the three PCA axes as criteria (we also used values of the original variables, but they were largely redundant). There is a high degree of variation in the habitat structure of every study plot, and the plot means do not differ significantly from each other.

To test whether an average habitat circle in a study plot tends to deviate from the central point of the habitat space, we compared the position of the plot means with origo of the ordination. The origo is an approximation of the central point of habitat space, as factor scores are normally distributed along the PCA-axes. We used a point estimate of the origo, based on all 206 habitat circles, but the exact significance level is less interesting than the general trend of comparisons. The results are included in Table 3, and they can be summarized as follows:

1) Foderholmen is close to the average in the horizontal denseness of habitats and tree height, but has a slightly higher than average proportion of conifers, particularly in the bush layer (thick *Juniperus* undergrowth).

2) The habitats of Gåsholmen are horizontally open due to grazing by a few sheep and calves. Tree height and the proportion of conifers are close to the average.

3) Bockholm-E is clearly different from the other plots, being characterized by relatively tall trees and a very high proportion of conifers.

4) Bockholm-W mainly includes open, bushy habitats, due to grazing by sheep. Horizontal denseness is close to the average, but trees are low and the proportion of conifers is low.

5) The Ulversö study plot has dense habitats, mainly consisting of deciduous trees and saplings. Tree height is close to the average. Variation within the plot is very high, however, caused by several outcrops of bare bedrock with small patches of rocky pine forest, the dense deciduous tree stands being in depressions among them.

Table 3. Location of the habitat circle means of the study plots along the three PCA axes. The means were compared with the origo of ordination (t-test, two-tailed); test results are included.

	Fact 1			Fact 2			Fact 3		
	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
Foderholmen	0.11	0.72	0.14 ns	0.01	1.07	0.20 ns	0.43	1.01	0.19*
Gåsholmen	–0.41	0.93	0.16*	0.05	0.94	0.16 ns	0.08	1.04	0.18 ns
Bockholm-E	–0.25	0.87	0.14 ns	0.32	0.96	0.15*	0.52	0.68	0.11**
Bockholm-W	0.07	0.97	0.12 ns	–0.31	0.95	0.12*	–0.30	0.90	0.11*
Ulversö	0.48	1.22	0.19*	0.12	1.02	0.16 ns	–0.42	1.06	0.17**

Table 4. Habitat spectra of the 17 species on the PCA axes, with comparisons of the means with the ordination origo (t-test, two-tailed).

	Fact 1			Fact 2			Fact 3		
	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
Anthus trivialis	–0.26	0.71	0.20 ns	0.13	1.01	0.29 ns	0.27	0.85	0.24 ns
Prunella modularis	–0.11	0.76	0.18 ns	0.04	0.84	0.20 ns	0.04	1.10	0.27 ns
Erithacus rubecula	0.39	0.78	0.21 ns	0.22	0.77	0.21 ns	0.12	0.76	0.20 ns
Luscinia luscinia	0.15	0.95	0.26 ns	–0.14	0.81	0.22 ns	–0.37	0.96	0.27 ns
Turdus merula	0.12	0.75	0.16 ns	0.46	0.94	0.21*	0.28	0.87	0.19 ns
T. iliacus	0.20	0.84	0.18 ns	0.17	0.93	0.21 ns	0.22	1.04	0.23 ns
Sylvia nisoria	0.76	0.89	0.27*	–0.26	0.77	0.23 ns	–0.82	1.22	0.37*
S. curruca	0.14	1.05	0.21 ns	–0.29	0.64	0.13*	–0.03	1.16	0.24 ns
S. communis	0.06	0.83	0.15 ns	–0.48	0.93	0.17**	–0.36	0.95	0.17*
S. borin	0.75	1.05	0.18***	0.27	0.99	0.17 ns	–0.68	0.94	0.16**
Phylloscopus trochilus	0.09	0.79	0.11 ns	0.44	1.02	0.14**	0.04	0.81	0.11 ns
Regulus regulus	–0.24	0.61	0.16 ns	0.87	1.34	0.34*	0.08	0.35	0.09 ns
Muscicapa striata	0.08	1.03	0.20 ns	0.47	1.24	0.24 ns	0.12	1.03	0.20 ns
Parus montanus	–0.10	0.87	0.16 ns	0.34	1.14	0.20 ns	0.44	0.76	0.14**
P. major	0.04	0.85	0.26 ns	0.62	1.24	0.37 ns	–0.18	1.11	0.33 ns
Fringilla coelebs	0.20	1.01	0.09*	0.12	1.01	0.09 ns	–0.04	0.97	0.09 ns
Emberiza citrinella	–0.31	0.95	0.24 ns	0.14	1.12	0.28 ns	–0.19	1.13	0.28 ns

