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Habitat associations of breeding peatland passerine species in eastern Finland

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We studied breeding bird assemblages in three different types of peatland habitat: open, shrub, and forests. We measured ten habitat variables in breeding territories and assessed nine microhabitat characteristics for fourteen passerine species found in these peatlands. *Motacilla flava* and *Anthus pratensis* were most abundant in the open habitats. Species most abundant in shrub habitats were *Emberiza schoeniclus* and *Acrocephalus schoenobaenus* while *Phylloscopus trochilus*, *Fringilla coelebs* and *Anthus trivialis* were most abundant in forested peatlands. Discriminant function analysis of microhabitat use revealed differences between two *Fringilla* species (*F. coelebs* and *F. montifringilla*) and within species (between foraging and singing sites for *Motacilla flava* and *Anthus trivialis*). Using quantitative vegetation data and habitat associations of the bird species we propose a qualitative model that predicts the changes in the bird assemblage along with the changes in the environment. Such a model would be useful in the environmental management of peatland habitats.

1. Introduction

A breeding bird community is made up of species that have different requirements for various habitat characteristics (Wiens 1989). The causes leading to observed habitat associations may occur in different spatial and/or temporal scales. Although we know that habitats differ in many ways, finding the components of variation that are crucial for the observed habitat associations of species has proven to be a difficult task (e.g. Wiens 1989, Orians & Wittenberger 1991). Obviously, the first step in doing this is to use quantitative characteristics in the environment that are related to distributions of different species.

The patterns of organization in bird communities have been explored in grasslands (Wiens 1969), shrubsteppe (Wiens & Rotenberry 1981), deserts (Folse 1982), Mediterranean chaparral (Cody 1974), and forests (James 1971, Anderson & Shugart 1974, Rabenold 1978, Prodon & Lebreton 1981, Spindler & Kessel 1980, James

& Wamer 1982). Here we extend the study to northern peatlands with a major emphasis on a quantitative description of the distribution of species in relation to habitat structure. Although data on breeding populations have been gathered in peatlands in northern Europe (e.g. Renno 1958, 1974, Kumari 1972, Dyrcz et al. 1972, 1973, Nilsson 1977, 1980, Veromann 1980, Kolmodin & Nilsson 1982, Boström & Nilsson 1983), and especially in Finland (e.g. Sammalisto 1955, Häyrinen 1970, Hakala 1971, Järvinen & Sammalisto 1976, Häyrinen et al. 1986, Järvinen et al. 1987, Kouki & Häyrinen 1991), little quantitative data exist on vegetation structure. Because it is generally recognized that birds use habitat structure to select breeding territories (MacArthur & MacArthur 1961, Hildén 1965, James 1971, Anderson & Shugart 1974, Smith 1977, Haila et al. 1980, Rotenberry & Wiens 1980, Wiens 1989, Orians & Wittenberger 1991), we focus our efforts on a quantitative and structural description of the habitats selected and used by the peatland avifauna. The main objectives of this study were to: (1) gather population data on birds; (2) quantify the vegetation structure associated with the territories of breeding bird species; and (3) identify the specific portions of the vegetation used by birds (hereafter referred to as microhabitat).

2. Study areas

We defined three peatland habitat types based on the structure of the vegetation: (1) open — dominated by low-lying Ericaceae species, sedges (*Carex* spp.), mosses, open water pools, and a few scattered trees or shrubs; (2) shrub — dominated by *Salix*, *Alnus*, or *Betula* shrub species from 0.5 to 4 m high, often with an understory of sedges or forbs (e.g. *Potentilla*, *Galium*, and *Lysimachia*); and (3) forest — dominated by conifers (*Pinus* or *Picea*) with an understory of Ericaceae species, scattered sedges, scattered shrubs (e.g. *Betula*), and a moss ground layer.

One open area, two shrub stands, and two forest areas were selected for territory mapping: (1) an 18 ha (450 m × 450 m) stand in an open peatland at Koivusuo (O1) (62°56′N, 31°25′E), (2) a 6 ha (400 m × 150 m) shrub stand located at the northwestern edge of Siikalahti (S1) (61°33′N, 29°35′N), (3) an 8 ha (400 m × 200 m) shrub stand located at the southern edge of Siikalahti (S2), (4) a 17.5 ha (500 m × 350 m) forest stand at Koivusuo (FP), and (5) a 10 ha (500 m × 200 m) stand of *Picea* and *Pinus* at Timmosuo (FM) (62°50′N, 30°50′N).

Three open areas and one forest area were selected for transect counts: (1) 3 km in an open peatland at Korvinsuo (O2) (62°45′N, 30°55′N), (2) 2 km in an open peatland at Pitkänlahdensuo (O3) (62°45′N, 30°55′N), (3) 5 km in an open peatland at Koivusuo (O4), and (4) 4 km in a forest area at Timmosuo (FV). All study areas were located in eastern Finland.

3. Methods

3.1. Bird censusing

In counting birds we used territory mapping (Anon. 1970, Svensson 1974, Dyrcz & Tomiałojc 1974) and Finnish line transect censuses (Järvinen & Väisänen 1975, 1976). Territory mapping was used to determine densities and to estimate territorial boundaries so that vegetation measurements could be related with species distributions (e.g. Haila & Hanski 1987). Line transect censuses were carried out to estimate population densities over a larger area and to provide supplementary data on habitat associations.

We censused territory mapping plots six times from 23 May to 24 June, 1981, except O1, which had very low population densities, and therefore was censused only four times. All census data were gathered during early morning hours (0400–1000) and time spent censusing each plot was approximately proportional to area. We required a minimum of two observations of a species before it was considered breeding on the plot. However, for the Yellow Wagtail *Motacilla flava*, which is often attracted to the censuser, we averaged the number of males observed.

