

# Foraging niches of foliage-gleaning birds in the northernmost taiga in Finland

Raimo Virkkala

Virkkala, R. 1988: Foraging niches of foliage-gleaning birds in the northernmost taiga in Finland. - *Ornis Fennica* 65:104-113.

The study area was located near the northern coniferous forest margin. Seven niche dimensions (habitat, tree species, tree size, feeding height in tree, tree part, foliage substrate, feeding technique) were recorded and these were combined in four multidimensional axes. The foliage-gleaning guild consisted of four species, which comprised 52-76% of the total bird community, depending on forest type. The Siberian Tit *Parus cinctus* and the Siberian Jay *Perisoreus infaustus* are specialists of virgin coniferous forests, whereas the Brambling *Fringilla montifringilla* and the Willow Warbler *Phylloscopus trochilus* are forest habitat generalists.

The multidimensional (seven-dimensional) foraging niches of the Siberian Tit and Siberian Jay were broader than those of the Brambling and Willow Warbler. Tree species, tree part and foliage substrate were the most important dimensions segregating the foliage-gleaning species from each other. The foraging niche of the Siberian Jay deviated most from those of the other species. Body size was connected with segregation of species on the microhabitat dimensions, especially on tree part and foliage substrate, but not on macrohabitat (habitat, tree species, tree size) and foraging height dimensions. Body size differences can be considered effective with respect to the foraging of the species.

The broad niches of the two sedentary species, the Siberian Tit and Siberian Jay, are suggested to be adaptations to the harsh physical conditions in these northern latitudes. The migratory species, the Brambling and Willow Warbler, preferred seasonally abundant foraging resources in deciduous trees and on leaves and needles. Due to forest management, the Willow Warbler has increased in northern Finland during recent decades, whereas the Siberian Tit and Siberian Jay have decreased. These population trends are discussed in relation to the foraging niches of the species.

Raimo Virkkala, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

## Introduction

The niche concept has become important in studying the structure of bird communities. The niche of a species may be considered within the framework of multidimensional space (Hutchinson 1957, Schoener 1974). Foraging patterns of species have been of key importance in analysing niche relations, and studies dealing with foliage-gleaning birds have been common, especially during recent decades (e.g., Alerstam et al. 1974, Nilsson & Alerstam 1976, Ulfstrand 1976, 1977, Hogstad 1978, Alatalo 1980, 1982a, Moreno 1981, Sæther 1982; but see Haftorn 1956, MacArthur 1958 for impressive early studies). Many studies have

stressed the importance of interspecific interactions, apparent as shifts in the foraging niches (for references, see Alatalo 1982b, Alatalo et al. 1986). Other important questions connected with the foraging niche organization of foliage-gleaning birds are seasonal dynamics (Alatalo 1980) and differences in foraging niches between sedentary and migratory species (Herrera 1978).

In this study I investigate the foraging niche organization of the foliage-gleaning guild in the northern taiga, near the northern coniferous forest margin. The most important questions addressed are:

1. How do the extreme northern conditions affect foraging niche breadths of species? Does the niche

breadth differ between sedentary and migratory species? 2. What are the most important niche dimensions segregating the species or on which dimensions are niche overlaps between species lowest? 3. How much do morphological differences among the species and/or species interactions influence the feeding niches? 4. Can regional changes in the bird fauna (see Järvinen & Väisänen 1979, Helle & Järvinen 1986, Virkkala 1987a) and changes on a local level between habitats (Helle 1985, Väisänen et al. 1986, Virkkala 1987b) be related to species-specific preferences on the microhabitat (within-habitat) level? Large-scale forest management in northern Finland has increased the numbers of species preferring forest edges and deciduous forests, whereas species of virgin coniferous forests have decreased (Helle & Järvinen 1986).

## Material and methods

### Niche dimensions

Foliage-gleaning birds were observed in northern Finnish Lapland, in the forests near Vuotso, Sodankylä (68°N, 27°E). The area is mainly covered by both virgin and managed coniferous forests. Foraging data were gathered between 19 June and 14 July in 1982, and 9 June and 24 July in 1983. The following niche dimensions were recorded:

**Habitat.** Four categories were separated: 1) pure pine forest, 2) pine-dominated forest (>50% of pine), 3) spruce-dominated forest (>50% of spruce), and lush birch-dominated forest (>50% of birch).

**Tree species.** The foraging-tree categories were: pine, spruce, birch, ground and air.

**Tree size:** tall tree (>5 m high), low tree (<5 m).

**Foraging height.** Relative foraging height in tree: lowest, second, third and top quarter.

**Tree part:** trunk; inner, middle and outer zone (in third parts) in the foliage.

**Foliage substrate:** branch (>25 mm in diameter), branchlet (12–25 mm), twig (6–12 mm), and leaf or needle base (<6 mm).

**Feeding technique:** glean, hang-glean, snatch, hover, and flycatch.

Niche dimensions were studied in the way presented by Alatalo (1980, 1982a), with the exception that I separated tree part and foliage substrate from each other, because twigs and leafed or needled twigs are also situated in the middle and inner foliage zones.

The niche dimensions can be considered hierarchical, as follows: between-habitat (1), within-habitat (2, 3), within-tree (4, 5), and within-foliage (6, 7) dimensions.