Preferences of individual species

We included in the analysis 17 species with more than 10 habitat description circles falling within their territories (Table 1). The circles coinciding with the territories of individual species describe their habitat spectra. First we compared the habitat spectrum of each species with overall habitat space, using factor scores on the three PCA-axes as criteria. The comparison is summarized in Table 4.

The habitat spectrum of every species is very widely dispersed in the habitat space, as is indicated by the high standard deviations (note that in the PCA-space the standard deviations of factor scores are standardized to one). This is further demonstrated in Fig. 2 using territory locations of *Fringilla coelebs* on Foderholmen as an example. The territories of an abundant generalist such as *F. coelebs* cover practically all habitat types found on the island, but habitats within the territories of every species breeding on the islands are highly variable (there is no chance of finding "pure" habitats for a one hectare territory on Foderholmen!).

The heterogeneity of the habitat spectra compared with the overall habitat space means that it is not statistically feasible to compare occupied habitat points with unoccupied ones (Rice et al. 1983, Capen et al. 1986). Habitats used by individual species on the islands simply do not fall into neat groups easily distinguishable from those not used. We inspected closer the preferences of individual species by comparing the means of their habitat spectra with the origo. A difference indicates that an average habitat circle tends to deviate from the center of the habitat space. The results are included in Table 4, and they can be summarized as follows:

1) Three species show preferences along the first

Fig. 2. Location of the territories of *Fringilla coelebs* (territory boundaries indicated) relative to the habitat configurations of Foderholmen (white = open cliffs, shaded = *Juniperus* scrubland, blackened = high vegetation, which actually comprises a mosaic of alder, birch, oak and pine stands and single trees).

PCA-axis which characterizes the horizontal thickness of habitats. *Sylvia borin* tends to have dense habitats in its territories, and *S. nisoria* and *Fringilla coelebs* show a slightly similar trend.

2) The second PCA-axis, related to tree height and density of large trees, seems to summarize habitat features that are important to several species. *Turdus merula, Phylloscopus trochilus* and *Regulus regulus* tend to favour habitat stands with tall trees, and *Sylvia curruca* and *S. communis* tend to avoid them.

3) The means of a few species deviate from the origo along the third PCA-axis. *Sylvia borin* and *S. nisoria* avoid conifers, and *Parus montanus* tends to favour them.

These broad preferences of individual species ought to be reflected in their numbers in the different study plots as well. Densities of the species show great variation over the plots (data in Table 1). However, the samples are small and variation may be spurious. Using the G-test we compared the distribution of pairs of individual species in the study plots with the null hypothesis of an even distribution. Only two species showed significant deviations (*S. communis*, $P<0.05$, and *E. citrinella*, $P<0.01$).

Interspecific differences

Generalists such as *F. coelebs* cannot be statistically significantly separated from the other species, as is evident from Fig. 2. For pairwise comparisons we used species belonging to the two main foraging guilds found in the island communities, ground insectivores and foliage insectivores. It is among members of the same guild that interspecific comparisons are ecologically most informative (for guild identities, see Haila & Järvinen 1983). We used the three PCA factors as input variables.

