

# Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland

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Six foraging niche dimensions (habitat, tree species, tree size, height in tree, tree part, feeding posture) were studied and multidimensional niche overlaps and breadths, which take into account the most important dependencies between niche axes, were calculated. The species studied were: *Parus montanus*, *P. cristatus*, *P. major*, *P. ater*, *Phylloscopus trochilus*, *Fringilla coelebs*, *F. montifringilla*, *Regulus regulus* and *Certhia familiaris*. The six-dimensional niche overlaps between common foliage-gleaning birds were 0.35–0.62, indicating relatively regular spacing of species in the multidimensional space, where all species overlap with one another in roughly the same proportions. Tree part was the most important axis for niche separation, perhaps owing to its close association with body size. The two most important axes, tree species and tree part, explained 77% of six-dimensional foraging niche differences in summer and up to 87% in winter. Foraging niche overlap was lower in winter than in summer, perhaps to avoid interspecific competition for limited food resources in winter. Resident foliage-gleaners were small and able to use versatile postures and to exploit needle twigs. Summer visitors, at least partly, used resources rejected by residents (deciduous trees, low trees). Niche width with respect to foraging site decreased in winter, but posture versatility increased. Fewer foraging sites are profitable for birds in winter, but since food is scarce birds cannot be very selective within each foraging site; hence broad niche for microaxes, such as foraging posture. True multidimensional niche overlaps or breadths could not be estimated adequately by one-dimensional projections (summation or production).

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## 1. Introduction

Niche relations of foliage-gleaning passerines, tits in particular, have been extensively studied in Europe (Palmgren 1932, Snow 1949, 1954, Hartley 1953, Gibb 1954, 1960, Betts 1955, Haftorn 1956, Ulfstrand 1962, 1976, 1977, Gibb and Betts 1963, Ludescher 1973, Alerstam et al. 1974, Nilsson and Alerstam 1976, Ulfstrand and Nilsson 1976, Herrera 1978a, 1979, Hogstad 1978, Morse 1978). Furthermore some of the most important niche studies in America have dealt with foliage-gleaners (MacArthur 1958, Root 1967, Morse 1970, Rabenold 1978). These small birds are relatively easy to observe in the field, their foraging site

niche can be quantified along several dimensions (habitat, tree, location in tree etc.), and they are abundant and forage almost uninterruptedly, facilitating gathering of data.

The niche space of animals has been conceived as multidimensional (Hutchinson 1957). However, when examining niche organization, multidimensionality has not been taken into account adequately. Multidimensional niche overlaps have been estimated roughly as averages (assuming totally dependent dimensions) or products (independent) of one-dimensional overlaps (see e.g. Cody 1974). Neither of these assumptions is realistic (May 1975, Alatalo and Alatalo 1977, Hanski 1978) as niche dimensions usually are partly, but not totally, dependent.

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In the present study I have used niche metrics that take into account dependencies between niche axes (May 1975, Alatalo and Alatalo 1977, 1979b) in order to measure niche overlaps and breadths in a six-dimensional niche space. Niche dimensions were selected so as to illustrate, as comprehensively as possible, the foraging site niche differences between foliage-gleaning species. I have studied several problems of the niche organization of foliage-gleaners, many of which concern competition in multidimensional resource niche space:

1. Morphological correlates of niche occupancy (see Karr and James 1975, Pearson 1977, Ricklefs and Cox 1977, Moermond 1979a).
2. Complementarity of niche axes (Cody 1974, Schoener 1974, Pianka 1976).
3. Which are the dimensions that segregate resource niches of different species, and does segregation involve several niche axes (MacArthur 1965, Levins 1968, Schoener 1974, Cohen 1979)?
4. Competition in winter and summer (Baker and Baker 1973, Ulfstrand 1977).
5. The role of residents and migrants in the community (Herrera 1978b).
6. Niche breadth in a seasonal environment (Levins 1968, Baker and Baker 1973).
7. How much do species overlap in their multidimensional foraging site niche (MacArthur and Levins 1967, Roughgarden 1976)?