I made at most five foraging observations per individual. The numbers of foraging records/individual averaged (in parentheses total number of observations): the Siberian Tit *Parus cinctus* 2.4 (418), Willow Warbler *Phylloscopus trochilus* 2.4 (155), Siberian Jay *Perisoreus infaustus* 1.9 (91), and Brambling *Fringilla montifringilla* 1.8 (160).

In the foraging sites of Siberian Tits quantitative habitat descriptions were carried out. In these sites the diameters of all the trunks were measured in an area of 600–900 m<sup>2</sup> (Virkkala 1985 and Virkkala & Liehu, in prep.), and the trunks over 7 cm in diameter were taken into account in calculating the expected tree species composition in the foraging sites.

### Niche metrics

For calculating niche breadths, I used the antilogarithm of Shannon's diversity measure ( $\exp H'$ ). Niche breadth in every dimension was standardized to be proportional to the largest niche observed (1.00) in a particular dimension. Multidimensional niche breadths were studied by combining the dimensions probably most dependent on each other (see Alatalo 1980, 1982a):

1. Habitat, tree species, tree size (20 classes).

2. Feeding height, horizontal tree part (17 classes).

3. Foliage substrate, feeding technique (11 classes).

In calculating the seven-dimensional niche breadth, I used the summation method for multidimensional dimensions (see Hanski 1978). Habitat, tree species and tree size are considered macrohabitat dimensions and the others microhabitat dimensions.

Pairwise overlaps between species were calculated by using percentage similarity,  $PS = \sum \min(p_{xi}, p_{yi})$ , which is the sum of the minimum relative frequencies over all the resource categories (Renkonen 1938, Hurlbert 1978, Alatalo & Alatalo 1979).

Multidimensional niche breadth and overlap are usually measured by using indices (see Colwell & Futuyma 1971, Alatalo & Alatalo 1977, Hanski 1978, Hurlbert 1978, Feisinger et al. 1981). Statistical testing of the results is difficult, because of the use of indices, and because the observations are not totally independent. Thus, the interpretation of the results is subjective (A. Järvinen, pers. comm.).

Table 1. Densities (pairs/km<sup>2</sup>) and number of observations of species (survey belt, in parentheses) according to line transect censuses. The total bird densities and proportion (%) of foliage-gleaning birds in different forest types are also presented. Species abbreviations: Siberian Tit = *Par cin*, Siberian Jay = *Per inf*, Brambling = *Fri mon*, Willow Warbler = *Phy tro*.

	<i>Par cin</i>	<i>Per inf</i>	<i>Fri mon</i>	<i>Phy tro</i>	Total	%
Virgin pine forest	2.8 (7)	1.2 (3)	29.1 (245)	9.5 (103)	61	69.6
Managed pine forest	0.5 (2)	0.3 (1)	16.5 (207)	12.1 (187)	57	51.9
Spruce forest	3.9 (13)	2.1 (7)	40.2 (450)	12.6 (185)	79	75.6
Birch forest	3.9 (5)	1.6 (2)	50.2 (214)	20.6 (214)	101	76.3
Mean	2.5	1.2	31.1	12.7	75	68.4

### Line transects

Densities of birds were calculated from line transect censuses carried out between 21 June and 3 July in 1982, and 15 June and 1 July in 1983. The calculations were based on the survey belt observations (see Virkkala 1987a, 1987b). The line transects were censused (in km) in different habitats, as follows:

virgin pine forest	21.8
managed pine-dominated forest	31.0
virgin spruce-dominated forest	29.6
virgin birch-dominated forest	12.0

On the basis of the censuses, the habitat amplitudes of the foliage-gleaning species were calculated as

$$B' = Y^2 / (A \sum (y_i^2 / a_i)),$$

where Y is the total number of observations of species, A is the total length of the line transect in km,  $y_i$  the number of observations in habitat type i, and  $a_i$  the length of the line transect in km in habitat type i. The value 1.00 indicates that each habitat type is utilised in proportion to its abundance (Hurlbert 1978).

## Results

### Bird densities in different forest types

Foliage-gleaning birds formed the most abundant feeding guild in these northern forests. They comprised 52–76% of the bird community in different forests (Table 1). For the proportion of other feeding guilds observed in these forests, see Virkkala (1987b: Table 5). In all types of forests, the two most numerous species were the Brambling and Willow Warbler. Besides these four main species (see Table 1), some less numerous foliage-gleaning birds were observed, such as the Willow Tit *Parus montanus* and

Goldcrest *Regulus regulus*. The habitat amplitudes (B') of the most common foliage-gleaning species were:

Siberian Tit	0.76
Siberian Jay	0.74
Brambling	0.89
Willow Warbler	0.94

In my data set, the Brambling and Willow Warbler seemed to have larger habitat amplitudes than the Siberian Tit and Siberian Jay. More generally also, the Brambling and Willow Warbler can be considered forest habitat generalists, whereas the Siberian Tit and Siberian Jay are specialists of old forests (see Virkkala 1987b).

### Foraging niche breadth

One- and multidimensional niche breadths are presented in Table 2. When all dimensions are considered, the Siberian Tit and Siberian Jay seem to have broader niches than the Brambling or Willow Warbler. The Willow Warbler and Brambling forage most often in birches and the Siberian Jay in coniferous trees (Table 3). The Willow Warbler is also most specialized on the tree-species dimension.