Line transect censuses followed the guidelines presented by Järvinen & Väisänen (1975, 1976), except that every transect was censused four times. We estimated densities with the formulae presented by Järvinen & Väisänen (1983) and we used correction values for forest passerines.

The method does not produce absolute densities, but gives approximately unbiased relative densities of different species. On average, single-visit censuses reveal about 60% of the breeding pairs in peatland habitats (Kouki & Järvinen 1980). Species recorded in the survey belt in a different habitat type than the one of interest (e.g. the Wood Warbler *Phylloscopus sibilatrix* recorded in an adjacent forest area while censusing an open peatland) were excluded.

3.2. Vegetation structure

We measured the structure of the vegetation with methods modified from those used by Wiens (1969), Rotenberry & Wiens (1980), and Wiens and Rotenberry (1981). The method is fully described in Niemi (1983, 1985) and Niemi & Hanowski (1984). Briefly, we identified five forms of vegetation within peatlands: (1) ground cover including moss and any vegetation less than 10 cm; (2) monocots > 10 cm, hereafter referred to as sedges because they were the predominant monocot within the study areas; (3) forbs > 10 cm, predominantly Ericaceae species such as *Ledum*, *Chamaedaphne*, and *Andromeda*, and others such as *Potentilla*, *Menyanthes*, and *Galium*; (4) shrubs > 30 cm but < 2.5 cm dbh, primarily *Salix*, *Alnus*, and *Betula*; and (5) trees > 2.5 cm dbh predominantly *Pinus*, *Picea*, and *Betula*. We measured nine variables associated with these vegetational forms and the percentage of open water (Table 1, Fig. 1).

3.3. Vegetation data and bird distribution

We randomly selected vegetation points by assigning numbers to each intersection of a 50 m × 50 m grid within each of the territory mapping plots. The number of points (i.e. intersections of the grid) selected was proportional to the area of the plot. These data were associated with a species if the vegetation point sampled was inside or overlapped territorial boundaries of the species.

Table 1. Ten habitat variables associated with each point sample.

Abbreviation	Variable	Description
OHT	Overall height	Estimated general height of vegetation in 100 m^2 surrounding point
GCV	Ground cover	Estimated percent cover of live vegetation less than 10 cm high in sq m surrounding point
TD	Tree density	Density of trees greater than 2.5 cm dbh measured by point-centered quarter method
WD	Shrub density	Density of shrubs greater than 30 cm high and less than 2.5 cm dbh measured by point-centered quarters
WHT	Shrub height	Mean height of the four closest shrubs measured for variable
WDFD	Forb density	Density of forbs greater than 10 cm high measured by point-centered quarter method
F1	Forb hits	Number of hits of forbs in 0-30 cm height interval
SD	Sedge density	Density of monocots greater than 10 cm high measured by point-centered quarter method
S1	Sedge hits	Number of hits of monocots in 0-30 cm height interval
OW	Open water	Estimated percent cover of water in 100 m^2 surrounding point

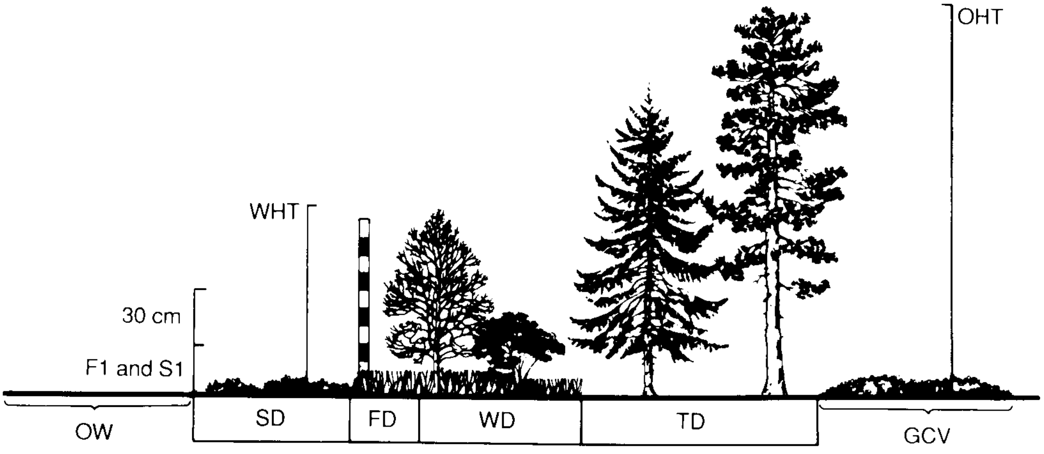

Fig. 1. Visual description of the vegetation measurements as described in Table 1.

Boundaries were inferred from the observations on species maps. Additional data to increase sample sizes for uncommon species were obtained in two ways. First, when a species was observed at least twice in four transect counts, vegetation data were gathered at some of these sites. These additional sites were selected randomly from the pool of sites in which each species was observed. At each of these sites, 5 additional vegetation points were sampled along a transect through the area in which the species was observed. Secondly, data were collected in selected wetland sites where a species was observed repeatedly throughout the breeding season. Territory boundaries could be defined with reasonable confidence only for passerines, therefore, we confined the analysis to those species. Vegetation data were collected for a minimum of five different territories for those species included in the analysis.