Short-term fluctuations in the foraging niches of the five most abundant species have been considered elsewhere (Alatalo 1980).

## 2. Material and methods

### 2.1. Field work

The material was gathered in the predominantly coniferous forests near the city of Oulu ( $64^{\circ}57'N$ ,  $25^{\circ}48'E$ ) in northern Finland between March 1975 and March 1976. The following six niche dimensions were studied:

1. Habitat determined in terms of tree species, tree height and soil within 25 m of the location of the observation. There were three important tree species in the forest: pine *Pinus silvestris*, spruce *Picea abies*, and Birch *Betula pubescens*. Habitat categories with their relative proportions in the forest (for estimation see Alatalo 1978b) were: pine forest (22.0%, pines over 5 m high); spruce forest (6.5%, over 5 m high); mixed coniferous forest (9.5%, spruce and pine each made up at least 20% of trees); mixed forest (29.8%, deciduous trees making up at least 20% of trees, pure deciduous forests were very rare); afforested swamp (15.2%, swamps with trees less than 5 m high, mostly recently drained); young forest (16.9%, dry ground and trees less than 5 m

high). The forest was very patchy with respect to these habitat types, birds often changing their habitats during the same observation period.

2. Tree. Foraging tree (or corresponding substrate) categories were: pine, spruce, birch, other deciduous tree (aspen *Populus tremula*, alder *Alnus glutinosa* and willow *Salix* sp.), ground, snow, air, other substrate.
3. Tree size: tall tree (over 5 m high), low tree (including bushes).
4. Height. Relative foraging height in tree: lowest, second, third and top quarter.
5. Tree part. The foraging stations in tree were classified as follows (cf. Alerstam et al. 1974): trunk, branch (diameter over 8 mm), twig (diameter less than 8 mm, in deciduous trees includes leaves), needle-laden twig, seed (cone or birch catkin).
6. Feeding posture according to the bird's position in space and with respect to twigs or branches: horizontal, horizontal and longitudinally along twig, horizontal and transversely on twig, head upwards, hanging upside down (includes head downwards), sited (one side up), hovering.

The six dimensions are roughly hierarchical from macrohabitat axes to microhabitat axes, and they may be grouped as macrosite (habitat, tree, tree size), microsite (site within trees: height, tree part) and feeding posture. Microsite + feeding posture will be referred to as microaxes.

During each month the same areas within the forest were visited, and short series of foraging observations were made on each foraging bird individual encountered. Within each series the foraging site was recorded at 15-s intervals. The number of records in each series was 4.0 on average. Several series were generally recorded on the same individual, and the average numbers of foraging records per individual during the same visit in winter were (for the scientific names, see Tab. 1): Willow Tit 7.5, Goldcrest 8.7, Crested Tit 13.4, Treecreeper 16.7, Great Tit 10.8, Coal Tit 22.7, all species 9.2. In summer the number of records per individual was smaller. Several observations per individual had to be taken because of the low density of birds in these northern forests during the winter (Tab. 1). Moreover appropriate multidimensional niche metrics requires a great deal of data owing to the large number of separate categories. The observations, for macrosites in particular, are not totally independent. Consequently, for tests which require independent observations, I used only one observation per each individual encountered.

Habitat distribution data, most likely to suffer from the dependency of observations, were compared with the results of a separate study on habitat selection, based on weekly line transects in the same forest area (Alatalo 1978b and unpubl. material). Relative frequencies of habitat use by birds correlated highly be-

tween the two independent procedures ( $r = 0.96$ ,  $P < 0.001$ ) for the four most abundant species. Along transects, observations were 20% fewer for spruce forests and mixed coniferous forests, but 20% more frequent for pine forests. The difference was mostly due to the relative scarcity of spruce and mixed coniferous forests along the fixed transects. Line transects provided information about the population densities.

In this paper, in order to give a general picture of niche organization, the monthly observations were pooled to represent the two major seasons: summer (May–September), winter (October–April).