The tree species composition was estimated in the foraging sites of Siberian Tits. When the observed foraging tree distribution is compared with the expected one (Table 4), it is found that in both the nesting (June) and fledgling period (July) Tits preferred coniferous to deciduous trees. The preference was particularly marked in the nesting period, but the difference was also statistically significant in the fledgling period, due to the much larger sample size. In birch-dominated forests Siberian Tits preferred coniferous trees, but in spruce- and pine-dominated forests they foraged according to the expected tree species composition (Table 4).

Table 2. One- and multidimensional niche breadths of species. The values have been scaled to be proportional to the largest niche on each dimension. Macrohabitat dimension = habitat — tree species — tree size; Microhabitat<sub>A</sub> = feeding height — tree part; Microhabitat<sub>B</sub> = foliage substrate — feeding technique. For abbreviations of species names, see Table 1.

One-dimensional							
	Habitat	Tree species	Tree size	Feeding height	Tree part	Foliage substrate	Feeding technique
<i>Par cin</i>	1.00	0.71	0.86	0.77	0.95	0.47	0.76
<i>Per inf</i>	0.65	0.74	0.79	1.00	1.00	1.00	0.13
<i>Fri mon</i>	0.93	1.00	0.86	0.39	0.68	0.57	0.25
<i>Phy tro</i>	0.89	0.46	1.00	0.47	0.27	0.23	1.00
Multidimensional							
	Macrohabitat	Microhabitat <sub>A</sub>	Microhabitat <sub>B</sub>	Total			
<i>Par cin</i>	1.00	0.69	1.00	1.00			
<i>Per inf</i>	0.29	1.00	0.46	0.91			
<i>Fri mon</i>	0.97	0.26	0.47	0.61			
<i>Phy tro</i>	0.86	0.13	0.72	0.49			

Table 3. Percentage distribution of feeding of species in different tree species, on the ground and in the air.

	Spruce	Pine	Birch	Ground	Air	n
<i>Par cin</i>	24.2	38.3	31.3	6.2	0.0	418
<i>Per inf</i>	33.0	33.0	6.6	27.5	0.0	91
<i>Fri mon</i>	18.1	22.5	43.8	10.0	5.6	160
<i>Phy tro</i>	13.5	25.2	58.1	2.6	0.6	155

On the tree-part dimension (Fig. 1) the Siberian Tit most often foraged on the trunk and in the outer foliage zone, the Siberian Jay in the middle zone, the Brambling in the middle and outer zone, and the Willow Warbler almost entirely in the outer zone (Fig. 1). The Brambling, Willow Warbler and Siberian Tit prefer the upper half of the tree, whereas the Siberian Jay forages evenly in the whole tree (Fig.

Table 4. Observed and expected tree species composition (%) in foraging sites of Siberian Tits during the nesting and fledgling period and in spruce-, pine- and birch-dominated forests. In parentheses absolute numbers of tree species on which  $\chi^2$ -tests between observed and expected tree species distributions are based.

	Pine		Spruce		Birch		P
Nesting period							
Observed	32.5	(13)	60.0	(24)	7.5	(3)	0.001
Expected	34.1	(119)	24.7	(67)	41.2	(93)	
Fledgling period							
Observed	42.7	(119)	24.0	(67)	33.3	(93)	0.001
Expected	31.3	(728)	30.3	(705)	38.4	(892)	
Pine-dominated forests							
Observed	83.3	(120)	3.5	(5)	13.2	(19)	ns
Expected	79.3	(677)	4.4	(38)	16.3	(139)	
Spruce-dominated forests							
Observed	3.0	(3)	60.6	(60)	36.4	(36)	ns
Expected	1.9	(17)	62.3	(553)	35.8	(318)	
Birch-dominated forests							
Observed	11.8	(9)	34.2	(26)	54.0	(41)	0.001
Expected	5.8	(34)	19.6	(114)	74.6	(435)	