Ground insectivores abundant enough in the study areas for meaningful comparisons include two thrushes (*Turdus merula* and *T. iliacus*) and four smaller species (*Anthus trivialis, Prunella modularis, Erithacus rubecula* and *Luscinia luscinia*). The two thrushes were compared, and so were the three small species of dense habitats (excluding *A. trivialis*, a species of open habitats). None of the comparisons revealed significant differences along any of the PCA axes.

Abundant foliage insectivores in the study areas include four *Sylvia*-warblers, *Phylloscopus trochilus, Regulus regulus* and *Parus montanus*. Pairwise comparisons are summarized in Table 5. They roughly constitute a continuum from scrubland species with no differences among each other (*S. nisoria, S. curruca* and *S. communis*) to species of wooded habitats and mutually similar habitat demands (*P. trochilus, R. regulus* and *P. montanus*). *S. borin* is an intermediate case, separated from almost all of the other species. *S. curruca* accepts more wooded habitats than the other scrubland species and occupies territories similar to those of *P. montanus* on the islands.

Table 5. Pairwise comparisons of habitat spectra of members of the foliage-gleaning guild (complete species names in Table 1) by the stepwise discriminant analysis. The significance of their mutual separation relative to the PCA axes (PC1, PC2 and PC3) was evaluated by ANOVA at each step; symbols: o = P>0.01, x = P<0.01, H = P<0.001.

	Syl nis			Syl cur			Syl com			Syl bor			Phy tro			Reg reg		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Syl cur	o	o	o															
Syl com	x	o	x	o	o	o												
Syl bor	o	o	o	o	o	H	x	H	o									
Phy tro	o	o	x	o	x	o	o	H	x	x	o	H						
Reg reg	H	o	o	o	H	o	o	H	o	H	o	o	o	o	o			
Par mon	x	o	H	o	o	o	o	H	H	x	o	H	o	o	o	o	o	o

The comparisons give a similar picture to Table 4. Broad preferences for different environmental types separate the species, but with considerable overlap. Tree height and foliage cover, related to the second PCA axis, seem to be the most important environmental characteristics segregating habitats of the species.

Sylvia warblers

We directed particular effort to observing the territory patterns and habitat use of *Sylvia* warblers as Cody (1978, 1985) argued that interspecific territoriality is a major factor affecting the site selection of *Sylvia* warblers in northern Europe.

For special study of the territory selection of *Sylvia* warblers we used two study areas where several species co-occurred: (1) Bockholm-W is dominated by open scrubland, with a few alder stands, separated by open cliffs (see Fig. 1). The *Sylvia* community of Bockholm-W comprised 26 pairs of four species. (2) The northern part of the Ulversö study plot consists of low but dense, mainly *Juniperus* thickets interrupted by small stands of deciduous trees. 13 pairs of *Sylvia* warblers belonging to four species occupied territories in an area of about 8 ha. The area is next to an open meadow.

We made visits to the two areas from 21 May through to 28 June, spending approximately 40 hours in 8 days in Bockholm-W, and 20 hours in 10 days in the Ulversö *Sylvia* area. Fig. 3 shows the