## 2.2. Niche metrics

Components of diversity, according to Alatalo and Alatalo (1977, 1979a), were used to illustrate niche segregation and to measure interactions or dependences of dimensions in niche segregation. I used the antilogarithmic Shannon's entropy ( $\text{expH}'$ ) as the diversity index. Standardizing the average within-category diversity by the species diversity of the guild in the whole forest gives a measure of the average overlap between species ( $L$ ). In this average niche overlap each species becomes weighted by its abundance (Alatalo and Alatalo 1979c). The interaction component of diversity ( $R$ ) measures redundancy or interactive complementarity between axes in segregating species.

When considering resource use overlaps between two species ( $C$ ) or between a species and the rest of the guild ( $G$ ) I used a simple measure of proportional overlap (e.g. Colwell and Futuyma 1971 Eq. 3, Hurlbert 1978 Eq. 1), which is the sum of the minima of the relative frequencies over all categories (recommended by Alatalo and Alatalo 1979c). The overlap between a species and the guild ( $G$ ) was calculated by excluding the species itself from the guild data.

Niche breadth ( $B$ ) was measured by the  $\text{expH}'$ . Original  $\text{expH}'$ -values were standardized by dividing them by the  $\text{expH}'$ -breadths of the pooled annual data for the whole guild. The procedure facilitates the between-dimensions comparisons of niche breadths even though the number of categories varies. Niche breadth 1.00 indicates that the species used the dimension(s) as broadly as the whole guild during the whole year.

May (1975, see also Alatalo and Alatalo 1977, Hanski 1978) stressed that when more than one resource dimension is involved, there is in general no substitute for measuring the species' full multidimensional utilization functions. Each possible combination of one-dimensional categories has to be used as a separate category when estimating multidimensional niche overlaps or breadths. Products or averages of one-dimensional overlaps are very rough approximations of true niche overlap in multidimensional space. The product usually underestimates the true multidimensional overlap, and the average (summation measure)

overestimates it. Basically this is due to the fact that niche axes seldom are totally independent or dependent.

My data allow full multidimensional measurement, as each observation comprised all six niche dimensions. However, in practice, the full multidimensional analysis was impossible since the six-dimensional matrix contains 6168 separate categories. The number of observations per category will become too small to give reliable results, underestimation of overlap and niche breadth being inevitable (cf. Feinsinger 1976).

One can overcome this difficulty by employing full multidimensional utilization functions only between those dimensions which are most dependent on each other (Alatalo and Alatalo 1979b). I included full multidimensional utilization functions within three groups of dimensions:

1. Habitat, tree, tree size (24 categories).
2. Tree, tree size, height, tree part (128 categories).
3. Tree part, feeding posture (40 categories).

Subsequently a six-dimensional data matrix based on independency between these three matrices was constructed. In other words I assumed that firstly each bird species used the same tree species of similar size in the same fashion in all habitats. This is a realistic assumption, since the structure of each tree species did not vary greatly between habitats, and birds seemed to forage similarly in the same tree species regardless of habitat. Secondly I assumed feeding posture to be dependent on tree part only, this being justified by the redundant interaction between these two axes in niche segregation ( $R = 0.12–0.18$ , measuring the niche segregation in feeding posture, which is given by tree part as well). The interactions between feeding posture and other axes than tree part were much lower (0.003–0.02). As the two assumptions are strongly supported by data, I have been able to use almost full six-dimensional utilization functions.

Constructing a new matrix based on some independence assumptions and subsequent use of full multidimensional analysis is a different procedure than calculating products of one-dimensional overlaps, since the most important dependencies between axes are retained. Only some conditional (partial) dependencies have been disregarded, e.g. habitat and tree part remain dependent through their dependency to tree and tree size. Furthermore even if axes were independent, products may give different results than full multidimensional calculus (see May 1975). Nor is the modification of product overlap used by Feinsinger (1976) comparable to my way of analysis.