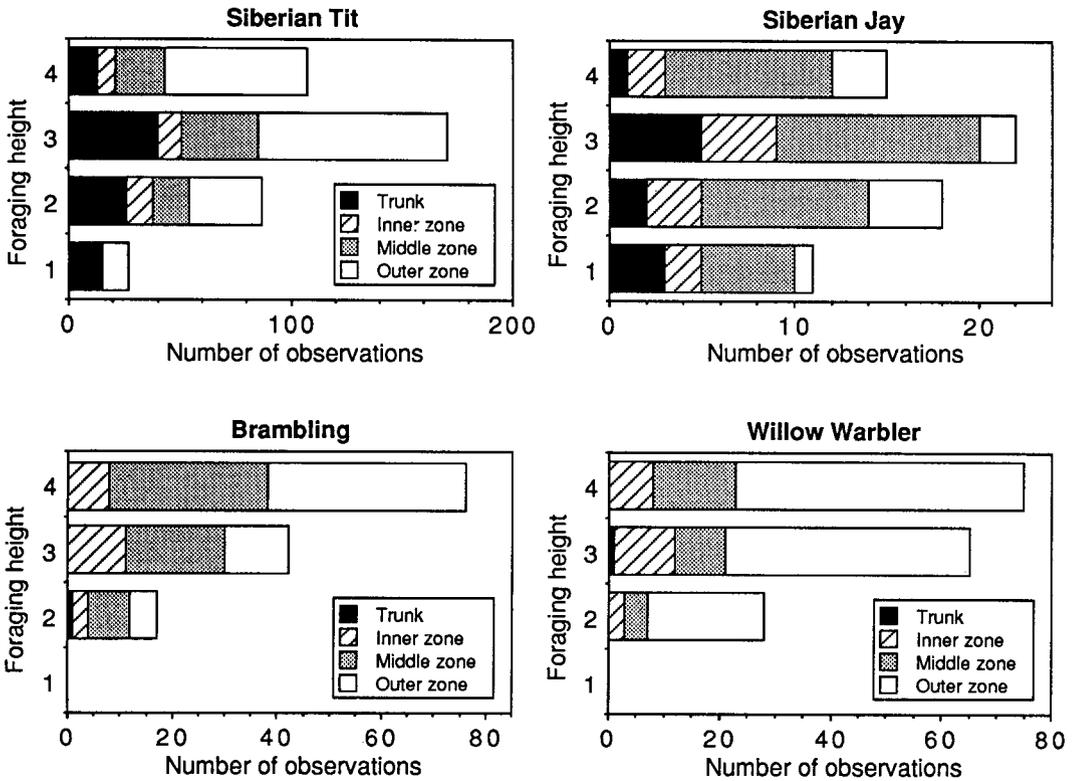


Fig. 1. Foraging of the species in the trees. 1 = lowest quarter, 2 = second, 3 = third, and 4 = top quarter.

Table 5. Percentage distribution of feeding of species on different substrates in the foliage. Diameters of substrates presented (in mm).

	Leaf or needle base (<6)	Twig (6-12)	Branchlet (12-25)	Branch (>25)	n
<i>Par cin</i>	65.6	17.2	12.6	4.6	302
<i>Per inf</i>	10.7	35.7	30.4	23.2	56
<i>Fri mon</i>	44.2	42.8	10.1	2.9	138
<i>Phy tro</i>	79.3	14.7	4.0	2.0	150

1). The Siberian Tit and Willow Warbler use mainly the leaf or needle base in the foliage (Table 5), the Brambling both the leaf or needle base and twigs, and the Siberian Jay prefers thicker branches.

On microhabitat dimensions (except feeding technique), the Siberian Jay has the broadest niche in the guild (Table 2). Probably due to their fairly large size for foliage-gleaners, Siberian Jays and Bramblings are very stereotypic in feeding technique.

*Foraging niche overlaps and segregation*

When multidimensional species-pair niche overlaps are considered, the foraging niche of the Siberian Jay is most segregated from those of the other species, (Table 6). The values of the niche overlaps are between 0.31 and 0.65 for the Siberian Jay, but between 0.60 and 0.76 for the other species. Along the one-dimensional axes, the average between-species overlap is smallest on the dimensions of tree species, tree part and foliage substrate.

**Discussion**

*Niche breadth and habitat amplitude*

Although the Brambling and Willow Warbler are the two most abundant species in these forests, their total niches are narrower than those of two clearly rarer species, the Siberian Jay and Siberian Tit. The correlation between abundance and foraging niche breadth is not positive ( $r=-0.69$ ,  $df=2$ , ns). Compared

Table 6. Species-pair overlaps on one- and multidimensional axis (see Table 2).

	One-dimensional						
	Habitat	Tree species	Tree size	Feeding height	Tree part	Foliage substrate	Feeding technique
<i>Par cin-Per inf</i>	0.83	0.70	0.98	0.86	0.58	0.45	0.64
<i>Par cin-Fri mon</i>	0.77	0.78	1.00	0.71	0.68	0.74	0.69
<i>Par cin-Phy tro</i>	0.89	0.73	0.96	0.80	0.72	0.86	0.69
<i>Per inf-Fri mon</i>	0.82	0.57	0.98	0.66	0.74	0.59	0.92
<i>Per inf-Phy tro</i>	0.80	0.48	0.94	0.74	0.37	0.31	0.65
<i>Fri mon-Phy tro</i>	0.86	0.83	0.96	0.91	0.63	0.65	0.73
Mean	0.83	0.68	0.97	0.78	0.62	0.60	0.72

	Multidimensional			
	Macrohabitat	Microhabitat <sub>A</sub>	Microhabitat <sub>B</sub>	Mean
<i>Par cin-Per inf</i>	0.65	0.54	0.43	0.54
<i>Par cin-Fri mon</i>	0.73	0.58	0.65	0.65
<i>Par cin-Phy tro</i>	0.71	0.62	0.59	0.64
<i>Per inf-Fri mon</i>	0.49	0.55	0.59	0.54
<i>Per inf-Phy tro</i>	0.47	0.33	0.31	0.37
<i>Fri mon-Phy tro</i>	0.76	0.60	0.65	0.67
Mean	0.64	0.54	0.54	

with the scarce sedentary species, the Siberian Tit and Siberian Jay, the abundant migratory Brambling and Willow Warbler are macrohabitat (between-habitat) generalists, but microhabitat specialists. The narrow habitat amplitude of the sedentary species may be caused by the fact that the populations of these species are strongly regulated by winter, and they therefore nest only in the most productive, optimal habitats (R. Alatalo, pers. comm.).