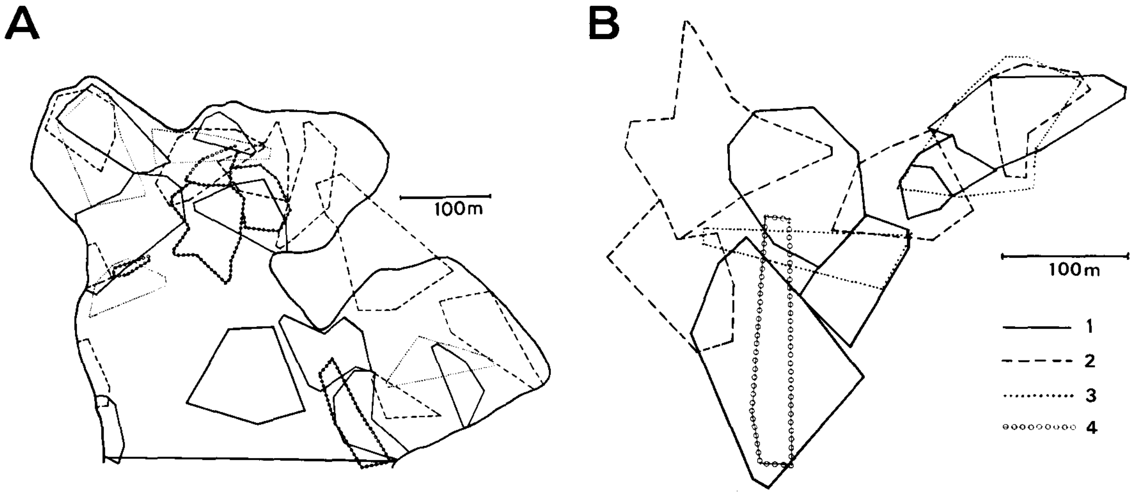

Fig. 3. Location of *Sylvia* territories relative to each other in the two areas of detailed territory mapping. (A) Bockholm-W; habitat configurations are shown in Fig. 1. (B) *Sylvia* area of the Ulversö plot; the area is bounded by an open meadow in the north and west, and by open cliffs in the south-east.

Table 6. One- and two-species combinations of the *Sylvia* warblers observed in the two areas of detailed territory mapping. See text and Fig. 3 for details.

	n	Alone	Overlap with				
			S nis	S cur	S com	S bor	S atr
Syl nis	4	0	–	0	2	3	0
Syl cur	6	2	0	–	3	4	0
Syl com	13	6	2	4	–	5	0
Syl bor	15	3	2	8	5	–	1
Syl atr	1	0	0	0	0	1	–

location of *Sylvia* territories in the areas relative to each other according to observations made on the movements of individual males. The territory borders are naturally unclear, but we directed particular effort to observing males in areas where territories of different species overlap. Vegetation patterns of Bockholm-W are shown in Fig. 1. Table 6 summarizes the types of one- or two-species combinations included in Fig. 3. As a two-species combination we interprete each case where more than a third of the area of a territory is covered by territories of another species.

The following three-species combinations occurred in the *Sylvia* areas: *S. curruca* (one territory) — *S. communis* (two territories) — *S. borin* (three territories) in a tangled configuration in Ulversö (Fig. 3B); *S. curruca* — *S. communis* — *S. borin* (one territory each) at two sites in Bockholm-W; and *S. nisoria* (two territories) — *S. communis* — *S. borin* in Bockholm-W (Fig. 3A).

These site selection patterns do not reveal any traces of interspecific territoriality. Observation data on the movements of warblers confirm the overlap. Different species were frequently observed in the same bushes and tree stands, sometimes simultaneously. We recorded three cases of interspecific aggressive behaviour (*S. curruca* — *S. communis; S. communis* — *S. borin*), but all of these occurred where there were short distances between birds that apparently found themselves too close to each other. It is hard to attach any deep ecological significance to these cases in terms of niche segregation. We also conducted playback experiments but with virtually no response from males of other species.

Cody (1978) explicitly names two pairs of *Sylvia* species that he suggests are interspecifically territorial: *borin* — *nisoria* and *communis* — *nisoria*; the pair *borin* — *curruca* is claimed to show "partial exclusion". It is hard to define unambiguous criteria for interspecific territoriality. Consequently, testing the claim is difficult (for discussions, see e.g. Murray 1971, 1976, Rice 1978). However, according to our data these species pairs are not interspecifically territorial (see Fig. 3 and Table 5).

Year-to-year variation

Year-to-year changes in territory location potentially confound territory selection patterns that look deterministic in a single year. Ornithologists often routinely assume that suitable habitats are saturated by breeding birds, but this is not necessarily the case (Wiens 1983, Enemar et al. 1984, James & Boecklen 1984, Capen et al. 1986). Cody (1978) concluded that *Sylvia atricapilla* and *S. curruca* were held back from suitable habitats at his study site because of the presence of other *Sylvia* warblers. Such a conclusion is totally unfounded as only a year's observational data was used. There is no way of knowing that any pairs ever tried to occupy the rest of the habitat deemed "suitable" by the ornithologist.