3.4. Microhabitat data on habitat use

We recorded the specific portions of the vegetation used by birds with a technique modified from that by Sabo (1980). The following variables were recorded when an individual was encountered: (1) species; (2) sex, if identifiable; (3) behavior as singing or feeding; (4) height in 1 m intervals; (5) height of vegetation used in 1 m intervals; (6) vegetation type as (a) open ground or moss; (b) sedge or grass; (c) low shrub (< 1 m high), (d) high shrub (1–4 m high), (e) small tree (> 4 m high, < 7.5 cm dbh); and (f) large tree (> 7.5 cm dbh); (7) plant genus used as (a) *Picea*, (b) *Pinus*, (c) *Salix*, (d) *Alnus*, (e) *Betula*, (f) *Ledum*, (g) *Andromeda*, (h) *Chamaedaphne*, (i) *Vaccinium*, (j) *Calluna* and (k) monocot; (8) perch substrate size as (a) leaf-needle base (< 6 mm diameter), (b) twig (6–12 mm diameter), (c) branchlet (12–25 mm diameter), (d) branch (> 25 mm diameter), or (e) ground; and, if in a tree or shrub, (9) distance from the bole or axis in dm. We collected a series of observations from each individual (up to five observations, each separated by at least 30 seconds), but because these observations are not independent, in the analyses we used a data set generated by randomly-selecting one observation from each series of observations.

3.5. Statistical analysis

Prior to all analyses, we calculated the mean, median, range, skewness, kurtosis, and coefficient of variation of variables used in statistical analyses. All habitat variables were skewed to the right and therefore we performed the analysis on logarithmically-transformed data. We used principal components analysis (PCA) to explore the covariation among the vegetation variables. By applying PCA we reduced the dimensionality of these data with minimal loss of information.

All PCA analyses were calculated using FACTOR of SPSS (see Nie et al. 1975) with the PA1 method and no rotation.

To examine habitat or microhabitat differences between species, we used discriminant function analysis (DFA). By using the DFA, we tried to find the linear combinations of the original variables that separate the groups. Therefore, groups were always defined before the analysis was applied. We used the Wilks lambda criterion in the stepwise procedure of subprogram DISCRIMINANT in SPSS for these analyses. The discrimination analysis of the microhabitat data were confined to the continuous variables measured. These included height of bird, height of vegetation used, and the distance of the bird from the bole.

Both techniques, since they were used in an exploratory fashion, require few formal assumptions of the data used (James & McCullogh 1990), and this was one of the reasons we preferred them. There are some alternatives to the DFA and PCA, usually with more stringent assumptions and limitations. We could have used multiple logistic regression instead of DFA, but since we confined the analysis to the continuous variables, we probably would not have gained much by applying it in the present case. We stress that the techniques applied are meant only for descriptive purposes and any inference about causation leading to observed patterns are beyond the scope of this paper.

4. Results

4.1. Bird censuses

Willow Warbler *Phylloscopus trochilus*, Chaffinch *Fringilla coelebs*, and Tree Pipit *Anthus trivialis* were most abundant in forested peatlands (Tables 2 and 3). Sedge Warbler *Acrocephalus schoenobaenus*, Reed Bunting *Emberiza schoeniclus*, and Snipe *Gallinago gallinago* were the predominant species in the two shrub stands (Table 2) accounting for more than 90% of the breeding individuals in each plot. The Yellow Wagtail and Meadow Pipit *Anthus pratensis* were most abundant in open peatlands (Tables 2 and 3). Bird density was highest in the shrub areas and lowest in the open peatlands (Table 2).

4.2. Habitat structure

We derived the major axes of variation in the habitat variables from a PCA of the pooled vegetation data. The interpretation (Table 4) and graphic display (Fig. 2) of peatland habitat structure was based on correlations of the original variables with the principal component axes. Principal component 1 (PC 1) was positively correlated with increasing overall height, tree density, forb density, forb hits, shrub height, and

Table 2. Breeding bird densities (pairs/10 ha) in the five territory mapping plots. For mapping codes, see text.

	O1	SW1	SW2	FP	FM
Botaurus stellaris			1		
Anas platyrhynchos		1	1		
A. crecca		1			
Aythya ferina		1	1		
Tetrao tetrix				1	
Rallus aquaticus			1		
Fulica atra		1			
Pluvialis apricaria	1				
Numenius phaeopus	1				
Gallinago gallinago	1	2	5		
Alauda arvensis			1		
Parus montanus				1	
Erithacus rubecula					1
Phoen. phoenicurus					2
Acroc. schoenobaenus		32	27		
Sylvia borin			1	1	
S. curruca				1	
Phylloscopus trochilus		1	1	4	3
Regulus regulus				3	
Muscicapa striata				1	
Ficedula hypoleuca				1	
Anthus pratensis	4				
A. trivialis				2	1
Motacilla flava	3				
Carduelis spinus				1	1
Carpodacus erythrinus			1		
Fringilla coelebs				2	4
F. montifringilla				1	1
Emberiza rustica				1	2
Emberiza schoeniclus		10	8		
Total density (pairs/10 ha)	10	49	43	19	16
Total breeding species	5	7	11	13	8

negatively correlated with percent open water, sedge density, and sedge hits (Table 4). In general, this axis progressed from open peatlands with open water pools and sedge on the left front, to forested peatlands with moss ground cover and a higher density of forbaceous (primarily Ericaceae) cover on the right (Fig. 2). PC 2 was positively correlated with increasing shrub density and increasing sedge hits (Table 4). PC 3 was primarily related with ground cover and to a lesser extent with sedge density, forb hits, shrub density, and shrub height. PC 1 and PC 2 were easiest to interpret and we have confined the remaining portion of the analysis to these two axes. The mean centroid of each bird species was calculated from the factor scores for each point sample collected within a species territory (Fig. 2).

Table 3. Breeding bird densities (pairs/km^2) in the four transect areas calculated by formulas in Järvinen & Väisänen (1983). Only those species with densities greater than 1 pair/km^2 are included.