The broad niches of the sedentary Siberian Tit and Siberian Jay might be an adaptation to an unpredictable environment with harsh winters (see Levins 1968). During normal winters the availability of prey items is probably low and the daylight period is short. Thus the sedentary species cannot be specialized in their foraging patterns. For instance, the range of the Coal Tit *Parus ater* does not reach the northern limit of its preferred spruce forest. Snow (1954, 1955) argues that the specialized foraging of the Coal Tit is due to the fine beak of the species, which is probably an adaptation to collecting small food particles. This might limit the ability of the species to obtain enough food to survive the intense cold. According to Alatalo (1982a), near the northern limit of its range (65°N), the Coal Tit has the narrowest niche of the foliage-

gleaners in winter (excluding the trunk-gleaning Treecreeper *Certhia familiaris*).

Nilsson & Alerstam (1976) studied the foraging niches of the Tit guild in northern Finland (66°N) in autumn. They observed that the Siberian Tit and Siberian Jay had the broadest niches (generalists) in the guild, which contained four additional species: the Willow Tit, Great Tit *Parus major*, Crested Tit *Parus cristatus* and Treecreeper. My study area is situated north of the boundaries of the Crested Tit and Treecreeper; the Great Tit occurs only near human settlements and the Willow Tit is very rare in summer. The study of Nilsson & Alerstam (1976) supports the idea that the northern distributions of the Siberian Tit and Siberian Jay are reflected in their broad feeding niches and generalized microhabitat selection.

As the Siberian Tit is the only abundant Tit species in this area in summer, interspecific competition may not greatly affect its niche size (R. Alatalo, pers. comm.).

The migratory species, the Brambling and Willow Warbler, are concentrated on seasonally abundant foraging resources, e.g., on deciduous trees and leaf or needle bases. Alatalo (1982a) reported that in

northern Finland summer visitors often exploit resources seldom used by residents, e.g., those found in deciduous trees.

The Siberian Jay is clearly heavier than the other species in the guild, and in consequence its body size varies more widely among individuals. The Siberian Jay can thus utilize a larger range of prey items, which probably increases its foraging niche breadth in relation to those of the other smaller species (see Schoener 1974). The Siberian Jay is also very versatile in foraging (but not in feeding technique), eating both insects and spiders in the trees, berries, small mammals, etc. (von Haartman et al. 1963–72).

#### *Resource partitioning and species interactions*

Along multidimensional (two- and three-dimensional) axes, the species-pair overlaps seemed to be fairly large (values between 0.31–0.76). The values are of the same magnitude as in the study of Alatalo (1982a; values between 0.35–0.63), although he measured full six-dimensional overlaps. According to Alatalo (1982a), his results reflect relatively regular spacing of species in the multidimensional space. In my study the Siberian Jay was the most segregated of the species: its mean species-pair overlaps were lowest along all three multidimensional axes and on five out of seven one-dimensional axes.

Similar-sized species tend to forage similarly (Cody 1974) and within a foraging guild body size correlates positively with average prey size (Hespenheide 1971). In this study there were great differences in body size among foliage-gleaning species, the heaviest species, the Siberian Jay, weighing 82 g and the lightest, the Willow Warbler, 9.4 g (according to von Haartman et al. 1963–72). In order to estimate the effect of morphological differences on the segregation of species, I studied the correlations of species-pair weight relations and species-pair overlaps on every dimension (Table 7). Statistically significant negative correlations existed on the dimensions of tree part and feeding substrate, and on both multidimensional microhabitat axes. Thus, body size was connected with segregation of species on microhabitat dimensions, especially horizontally (tree part, foliage substrate), but not on macrohabitat or vertical (foraging height) dimensions. This result is basically the same as that of Alatalo (1982a).

Body size differences are clearly reflected in feeding in the foliage: the Siberian Jay prefers twigs

Table 7. Correlations between all species-pair weight relations and species-pair niche overlaps ( $df = 4$ ) over all the dimensions. The weights of the species, taken from von Haartman et al. (1963–72), are as follows: Siberian Tit 11.7 g, Siberian Jay 82.0 g, Brambling 22.1 g and Willow Warbler 9.4 g.

Dimension	Correlation	P
Habitat	-0.35	ns
Tree species	-0.72	ns
Tree size	-0.42	ns
Feeding height	-0.03	ns
Tree part	-0.85	0.05
Foliage substrate	-0.97	0.01
Feeding technique	-0.32	ns
Macrohabitat	-0.69	ns
Microhabitat <sub>A</sub>	-0.87	0.05
Microhabitat <sub>B</sub>	-0.95	0.01

and branches; the second heaviest species, Brambling, forages on both leaf or needle bases and twigs; the light Siberian Tit and Willow Warbler clearly prefer leaf or needle bases (Table 6). The stereotypic feeding techniques of the Siberian Jay and Brambling (mainly gleaning) are probably also connected with the large size of these species compared with the Siberian Tit and Willow Warbler.