Ultimately this assumption should be tested by experiments (see Garcia 1983), but a simpler test, although not as accurate, can be made by comparing territory patterns in the same plots in different years. There may be stochastic year-to-year variation in the number of pairs and their territory locations within single plots (e.g., Danilov 1980, Rice 1981, Rice et al. 1983, Wiens 1983, Haila 1983, 1986, Svensson et al. 1984, Holmes et al. 1986, Rotenberry 1986). The existence of such variation would contradict the assumption of deterministic habitat saturation.

Two of the study islands, Gåsholmen and Bockholm, were censused by the mapping method in 1980 (Haila & Kuusela 1982). In addition, 6.4 km of line transects were censused in both 1980 and 1983, by Y. Haila, on Ulversö along identical routes. Census results of 1980 and 1983 are presented in Table 7.

Haila (1983) suggested that population sizes of different species on any single island in the Åland archipelago vary randomly around an expected size, determined by the regional abundance of the species and habitat composition of the island. It is expected that species number in a sample from the islands increase regularly whether sample size is increased in space, by censusing several similar islands in a single year, or in time, by censusing the same island in several years. Rarefaction curves based on data from similar islands can be used to predict how much the total species number, in the total sample, ought to increase when an island is censused in two years.

Table 7. The census results from Gåsholmen (Gh), Bockholm (Bh), and 6.4 km of line transects on Ulversö in 1980 and 1983. Number of territories and, for the line transects, total number of observations are given.

	Gh		Bh		Transect	
	80	83	80	83	80	83
Anthus trivialis	0	2	3	3	18	9
Motacilla alba	3	2	5	3	3	4
Prunella modularis	0	1	1	5	8	2
Erithacus rubecula	3	0	7	5	9	8
Luscinia luscinia	1	1	3	8	9	6
Oenanthe oenanthe	2	2	3	1	6	6
Turdus merula	3	3	9	4	29	15
T. philomelos	0	1	6	4	12	18
T. iliacus	4	3	5	6	12	18
Hippolais icterina	0	1	2	0	3	4
Sylvia curruca	2	3	3	6	7	6
S. communis	1	1	6	9	24	25
S. borin	1	1	12	13	26	28
Phyllosc. trochilus	3	5	9	7	40	42
Regulus regulus	1	1	1	4	7	6
Muscicapa striata	2	2	4	5	11	7
Parus montanus	3	1	5	5	11	4
P. caeruleus	1	1	2	0	7	1
P. major	0	1	1	4	12	6
Fringilla coelebs	20	19	58	48	80	108
Carduelis chloris	1	0	4	2	10	15
Emberiza citrinella	1	0	9	9	26	23
Total species	19	23	33	36		
"immigrations"		7		7		
"extinctions"		3		4		

Data from Gåsholmen and Bockholm present a test for this prediction. The expected net increase in species number in the pooled sample of two years compared with a data set from a single year is for Gåsholmen 6.2, and for Bockholm 7.8 (Haila 1983: 342). The observed figures were for Gåsholmen –3, +7 and for Bockholm –4, +7. The agreement is good.

We also compared population changes on the two islands with each other (data in Table 7). The direction of change was similar for 7 species, the opposite for 4 species, and the number of pairs stayed unchanged on one or both of the islands for 11 species. Figures show that changes in neighbouring local, small populations do not necessarily coincide, which agrees with the assumption of stochastic variation.

The mapping data of 1980 and 1983 also allow a comparison of the territory locations of individual species on the two islands. In the following tabulation we compare the territories of the four *Sylvia* warblers occurring on the two islands in 1980 with those in 1983. The mapping of territories was less detailed in 1980. We compared the original field notes of 1980 with the territories of 1983, and recorded a non-overlap only if all of the 1980 observations were outside of the 1983 territories.