	O2	O3	O4	FV
Tetrao urogallus				3.4
T. tetrix	1.5	0.8	0.5	2.3
Lagopus lagopus	1.1		1.1	
Vanellus vanellus	4.5	6.3	10.6	
Pluvialis apricaria	3.7	2.8	3.1	0.7
Numenius phaeopus	6.2	4.1	9.4	0.2
N. arquata	2.4	0.9	1.6	
Tringa glareola	0.3	0.8	7.2	3.3
Capella gallinago	0.7	0.5	3.4	1.6
Philomachus pugnax	3.1	6.1	31.1	
Cuculus canorus	0.4			1.4
Dendrocopos major		0.6		1.7
Alauda arvensis		0.8	2.3	
Parus major				2.1
P. montanus			1.7	
Erithacus rubecula				1.3
Saxicola rubetra	0.4	0.7		1.3
Turdus iliacus	0.6	1.3		2.3
T. philomelos				2.4
Acroc. schoenobaenus			1.4	
Sylvia borin		1.4	0.6	0.9
Phylloscopus trochilus	7.8	10.8	0.8	19.4
Regulus regulus				1.8
Muscicapa striata				2.5
Anthus pratensis	11.0	13.9	14.8	2.7
A. trivialis	2.8	4.0	2.2	12.8
Motacilla alba		0.9		2.1
M. flava	35.7	33.4	6.2	4.9
Lanius collurio				1.7
Carduelis spinus				2.1
Fringilla coelebs	2.6	6.9	2.7	18.2
F. montifringilla				1.4
Emberiza rustica				2.3
Total density (pairs/km^2)	88	105	102	104
Total species	27	30	22	43

4.2.1. Bird-habitat distribution

Although both the Yellow Wagtail and the Meadow Pipit are shown on the extreme left of Fig. 2, they occurred in different habitats (DFA, $P < 0.05$). Meadow Pipit was found associated with treeless peatlands, open water pools, and sparse shrubs or forbs (Tables 5 and 6). In contrast, the Yellow Wagtail was found in peatlands with a few scattered *Pinus* trees, but also with sparse shrubs and forbs (Tables 5 and 6). In a DFA of habitat variables gathered within the territories of these two species, the three best discriminating variables were a higher tree density, less sedge hits, and higher ground cover associated with Yellow Wagtail territories (Table 5).

Table 4. Correlation coefficients of the original habitat variables (Table 1) with the first three principal components from a principal components analysis of the pooled habitat data gathered in eastern Finnish peatlands (n = 250). All habitat variables logarithmically-transformed prior to analyses.

Habitat variables	Principal components 1	2	3
Overall height	0.87	0.03	0.09
Tree density	0.85	–0.01	0.03
Shrub height	0.70	0.29	–0.30
Shrub density	0.49	0.64	–0.35
Forb density	0.76	0.15	0.22
Forb hits	0.74	–0.01	0.32
Sedge density	–0.58	0.60	0.35
Sedge hits	–0.49	0.73	0.21
Ground cover	0.50	–0.10	0.75
Open water	–0.80	–0.16	0.04
Explained variation %	48.1	14.3	11.0
Cumulative variation %	48.1	62.4	73.4

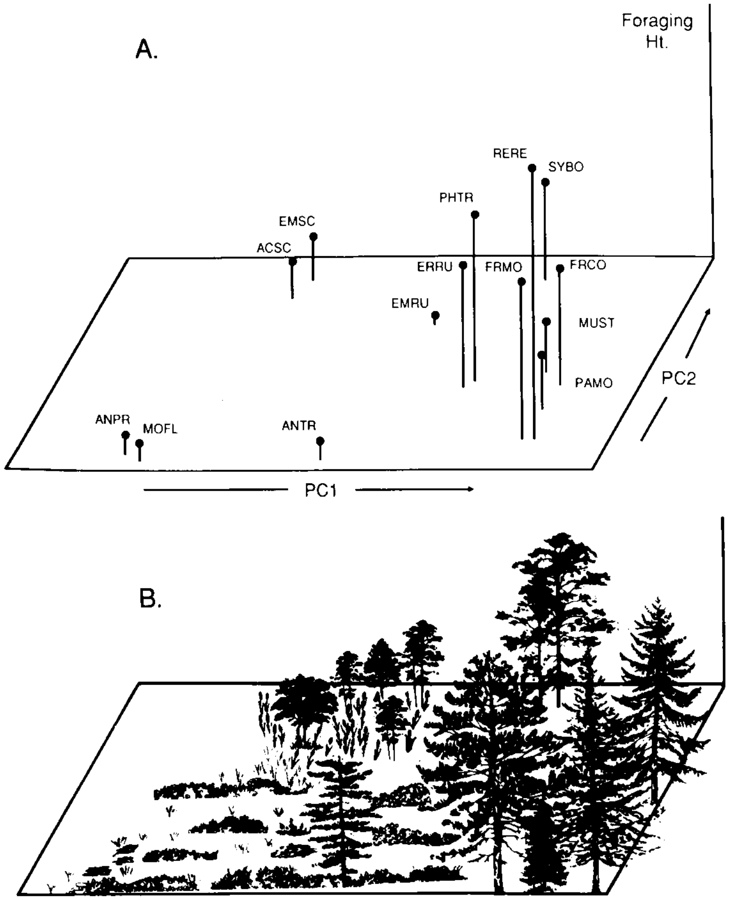

Fig 2. Bird species distribution projected on the axes representing the habitat variation (A) and graphical interpretation of the peatland vegetation (B) in the same space (A). The x-axis and y-axis are the first (PC1) and second (PC2) principal components based on the habitat variables (see Table 6.) The z-axis is based on the mean foraging height for bird species (A), while (B) is based on the mean overall height of the vegetation within each stand. PC1 and PC2 are scaled according to the amount of variation they explain. Codes for species are as follows: ANPR = the Meadow Pipit, MOFL = the Yellow Wagtail, ACSC = the Sedge Warbler, EMSC = the Reed Bunting, EMRU = the Rustic Bunting, ERRU = the Robin, PHTR = the Willow Warbler, RERE = the Goldcrest, FRMO = the Brambling, SYBO = the Garden Warbler, FRCO = the Chaffinch, MUST = the Spotted Flycatcher, PAMO = the Willow Tit.