Competition between species should be observed as complementarity of different dimensions (Schoener 1974). This means that a high value for pairwise overlap or niche breadth on one dimension should be compensated by a low value on another dimension. Of the niche breadth correlations between two dimensions (24), ten were positive, fourteen negative, and none of them was statistically significant. The correlations between mean species overlaps show eight negative and sixteen positive correlations, of which only two are statistically significant (habitat/feeding height,  $r=0.969$ ,  $P<0.05$ , tree species/feeding substrate,  $r=0.996$ ,  $P<0.001$ ,  $df=2$ ). My data do not thus indicate any complementarity between niche dimensions. However, the dimensions selected for the study are not totally independent, which affects the result (Schoener 1974).

The size differences among the species are considerable, and thus species interactions are not very likely, because competitive interactions usually occur between similar-sized species. Connell (1975, 1980) proposed that interspecific competition more probably occurs in moderate but not in very harsh environments, because the extreme physical conditions

reduce populations below the carrying capacity of the resources. In my study area, situated near the northern coniferous forest margin, the physical conditions can without doubt be considered very harsh.

In a recent study, Alatalo & Carlson (1987) showed that interspecific competition was involved in the food-storing behaviour of the Siberian and Willow Tits, the Siberian Tit being the dominant species. They studied the hoarding-site preferences of the two species in northern Sweden by comparing two areas, one with only the Willow Tit, the other with both species. The Willow Tit changed its hoarding sites in the presence of the Siberian Tit. However, the study did not contain any samples from areas where the Siberian Tit was the only species and it is thus possible that the Siberian Tit changes its hoarding sites in the presence of the Willow Tit. Besides being considered a consequence of interspecific competition, these results can also be interpreted as spatial isolation on the microhabitat level (see Schoener 1974). These two species are similar in size and morphology, and there are several observations of interbreeding (Hildén & Ketola 1985, Järvinen et al. 1985, Järvinen 1987). Thus microhabitat isolation is possible in an area of sympatry.

In my study area the Willow Tit occurs relatively abundantly after migrations in autumn and winter (for densities, see Virkkala 1987b), but most individuals disappear in the spring. I suggest this is due to a lack of the preferred breeding habitats of Willow Tits in this area: lush, deciduous forests along riversides have been destroyed by water-power construction. Near the northern margin of their ranges species are usually found in the most productive habitats, so that habitat selection, as also microhabitat selection, differs from that in more southern areas (see Alatalo & Carlson 1987). This makes it difficult to show that niche shifts are due to interspecific competition, when species are compared in a large region of allopatry and sympatry.

#### *Consequences of foraging preferences*

Due to forest management, large-scale habitat changes have occurred in northern Finland during the last 30–40 years (Järvinen et al. 1977, Helle & Järvinen 1986). Clear-cuttings and thinnings have increased the amount of deciduous trees and bushes, while earlier uniform virgin coniferous forests have been reduced and fragmented. In addition, deciduous

trees and bushes have increased at the edges of fragments of coniferous forests and on the drained mires (Väisänen & Rauhala 1983, Väisänen et al. 1986). These changes in the structure of northern forests have caused changes in the abundance of many bird species during the recent decades. For instance, the Willow Warbler, which prefers deciduous forests, has increased, and the Siberian Jay and Siberian Tit, which prefer virgin coniferous forests, have decreased (Järvinen & Väisänen 1979, Väisänen et al. 1986). Tree species preferences of foraging Willow Warblers, Siberian Tits and Siberian Jays can thus be connected with the changes in the structure of northern forests.

Willow Warblers prefer birches for foraging, whereas Siberian Jays and Siberian Tits favour coniferous trees (the Siberian Tit especially during the nesting period, see Table 4). The species richness of macrolepidopteran larvae (Niemelä et al. 1982) and the density of invertebrates (Hågvar 1976) on birch are highest in mid and late summer (July–August). At these latitudes, the Willow Warbler starts breeding in late June (J. Tiainen and J. Tuomenpuro, unpubl.) at the time when birches are coming into leaf. During the nestling and fledgling period (July) of Willow Warblers, birches provide a surplus of food. Siberian Jays breed in April–May and Siberian Tits in May–June (see von Haartman et al. 1963–72), when the birches have clearly smaller numbers of invertebrates. Although Siberian Jays and Siberian Tits take food on the ground in the spring, they more regularly forage in the trees (my own observations). The Siberian Tit has been observed to prefer coniferous to deciduous trees when foraging in late autumn (Nilsson & Alerstam 1976), and also in late winter for hoarding (Alatalo & Carlson 1987). In Norway the Willow Warbler preferred birches in mixed forests in the later part of the breeding season (July), probably as a consequence of an increase in the amount of food available (Angell–Jacobsen 1980). The decrease of old coniferous trees is thus disadvantageous to the foraging of the Siberian Tit and Siberian Jay, whereas the increase of deciduous trees due to silvicultural practices favours the foraging patterns of the Willow Warbler.

*Acknowledgements.* R. Alatalo, Y. Haila, A. Järvinen, O. Järvinen, S. G. Nilsson, J. Tiainen and K. Vepsäläinen read my manuscript and made many valuable comments. This study was supported financially by the Emil Aaltonen Foundation and the Academy of Finland.