Species	Number of pairs 1980		Overlapping with 1983	
	Gh	Bh	Gh	Bh
S. nisoria	–	1	–	1
S. curruca	2	3	2	1
S. communis	1	6	0	1
S. borin	1	12	1	11

The figures indicate that the territory locations vary a great deal from year to year. We discuss further the differences between the species in the Discussion.

Discussion

Overlap vs. segregation

Our results indicate a smaller degree of interspecific habitat segregation than has usually been reported. The pattern may be mainly due to the peculiar mosaic structure of the study area, but the overlap in space is not an artefact. For instance, the 44 territories of 19 species crowded into the seven hectares of available space on Foderholmen necessarily overlap. The mosaic structure of the habitats brings together species that in "pure" habitats would be unlikely to coexist (e.g., *Erithacus rubecula* and *Luscinia luscinia*, or *Sylvia curruca* and *Parus montanus*).

The result has implications concerning interpretations of interspecific differences in habitat selection patterns. Some authors (e.g., Anderson & Shugart 1974, Cody 1974, 1978, 1985) have regarded the distribution of species along habitat gradients as a form of resource partitioning. Such apparent segregation in space may, however, be due to the different environmental requirements of different species. When appropriate habitat elements occur together, "segregation" no longer occurs.

The data show somewhat different preferences in different species. James (1971) used the term "niche-gestalt" to describe a response to a basic configuration of the environment by a particular species. The concept agrees with Hildén's (1965) "proximate factors" of habitat selection. Broad preferences emerging in the data presumably correspond to the niche-gestalts of the species. It is less important, what in addition to the niche-gestalt belongs to spatial configuration (for instance, open cliffs separating small habitat stands from each other). This explains why forest birds are efficient in colonizing the study islands where "forests", in the conventional, contiguous sense of the term, are actually lacking (see also Haila & Järvinen 1983, Haila et al. 1983).

Relationships among *Sylvia* warblers can be analyzed in terms of their niche-gestalts. *S. curruca, S. communis* and *S. borin* have clearly different preferences, and in "pure" contiguous stands they mainly segregate to different habitats (for the Åland Islands, see Palmgren 1930, Haila et al. 1980).

S. curruca is particularly adapted to habitats with a mosaic-like structure. It has a wide habitat range on the Åland mainland (Haila et al. 1980).

S. nisoria is a scrub-warbler with a peculiar niche-gestalt. Observations from the Vargskär area in 1976–1983 include about 40 territories at 10 sites, each one of them comprising a *macchia*-like mosaic of low *Juniperus* bushes and deciduous thickets (*Crataegus, Rosa, Prunus*).

S. borin is a resident of closed habitats, and the high between-year overlap in its territory locations on Gåsholmen and Bockholm compared with the other species is understandable, for there are few patches of dense deciduous woods on the islands.

S. atricapilla is scarce in the archipelago because tall trees are lacking (see Haila & Järvinen 1983, Haila et al. 1983).

The data on *Sylvia* warblers show that they may occur together in all combinations provided the environment simultaneously fulfils the niche-gestalt of several species (see also Zbinden & Blondel 1981, Blondel 1985). For some species-pairs this is improbable (*communis* and *atricapilla*), but most of the others were actually found.

Cody (1978, 1985) failed to appreciate differences in habitat preferences among *Sylvia* warblers. His measurements of the habitat structure were based on only one vegetation profile, obtained at the estimated territory center. He estimated only within-habitat heterogeneity, but the between-habitat component is, according to our data, equally important.

Neither did Cody (1978, 1985) take into account the fact that some of the species are scarce and cannot, because of scarcity alone, be realistically expected to coincide with the other species. This problem is magnified when all Sylviids are considered together. For instance, *Hippolais icterina, Phylloscopus collybita* and *P. sibilatrix* are all relatively scarce in the archipelago, and have niche-gestalts very different from those of the scrubland warblers. Drawing conclusions concerning their interspecific relationships in ecological time, using only observational data (let alone data from only one breeding season) is not valid.