The Sedge Warbler and Reed Bunting were both abundant within shrub habitats and vegetation associated with their territories was similar (Tables 5 and 6). Both species were associated with a high density of *Salix* shrubs and a high density of sedges. The Garden Warbler *Sylvia borin* was also associated with shrub vegetation. The species was not common in peatlands and only occurred in areas of tall shrubs and high sedge density. The Garden Warbler was found in areas of the thickest vegetation in terms of shrubs and trees and often on the edge of two peatland types (Table 5 and Fig. 2).

Of the forest species, the Tree Pipit was found in the open portions of the forest, while the Rustic Bunting *Emberiza rustica* and the Willow Warbler were often on forest edges (Tables 5 and 6 and Fig. 2). These forest-dwelling species were all grouped together and all had similar habitat associations (Fig. 2).

DFA was used to explore differences in the habitats selected by the Chaffinch and Brambling *F. montifringilla*. The results were insignificant (P > 0.05) and none of the ten habitat variables or combinations of variables could be used to distinguish between territories used by either species.

4.3. Microhabitat distribution

Microhabitat data were summarized according to sex and behavior for those species with a sample size of n > 10 (Table 7). The species were subdivided into three groups for analysis: (1) sexually dimorphic species were used to explore differences in male foraging and singing sites (included the Yellow Wagtail and the Chaffinch); (2) species with monomorphic plumage were used to explore differences in singing and foraging sites (included the Garden Warbler and the Willow Warbler); and (3) other species (most not sexually dimorphic) of which we had small sample sizes and thus they were not amenable to statistical analysis (included Willow Tit *Parus montanus*, Robin *Erithacus rubecula*, Redstart *Phoenicurus phoenicurus*, Meadow and Tree Pipits, Goldcrest *Regulus regulus*, Spotted Flycatcher *Muscicapa striata*, Sedge Warbler, and Rustic Bunting).

4.3.1. Microhabitat distribution — pipits and wagtails

All three motacillids, Yellow Wagtail, Tree Pipit, and Meadow Pipit, were ground foragers (Table 7). Yellow Wagtail was found primarily singing from small (mean height = 4.8 m) *Pinus* trees. Foraging sites (height of bird and height of vegetation) used by male and female Yellow Wagtail did not differ (DFA). Foraging and singing sites used by the Yellow Wagtail were different (DFA, $P < 0.01$). This species sang from the tops of trees but foraged on the ground.

4.3.2. Microhabitat distribution — warblers

Singing and foraging sites of the Garden Warbler were different (DFA, $P < 0.05$, Table 7). None of the three variables (height of bird, height of vegetation, or distance from central axis) were significantly different alone, but the combination of height of bird and distance from the central axis was significant. Garden Warbler appears to forage more often in deciduous trees, lower in the vegetation, and from smaller perches on the

Table 5. Habitat characteristics of breeding passerines in eastern Finland. See Table 1 for descriptions of variables. Ground cover of live vegetation and open water percentages are estimated from the areas indicated surrounding a sample plot.

		Habitat variable									
Species	N	Ground cover[a]	Sedge density[b]	Sedge hits[c]	Forb density[b]	Forb hits[c]	Shrub density[d]	Shrub height[e]	Open water[f]	Overall height[g]	Tree density[h]
Erithacus rubecula	21	76	40	4	105	9	10	101	–	14.8	24
Phoenicurus phoenicurus	13	80	7	1	136	10	10	97	–	12.8	17
Acrocephalus schoenobaenus	40	38	167	9	43	5	31	86	8	4.1	3
Sylvia borin	13	58	156	8	131	8	40	123	2	9.6	28
Phylloscopus trochilus	59	69	13	4	105	8	17	103	2	10.3	20
Regulus regulus	21	82	3	1	100	9	9	107	–	13.7	21
Muscicapa striata	20	82	10	3	124	11	17	93	–	13.2	20
Anthus pratensis	42	55	96	6	2	2	1	23	23	1.3	0
A. trivialis	40	71	49	6	64	9	27	79	–	7.7	16
Motacilla flava	31	66	79	4	25	3	1	35	18	1.8	1
Fringilla coelebs	39	74	7	3	117	9	10	104	–	12.9	20
F. montigringilla	22	71	6	2	161	10	11	105	–	12.8	24
Emberiza rustica	23	60	15	5	95	9	26	98	–	8.1	20
E. schoeniclus	34	40	170	8	42	5	20	87	6	5.5	4

[a] % of 1 m^2 (mean), [b] stems/m^2 (median), [c] number (mean), [d] stems/25 m^2 (median), [e] cm (mean), [f] % of 100 m^2 (mean), [g] m (mean), [h] stems/100 m^2 (mean).

outer edges of trees and shrubs in contrast with its singing sites. The singing sites of Willow Warbler were primarily in *Pinus* trees (mean height = 9.4 m) and these sites were different ($P < 0.05$) from foraging sites that were in deciduous trees and in small perches at the outer extremities (Table 7). The Goldcrest was almost exclusively associated with tall *Picea* trees (mean height = 15.4 m) and the Sedge Warbler with *Salix* shrubs (Table 7).