## Selostus: Millaiset ovat lehvästössä ruokailevien lintujen ekolokerot Pohjois-Lapissa?

Mittasin Sodankylän Vuotson ympäristössä kesä-heinäkuussa 1982–83 lehvästössä ruokailevien lintujen ruokailulokeron seitsemän eri dimensiota (elinympäristö, puulaji, puun koko, ruokailukorkeus puussa, puun osa, lehvästön osa, ruokailutapa), jotka yhdistin neljäksi moniulotteiseksi akseliksi. Lehvästökiltaan kuului neljä lajia, joiden osuus kokonaislintuheydestä eri metsätyypeillä vaihteli 52–76%:iin. Lehvästökiltaan kuului neljä lajia, joiden osuus kokonaislintuheydestä eri metsätyypeillä vaihteli 52–76%:iin. Lehvästökiltaan lajit ja ruokailuhavaintojen määrät olivat: lapintiaainen (N=418), kuukkeli (N=91), järripeippo (N=160) ja pajulintu (N=155). Paikkalinnut lapintiaainen ja kuukkeli ovat erikoistuneet vanhoihin havumetsiin, kun taas muuttolinnut järripeippo ja pajulintu ovat metsien yleislajeja.

Lapintiaisen ja kuukkelin seitsenulotteiset ravinnonhankintalokerot olivat laajempia kuin järripeipon ja pajulinnun. Lajien lokeroiden päällekkäisyys oli pienin puulajin, puun osan ja lehvästön osan suhteen. Kuukkelin ravinnonhankinta erosi selvimmän muista lajeista. Lajien kokoerot vaikuttivat ravinnonhankintaan mikrohabitaattitasolla (puun osa ja lehvästön osa), mutta ei makrohabitaattitasolla (elinympäristö, puulaji, puun korkeus) eikä ruokailukorkeuden suhteen.

Paikkalintujen laajojen ruokailulokeroiden oletettiin olevan sopeutuvia pohjoisiin ankaariin ympäristöolosuhteisiin. Lapintiaainen ja kuukkeli suosivat havupuita ruokaillessaan. Muuttolinnut sen sijaan hankkivat ravintonsa erityisesti kesällä runsasarvintoisista lehtipuista sekä lehti- ja neulasoksilta. Metsätalouden seurauksena vanhat havupuut ovat vähentyneet ja lehtipuut enentyneet Pohjois-Suomessa. Metsätalouden aiheuttama metsien rakennemuutos on epäedullista lapintiaisen ja kuukkelin ravinnonhankinnalle, mutta suosii pajulintua.

## References

- Alatalo, R. V. 1980: Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. — *Oecologia* (Berl.) 45:190–196.
- Alatalo, R. V. 1982a: Multidimensional foraging niche organization of foliage-gleaning birds. — *Ornis Scand.* 13:56–71.
- Alatalo, R. V. 1982b: Evidence for interspecific competition among European tits *Parus* spp.: a review. — *Ann. Zool. Fennici* 19:309–317.
- Alatalo, R. V. & Alatalo, R. H. 1977: Components of diversity: multivariate analysis with interaction. — *Ecology* 58:900–906.
- Alatalo, R. V. & Alatalo, R. H. 1979: On the measurement of niche overlap. — *Aquilo Ser. Zool.* 20:26–32.
- Alatalo, R. V. & Carlson, A. 1987: Hoarding-site selection of the Willow Tit *Parus montanus* in the presence of the Siberian Tit *Parus cinctus*. — *Ornis Fennica* 64:1–9.
- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1986: Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of nonexperimental data. — *Amer. Nat.* 127: 819–834.
- Alerstam, T., Nilsson, S. G. & Ulfstrand, S. 1974: Niche differentiation during winter in woodland birds in southern Sweden and the island of Gotland. — *Oikos* 25:321–330.
- Angell-Jacobsen, B. 1980: Overlap in feeding pattern between Willow Warbler *Phylloscopus trochilus* and Brambling *Fringilla montifringilla* in two forest habitats in western Norway. — *Ornis Scand.* 11:146–154.
- Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton Univ. Press, Princeton.
- Colwell, R. K. & Futuyma 1971: On the measure of niche breadth and overlap. — *Ecology* 52:567–576.
- Connell, J. H. 1975: Some mechanisms producing structure in natural communities: a model and evidence from field experiments. — In: Cody, M. L. & Diamond, J. M. (eds.), *Ecology and evolution of communities*, pp. 460–490. Harvard Univ. Press, Cambridge, Mass.
- Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of competition past. — *Oikos* 35:131–138.
- Feisinger, P., Spears, E. E. & Poole, R. W. 1981: A simple measure of niche breadth. — *Ecology* 62:27–32.
- von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvoin I–II. — Otava, Helsinki.
- Haftorn, S. 1956: Contribution to the food biology of tits, especially about storing of surplus of food. Part IV. A comparative analysis of *Parus atricapillus* L., *Parus cristatus* L. and *Parus ater* L. — *Kgl. Norsk. Vidensk. Selsk. Skr.*, No. 4:1–54.
- Hanski, I. 1978: Some comments on the measurement of niche metrics. — *Ecology* 59:168–174.
- Helle, P. 1985: Effects of forest regeneration on the structure of bird communities in northern Finland. — *Holarct. Ecol.* 8:120–132.
- Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — *Oikos* 46:107–115.
- Herrera, C. 1978: Ecological correlates of residence and non-residence in Mediterranean passerine bird community. — *J. Anim. Ecol.* 47:871–890.
- Hespenheide, H. A. 1971: Food preference and the extent of overlap in some insectivorous birds, with special reference to the tyrannidae. — *Ibis* 113:59–72.
- Hildén, O. & Ketola, H. 1985: A mixed pair of *Parus cinctus* and *P. montanus* nesting in Kuusamo. — *Ornis Fennica* 62:26.
- Hogstad, O. 1978: Differentiation of foraging niche among tits, *Parus* spp., in Norway during winter. — *Ibis* 120:139–146.
- Hurlbert, S. H. 1978: The measurement of niche overlap and some relatives. — *Ecology* 59:67–77.
- Hutchinson, G. E. 1957: Concluding remarks. — *Cold Spring Harbour Symp. Quant. Biol.* 22:415–427.
- Hågvar, S. 1976: Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.). — *Norw. J. Ent.* 23:61–74.
- Järvinen, A. 1987: A successful mixed breeding between *Parus cinctus* and *Parus montanus* in Finnish Lapland. — *Ornis Fennica* 64:158–159.
- Järvinen, A., Ylimaunu, J. & Hannila, J. 1985: A mixed nesting pair *Parus montanus* and *P. cinctus* in Finnish Lapland. — *Ornis Fennica* 62:25–26.
- Järvinen, O. & Väisänen, R. A. 1979: Changes in bird populations as criteria of environmental changes. — *Holarct. Ecol.* 2:75–80.

- Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimisten 30 vuoden aikana. (Summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975). — *Silva Fennica* 11:284–294.
- Levins, R. 1968: Evolution in changing environments. — Princeton Univ. Press, Princeton.
- MacArthur, R. H. 1958: Population ecology of some warblers of northeastern coniferous forests. — *Ecology* 39:599–619.
- Moreno, J. 1981: Feeding niches of woodland birds in a montane coniferous forest in central Spain during winter. — *Ornis Scand.* 12:148–159.
- Niemelä, P., Tahvanainen, J., Sorjonen, J., Hokkanen, T. & Neuvonen, S. 1982: The influence of host plant growth form and phenology on the life strategies of Finnish macrolepidopterous larvae. — *Oikos* 39:164–170.
- Nilsson, S. G. & Alerstam, T. 1976: Resource division among birds in North Finnish coniferous forest in autumn. — *Ornis Fennica* 53:15–27.
- Renkonen, O. 1938: Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. — *Ann. Zool. Soc.* "Vanamo" 6:1–231.
- Sæther, B.-E. 1982: Foraging niches in a passerine bird community in a grey alder forest in Central Norway. — *Ornis Scand.* 13:149–163.
- Schoener, T. W. 1974: Resource partitioning in ecological communities. — *Science* 185:27–39.
- Snow, D. W. 1954: Trends in geographical variation in Palearctic members of the genus *Parus*. — *Evolution* 8:19–28.
- Snow, D. W. 1955: Geographical variation of the Coal Tit *Parus ater* L. — *Ardea* 43:195–226.
- Ulfstrand, S. 1976: Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. — *Ornis Scand.* 7:21–27.
- Ulfstrand, S. 1977: Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. — *Oecologia (Berl.)* 27:23–45.
- Virkkala, R. 1985: Lapintiaisen (*Parus cinctus*) ekologiasta hakatulla ja luonnontilaisella metsäalueella Metsä-Lapissa. — M. Sc. Thesis, Dept. Zoology, Univ. Helsinki, 121 pp.
- Virkkala, R. 1987a: Geographical variation in bird communities of old, intact forests in northern Finland. — *Ornis Fennica* 64:107–118.
- Virkkala, R. 1987b: Effects of forest management on birds breeding in northern Finland. — *Ann. Zool. Fennici* 24:281–294.
- Väisänen, R. A. 1983: Pohjois-Suomen maalinuston kannanmuutokset viime vuosikymmeninä. (Summary: Long-term population changes of the most abundant north Finnish land birds during the past 40 years.) — *Aureola* 8:58–65.
- Väisänen, R. A. & Rauhala, P. 1983: Succession of land bird communities on large areas of peatland drained for forestry. — *Ann. Zool. Fennici* 20:115–127.
- Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local populations in boreal forests? — *Ornis Scand.* 17:282–292.

Received 11 May 1988, accepted 4 August 1988

---

## New Zealand 1990 — a joint Nordic group

In December, 1990 the ornithologists of the world will meet in Christchurch, New Zealand. On 2–9 December the 20th International Ornithological Congress will take place on these remote slands. During the congress week there will be lectures, posters, discussion, workshops, films, exhibitions and social events. Both before and after this week there will be excursions to many areas of great interest to bird-watchers.

The Swedish Ornithological Society will, by this advertisement, investigate the possibility of organizing a joint Nordic journey to New Zealand. At this time we are interested only in obtaining preliminary letters of intent. If the number of interested persons is sufficient to reduce travelling costs substantially, we will continue to plan for a common Nordic group.

If you are interested to go to New Zealand, please let us know as soon as possible, and not later than 1 October, 1988. Write to:

Sören Svensson  
Department of Animal Ecology  
Ecology Building  
S-223 62  
Sweden