Adequate scale

Conclusions on bird-habitat relationships clearly depend on the scale in which (1) habitats are described, and (2) bird presences are recorded (see Wiens et al. 1987). Our data demonstrate that the between-site component in habitat variation is an important one, but its adequate quantification is not simple. Too broad a scale in habitat descriptions may average out those characteristics of the environment that are important for the birds.

There seem to be two alternative ways of finding an adequate scale in bird-habitat studies; for general discussions of scale problems see Wiens (1981), Wiens et al. (1986, 1987). Rotenberry & Wiens (1981), Wiens & Rotenberry (1981) outlined a synthetic approach involving an ordination of sites according to their habitat characteristics and drawing density contours of different species in the environmental space thus defined. This approach can be used for comparisons between different areas (study plots).

Sherry & Holmes (1985; see also Holmes 1981) emphasized that for an assessment of the processes or dynamics of habitat selection detailed data are needed on how birds use their habitats. In a mosaic environment such as our study areas, different species with spatially overlapping territories probably use different habitat elements, depending on their foraging adaptations. Their territories overlap on a two-dimensional map, but they may actually live in partially separate parts of a complex habitat configuration.

Interpretations of population changes depend on the scale of the study as well. Local populations may vary stochastically or because of local environmental effects, but entirely independently of regional population variation. This emphasizes the need for long-term studies and reference data of various spatial scales (Wiens 1981, Wiens & Rotenberry 1981, Haila & Hanski 1984, Gaud et al. 1986, Rotenberry 1986, Wiens et al. 1987).

An exception that indicates a rule?

The environment of the Vargskär archipelago is exceptional in its highly mosaic structure. The relationships — or rather, the lack of relationships — between habitat selection patterns of different species cannot be generalized *prima facie* to other environments.

However, patterns observed in Vargskär imply a general point that may be valid, but more difficult to observe, also in more uniform environments. Species breeding in Vargskär probably establish territories which are actually discrete in space, comprising a number of suitable habitat stands separated from each other by other types of habitats, usually open cliffs or low scrublands (see Fig. 2).

The situation may actually be similar in habitats that look uniform to the naked eye. It may be that "forest" *per se* is for many forest birds less important than particular structural elements in the forest that correspond to their breeding and foraging habits. Their territories, defined by how they actually make use of them, may consist of discrete patches also within a "uniform" habitat. The niche-gestalt of each species is confused in a complex matrix of macro-habitat characteristics.

This possibility has important management implications. It would mean that the relationship between macro-habitat features and the needs of particular bird species would be indirect, mediated through the niche-gestalt of the species. Describing macro-habitat features may be a relatively poor means of assessing the suitability of a particular plot for individual bird species. The niche-gestalts ought to be directly assessed.

The possibility also has theoretical implications: If different species actually live in a different spatial matrix, it is difficult to give "communities" defined on a two-dimensional map any other than a purely descriptive, "epiphenomenal" (Simberloff 1980, James & Boecklen 1984) meaning.

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Selostus: **Varpuslintujen biotoopinvalinnasta saariston laikuttaisissa elinympäristöissä**

Tutkimme varpuslintujen biotoopinvalintaa Vargskärin saaristossa Föglön pohjoisosassa Ahvenanmaalla kesällä 1983. Laskimme kartoitusmenetelmällä pesimälinnuston kolmelta pieneltä saarelta (7, 14 ja 38 ha) sekä 16 hehtaarin suuruiselta näytealalta Vargskärin suurimmalla saarella (580 ha). Valitsimme satunnaisesti näytealoilta 206 pistettä, joiden kohdalta arvioimme 0.04 hehtaarin suuruisen ympyrän alalta (1) puiden lukumäärän ja puulajisuhteet, (2) taimien lukumäärän ja puulajisuhteet, (3) kenttäkerroksen tärkeimpien kasvillisuustyyppien peittävyydet, (4) latvuskorkeuden, (5) latvusten peittävyyden sekä (6) pensaskerroksen tiheyden. Pääkomponenttianalyysiä käyttäen kuvasimme tutkimusalueiden "biotooppiavaruuden" rakenteen näiden mittausten pohjalta (taulukko 2). Tutkimusalueita luonnehtii biotooppien pienipiirteinen vaihtelu. Yhtenäiset kasvillisuustyypit ovat pienialaisia (0.02–0.05 ha), ja niiden välissä on avokallioita sekä matalaa pensastoa, etupäässä katajaa (kuva 1). Kunkin tutkimusalueen biotooppipisteet ovat näin ollen hyvin vaihtelevia (taulukko 3).