Table 6. Plant species composition within the territories of passerine species in peatlands of eastern Finland. All values are frequency values expressed as percentages. Acronyms: Pin = *Pinus sylvestris*, Pic = *Picea abies*, BeT = *Betula pubescens* or *B. pendula*, Sal = *Salix* spp., BeS = *Betula pubescens* or *B. nana*, Jun = *Juniperus spp.*, Vac = *Vaccinium* spp., Rub = *Rubus chamaemorus*, Emp = *Empetrum nigrum*, Cham = *Chamaedaphne calyculata*, Men = *Menyanthes trifoliata*, Led = *Ledum palustre*, And = *Andromeda polifolia*, Gal = *Galium* spp., Pot = *Potentilla palustris*, Lath = *Lathyrus* spp.

	Trees				Shrubs				
Species	Pin	Pic	BeT	Sal	Pin	Pic	BeS	Sal	Jun
Erithacus rubecula	37	38	24		30	17	8		16
Phoenicurus phoenicurus	63	13	21		46	13	27		8
Acrocephalus schoenobaenus			56	44				100	
Sylvia borin	33	2	60	2	16	4	67	9	2
Phylloscopus trochilus	43	24	26	5	25	19	30	11	9
Regulus regulus	32	52	13		17	39	24		20
Muscicapa striata	69	19	5	3	56	3	19		16
Anthus pratensis	100				43		53	4	
A. trivialis	88	9	3		60	8	30		
Motacilla flava	100				70		30		
Fringilla coelebs	35	38	23		38	18	25		13
F. montifringilla	56	31	14		21	18	44	7	6
Emberiza rustica	60	18	20		52	26	23	1	8
E. schoeniclus			51	49				100	

	Forbs								
	Vac	Rub	Emp	Cham	Men	Led	And	Gal	Lath
Erithacus rubecula	69	6		6		6			
Phoenicurus phoenicurus	60	6	12	8		15			
Acrocephalus schoenobaenus					19		3	67	12
Sylvia borin	64	9	2	10	3	2		7	
Phylloscopus trochilus	59	4	4	11	4	9		6	
Regulus regulus	68	10	4	8		11			
Muscicapa striata	56	1	7	4		23	3		
Anthus pratensis	7	15		13	35		34		
A. trivialis	44	1	9	17	20	17	5		
Motacilla flava	14	11		31	4	1	37		
Fringilla coelebs	71	6	8	5		6			
F. montifringilla	70	6	2	8		11			
Emberiza rustica	51	3	12	16		12			
E. schoeniclus					16			72	12

Table 7. Microhabitat characteristics of the 14 passerine bird species observed in peatlands. Variables: Beh = behaviour (S = singing, F = foraging), N = number of observations, Ht = mean height (m) of position of the bird, Vht = mean height (m) of vegetation used, Rat = ratio of Ht/Vht, Dist = distance (m) from central axis or bole. Vegetation type: 6 = ground, S = sedge or grass, SS = small shrub, LS = large shrub, ST = small tree, LT = large tree (see text for more details). Plant species: K = *Picea*, P = *Pinus*, D = deciduous, E = Ericaceae spp. Perch: 3 = 0–6 mm, 9 = 6–12 mm, 15 = 12–18 mm, 25 = > 25 mm diameter perch. For example, for *Motacilla flava* on the first line, 52% of the total 29 independent observations were in large shrubs, similarly 24% of the observations were in small trees.

Bird data								Vegetation type						Plant species				Perch			
Species		Beh	N	Ht	Vht	Rat	Dist	G	S	SS	LS	ST	LT	K	P	D	E	3	9	15	25
Group 1																					
M. flava	Male	S	29	4.5	4.8	0.9	–	–	–	–	52	24	24	–	–	100	–	21	41	31	7
		F	26	0.1	0.2	0.0	–	81	15	–	–	–	4	–	–	–	–	–	–	–	–
	Female	F	10	0.0	0.2	0.1	–	80	20	–	–	–	–	–	–	–	–	–	–	–	–
F. coelebs	Male	S	8	7.8	12.5	0.7	–	–	–	–	–	–	100	38	50	13	–	38	50	13	–
	Male	F	28	5.3	9.4	0.4	–	21	4	–	–	11	64	27	64	5	5	10	62	19	10
	Female	F	36	2.9	8.4	–	–	35	–	–	3	26	35	38	31	15	15	18	64	18	–
F. montifringilla	Male	S	28	9.6	13.9	0.7	–	–	–	–	4	14	82	14	75	11	–	11	32	29	29
		F	22	6.6	12.4	0.6	–	–	–	–	4	18	77	9	73	18	–	23	27	36	14
Group 2																					
S. borin	Male	S	10	6.4	8.2	0.7	0.5	–	–	–	30	40	30	–	38	63	–	20	80	–	–
	Both	F	24	5.3	8.8	0.6	0.9	–	–	–	38	29	33	–	19	81	–	58	38	4	–
P. trochilus	Male	S	25	8.8	9.4	0.9	0.3	–	–	–	8	56	36	8	68	24	–	28	56	12	4
	Both	F	44	7.3	12.2	0.6	1.1	–	–	5	–	45	50	9	21	67	2	50	43	5	2
Group 3																					
P. montanus	Both	F	24	5.3	6.8	0.8	0.8	–	–	8	8	63	21	4	79	13	4	25	67	8	–
E. rubeculus	Male	S	17	11.0	13.4	0.7	0.6	–	–	–	–	35	65	41	47	12	–	13	60	20	7
	Both	F	17	2.8	5.4	0.2	0.4	29	24	6	–	24	18	–	–	–	–	–	–	–	–
A. schoenobaenus	Male	S	16	1.5	2.2	0.7	0.4	–	6	38	50	–	6	–	–	100	–	40	40	13	7
	Both	F	11	1.6	3.0	0.5	0.6	–	–	18	73	9	–	–	–	100	–	45	36	9	9
R. regulus	Both	F	25	12.6	15.4	0.8	0.5	–	–	–	–	24	76	96	4	–	–	56	36	8	–
M. striata	Both	F	31	5.6	11.0	0.5	0.8	–	–	–	26	16	58	7	79	14	–	6	45	42	6
A. pratensis	Both	F	17	0.0	0.1	–	–	94	6	–	–	–	–	–	–	–	–	–	–	–	–
A. trivialis	Male	S	28	8.8	9.0	0.9	0.2	–	4	–	18	50	29	4	92	4	–	4	70	26	–
	Both	F	17	0.1	0.3	–	–	76	12	6	–	–	6	–	–	–	–	–	–	–	–
E. rustica	Female	F	9	0.1	0.8	0.0	–	89	–	–	–	–	11	–	–	–	–	–	–	–	–
E. schoeniclus	Male	S	21	2.6	3.3	0.8	–	–	–	10	71	14	5	–	10	90	–	33	48	14	5
		F	9	1.2	1.6	0.4	–	22	22	22	11	22	–	–	–	–	–	–	–	–	–

4.3.3. Microhabitat distribution — finches and sparrows

Chaffinch sang in large coniferous trees, while foraging sites were lower and in smaller trees or on the ground (Table 7). The foraging sites of the sexes were not different (DFA). However, foraging and singing sites of the Chaffinch were different ($P < 0.05$). The primary difference was height where individuals were observed foraging in smaller trees and in lower parts of the vegetation, but singing was often from the top portions of the tree.

Foraging sites of Chaffinch and Brambling differed ($P < 0.01$). Brambling was more frequently observed foraging in the outer edges of branches than Chaffinch (Table 7).

Rustic Bunting was very difficult to observe and most observations were on females foraging on the ground. Reed Bunting was most often recorded singing in large shrubs (Table 7).

5. Discussion

This paper includes estimates of population sizes of birds breeding in peatlands in eastern Finland. In regard to these estimates, our findings generally agree with previously published ones and we will not discuss these in detail but concentrate on our findings about habitat structure and habitat associations of species.

5.1. Peatland habitat structure

We have described three distinct habitat associations within peatlands of eastern Finland. Although we attempted to find large homogeneous study plots, the major axes of habitat variation as derived from PCA showed a relatively continuous gradient from open through shrub to forested stands. Thus, even though each plot is distinguishable as open, shrub, or forest, the habitat patches include heterogeneous vegetation. This adds noise to our data, but it includes an ecological message. Namely, many species were found in peatlands where the suitable habitat for a given species was very restricted. Examples include: (1) The Sedge Warbler in a small patch of shrubs in the predominantly open habitat of the O4 transect; (2) The Willow Warbler in an area of higher shrubs and small trees in the predominantly shrub stands, SW1 and SW2; (3) the Tree Pipit, the Willow Warbler, and the Chaffinch in small patches of trees or close to the wooded margins in the open peatland transects (O2, O3, and O4); and (4) the Goldcrest in small patches of *Picea* in the FV transect. We do not suggest that all habitat patches suitable to a species are occupied, but this emphasizes the influence of relatively small variations in habitat structure on the distribution and abundance of species (see also Järvinen & Väisänen 1980).

5.2. Habitat structure and prediction

The major axis of habitat variation derived from PCA was primarily related with overall height of the vegetation. This vegetation parameter has been suggested in several previous studies as the most important in relation to species distribution (Cody 1968, Wiens 1969, Rotenberry & Wiens 1980). In our case, vegetation height is an obvious component in separating the habitats; however, the specific density of trees, sedges, forbs, and floristic composition are likely important for the distribution of specific species. For instance, most of the forest species show frequencies of trees, shrubs, and forbs within their territories similar to the frequencies available in the stands. The Goldcrest, Robin, and Chaffinch, however, show trends in preference for *Picea* while the Tree Pipit, Spotted Flycatcher, and Redstart show tendencies for *Pinus*. Another interesting deviation is shown by the Meadow Pipit which had a high frequency of *Menyanthes trifoliata* within its territory despite the low frequency of the plant in three of the four open peatlands sampled. Certainly, some of these deviations may be related to chance, but some attention to floristic composition could be fruitful in future studies (see also Wiens & Rotenberry 1981, Wiens 1985).

Prodon & Lebreton (1981) present a model for predicting bird species response to changes in habitat structure based on correspondence analysis (Hill 1973). Here we present a similar descriptive model that can aid in predicting the response of bird species with changes in habitat structure (see also Niemi et al. 1983). The mean position for each species within the two-dimensional PCA space (Fig. 2) are preferred areas for the species within the peatlands we studied. In theory, any sample of vegetation points within a specific peatland stand, within the distribution of points where a species was found, could be considered suitable habitat for that species. If the stand changes over time or is altered (e.g. by drainage or logging), then this may result in a shift of the mean position of the stand either toward or away from a species mean. A shift toward the species mean would presumably be favorable for the species, while a shift away would have the opposite effect.

The advantages and disadvantages of using techniques such as principal components analysis, multiple regression, or correspondence analysis have been debated (i.e., Gauch et al. 1977, James & Wamer 1982). We believe that many species have non-linear responses to habitat gradients (i.e., species do not necessarily increase asymptotically with a suitable predictor variable). With continuous variables, specific hypotheses such as the differences in habitats selected by two congeneric species can be investigated with more powerful statistical tests like discriminant function analysis.

5.3. Microhabitat distributions

Our intent was to describe the specific aspects of the vegetation used by the common passerine species found within the peatland habitats. Similar techniques have been used in a variety of previous studies (e.g. Ulfstrand 1976, Alatalo 1980, Hutto 1981, Moreno 1981).