Selvitimme niiden 17 lajin biotoopinvalintaa, joiden reviireille osui vähintään 10 biotooppipistettä (taulukko 1). Kunkin lajin biotooppipisteet antavat kuvan lajille ominaisesta "biotooppispektristä". Useimpien lajien biotooppispektrit ovat erittäin vaihtelevia eivätkä poikkea saarten biotooppiavaruuden keskipisteestä (taulukko 4). Tämä johtuu mitä ilmeisimmin saarten maastotyyppien rikkonaisuudesta. Kunkin lintuparin reviirillä on suuri määrä erilaisia biotooppilaikkuja (kuva 2).

Erotteluanalyysiä käyttäen vertasimme hyönteissyöjien biotooppispektrejä pareittain toisiinsa; näihin vertailuihin sisällytimme lähellä maan pintaa sekä oksistossa ruokailevat lajit. Edellisen ryhmän lajien biotoopinvalinta ei tutkimusalueillamme poikkea toisistaan. Oksistossa ruokailevista lajeista sen sijaan erottuu ryhmä pensaikkobiotooppeja suosivia kerttuja sekä ryhmä puita kasvavia biotooppeja suosivia lajeja, joiden biotooppispektrit eroavat toisistaan (taulukko 5).

Erityisen tarkoin pyrimme kartoittamaan *Sylvia*-suvun kerttujen reviirien sijainnin toisiinsa nähden kahdella alueella (8 ja 22 ha), joilla oli yhteensä 39 viiden eri kerttulajin reviiriä (kuva 3). Eri lajien reviirit olivat huomattavan päällekkäisiä (taulukko 6). Tämä osoittaa, että *Sylvia*-suvun kertut eivät tutkimusalueellamme puolusta reviirejä toisia lajeja vastaan. Kahdella tutkimistamme alueista kartoitettiin pesimälinnusto myös kesällä 1980. Tulosten vertailu osoittaa, että useiden *Sylvia*-lajien reviirien sijainti vaihtelee vuodesta toiseen. Myös eri lintulajien parimäärät vaihtelivat vuosien 1980 ja 1983 vertailussa erisuuntaisesti eri tutkimusalueilla (taulukko 7). Ilmeisesti sattuma vaikuttaa siihen, kuinka monta paria tietylle alueelle vuosittain asettuu ja mihin ne sijoittavat reviirinsä.

Lukuisien varpuslintulajien reviirit ovat Vargskärin pikkusaarissa keskenään päällekkäisiä. Tämä johtuu saarten biotooppien mosaiikkimaisuudesta. Yhtenäisillä biotoopeilla monet Vargskärillä "päällekkäisinä" esiintyvät lajiparit (esimerkiksi punarinta ja satakieli, tai hernekerttu ja hömötiainen) esiintyvät toisistaan erillään, koska ne suosivat eri biotooppeja. Ilmeisesti lintujen reviirit koostuvat Vargskärin mosaiikkimaisemassa erillisistä laikuista, joita pesivä pari käyttää hyväkseen ja joiden välillä on esimerkiksi avokallioita tai katajikkoa. Arvelemme, että reviirit voivat yhtä lailla koostua erillisistä laikuista myös näennäisesti yhtenäisillä biotoopeilla, joskin tätä on vaikea havaita.

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