We regard differences in microhabitat use as a potential isolation mechanism between closely related species. A particularly interesting case here are the *Fringilla* species (the Chaffinch and the Brambling). Merikallio (1951) proposed that there is interspecific territoriality between the species. Our data were too scarce to make any judgments on interspecific territoriality, but the habitat associations were similar in both species. According to our results, the species differ in their microhabitat use. Because density patterns of the two species form a continuous spectrum over Finland (the Chaffinch being most abundant in the south, the Brambling in the north; Järvinen & Väisänen 1979) an interesting question concerns whether microhabitat distributions change as density patterns change.

6. Concluding remarks

Our study is concerned mainly with habitat associations of different species. We do not expect that all the patterns revealed are omnipresent even in Finnish peatlands. Even though we have used quantitative vegetation data in describing habitat associations, there are many potential fallacies if we try to assess habitat selection of the species. We would like to point out five factors that should be kept in mind while interpreting species-habitat patterns.

1. Our study was completed in different peatland habitats, but for many species (e.g. the Tree Pipit, the Goldcrest, and the Chaffinch) peatlands are inferior habitats in terms of population densities (von Haartman et al. 1963–72, Järvinen & Väisänen 1980, Hyytiä et al. 1983). Thus, our study reveals habitat associations of the species within peatlands, but does not describe habitat selection for specific species.

2. Populations do not exist in isolation (Haila et al. 1979), and population density and habitat selection are probably closely related (e.g. see Rosenzweig 1985, 1991, Wiens 1989, Kouki & Häyrinen 1991). Accordingly, habitat association patterns are dependent on changes of the species population across its entire range. For instance, in a forested area in Northern Finland, the bird assemblage changed considerably during a 70 year period despite the apparent constancy of habitat structure (Väisänen et al. 1986). This is also the reason why we really cannot conclude much about the processes leading to habitat selection by different species. These decisions most likely vary with density, and our data is both temporally and spatially too limited to draw conclusions about dynamic processes like habitat selection. We see that the next step toward understanding habitat selection of peatland birds requires more detailed investigation of the habitat characteristics in plots with varying densities.

The spatial dynamics of populations possibly concomitant with density changes should also shed light on the characteristics crucial for habitat selection.

3. The mosaic structure of habitats is typical for many biological environments and this variation in habitat structure contributes to the variation in the bird assemblage of an area (see examples in Sect. 5.1.). Although we have not considered the effect of area on habitat selection, we suggest that many species may select territories according to small-scale structural patterns and not necessarily according to the general vegetation structure (Wiens 1985, but see Orians & Wittenberger 1991).

4. To understand habitat associations we clearly need to know how a species uses its habitat. A good approach seems to be observation of microhabitat use by the different species, albeit many problems are involved in these studies (see Sect. 5.3., Orians & Wittenberger 1991). For example, the macrohabitat associations of the two *Fringilla* species seem to be similar while microhabitat distributions were different (Sect. 4.3.3.). Thus, these species seem to select the same macrohabitat, but use it in different ways.

Despite the problems and difficulties in studies of habitat distributions, there are several useful purposes for these studies in environmental management. Finnish peatlands are disappearing rapidly. At one time, peatlands covered about one third (100 000 km^2) of the country. At present, the total area of peatlands has decreased to about 40 000 km^2. To conserve these areas we clearly need more information on their faunas and floras. Descriptive models, such as presented here, could be useful in making projections about the populations of species that use peatlands. If we know the specific habitat requirements of the species and the degree of change in the environment (e.g. due to logging or peatland drainage) we should be able to predict approximate population responses to environmental changes.

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Selostus: **Soilla pesivien varpuslintulajien esiintyminen kasvillisuudeltaan erilaisissa suoympäristöissä Itä-Suomessa**

Tutkimme suolinnuston populaatiotiheyksiä ja lajien makro- ja mikrohabitaatteja Itä-Suomessa (Ilomantsissa, Lieksassa ja Parikkalassa). Tutkimusalueina oli avoimia, pensaikkoisia ja metsäisiä suotyyppejä. Lintutiheydet arvioitiin kartoitus- ja linjalaskentamenetelmillä. Pesimäpaikkojen (14 lajia) makrohabitaatin rakenne mitattiin kvantitatiivisesti kymmenen muuttujan avulla (kuva 1), jotka olivat kasvillisuuden korkeus, aluskasvillisuuden peittävyys, puiden tiheys, pensaiden tiheys, pensaiden korkeus, varpujen tiheys (horisontaalisesti ja vertikaalisesti), ruohojen tiheys (horisontaalisesti ja vertikaalisesti) ja avoveden määrä. Lajien mikrohabitaatin kuvaamiseen käytettiin yhdeksää jatkuvaa ja luokittelevaa muuttujaa.

Lajien pesimähabitaatit on esitetty kuvassa 2. Keltavästäräkki ja niittykirvinen olivat avoimien ympäristöjen valtalajit. Pajusirkku ja ruokokerttunen esiintyivät runsaimpina pensaikkoalueilla ja pajulintu, peippo ja metsäkirvinen puustoisilla habitaateilla.

Peippo ja järripeippo esiintyivät rakenteellisesti samanlaisissa ympäristöissä, mutta erosivat mikrohabitaatin käytön suhteen. Keltavästäräkin ja metsäkirvisen ruokailu- ja laulaupaikat olivat erilaiset.

Kvantitatiiviseen kasvillisuuden kuvaukseen ja lajien esiintymisen mukaisesti esitämme kvalitatiivisen mallin, jonka mukaan voidaan arvioida lintuyhteisön muutos, kun ympäristö muuttuu tietyllä tavalla (kuva 2). Tämäntyyppisiä malleja voitaneen käyttää mm. arvioitaessa ympäristömuutosten vaikutuksia.

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