### 3. Results

#### 3.1. Guild composition

I studied the foraging of the eight most abundant foliage-gleaning, strictly speaking foliage-, twig- and branch-gleaning, passerine birds that regularly fed on arthropods (some of them seeds in addition) in trees (Tab. 1). Besides I studied foraging of the trunk-gleaning Treecreeper. I excluded two least abundant foliage-gleaners, the Chiffchaff and the Lesser Whitethroat, from the data analysis, as the number of observations was small for them.

Three of the species are summer visitors, the Willow Warbler and the Chaffinch being the most abundant breeding birds of the forest (Alatalo 1978b). The Brambling breeds in the area, irregularly, its main breeding range being situated further north (Järvinen and Väistönen 1979). Both *Fringilla* species are typical foliage-gleaners in these forests in summer.

Only four of the species are regularly found all the year in these forests: Willow Tit, Goldcrest, Crested Tit, Treecreeper. During winter Great Tits obtain most of their food near houses outside the forest, and Coal Tits are only irregular winter visitors after autumn irruptions. A large proportion of the Goldcrest population is migratory.

#### 3.2. Macrosite utilization

Habitat types were determined in terms of tree and tree size, and these niche axes were clearly dependent on each other. For brevity, I present only the selection of tree and tree size by birds (Figs 1, 2). All species, except the Crested Tit, significantly changed their tree species utilization from summer to winter (independent observations,  $\chi^2$ -test,  $p < 0.05$ ). In pairwise comparisons species differed ( $p < 0.05$ ) from each other in their

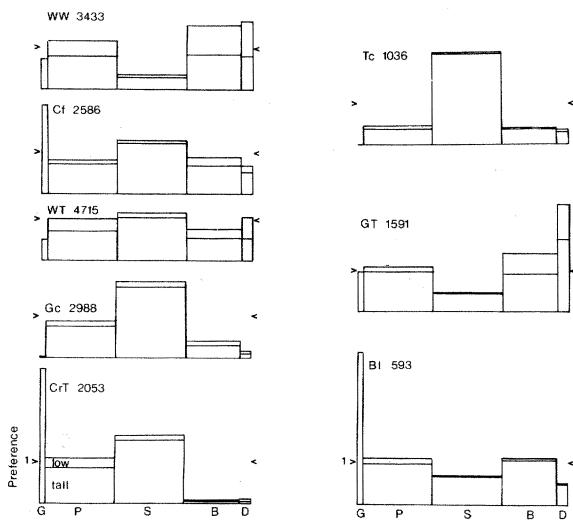


Fig. 1. The preference of foraging trees in summer (low trees in upper part of the bar). P = pine, S = spruce, B = birch, D = other deciduous tree, G = ground and other substrates. The breadth of the bar shows the tree use of the whole guild. The arrow indicates the level when tree was used by each species as frequently as by the guild (preference = 1). Numbers of observations after the abbreviation of the bird species name.

tree species and tree size selection, except the Brambling and the Chaffinch during summer. In summer pine, spruce and birch were used with almost equal frequency by the guild, whereas in winter coniferous trees were much preferred. The Willow Warbler and the Great Tit avoided spruce, preferring low trees during summer. The Willow Tit and the Chaffinch were generalists, whereas the Goldcrest and the Crested Tit preferred conifers, the latter almost exclusively so. The observations for the Brambling, compared with the

Tab. 1. Densities of the guild members in the forest during April 1975 – March 1976 (for census, see Alatalo 1978b). Weights from Haartman et al. (1963–72).

Species	Abbreviation	Weight (g)	Summer	Ind. $\text{km}^{-2}$
			Winter	
Willow Warbler, <i>Phylloscopus trochilus</i> L. ....	WW	9.4	60.5	–
Willow Tit, <i>Parus montanus</i> Conrad .....	WT	11.2	39.6	19.2
Goldcrest, <i>Regulus regulus</i> (L.) .....	Gc	5.7	29.9	7.5
Chaffinch, <i>Fringilla coelebs</i> L. ....	Cf	22.0	29.6	(0.2) <sup>1</sup>
Brambling, <i>Fringilla montifringilla</i> L. ....	Bl	22.2	8.6	–
Crested Tit, <i>Parus cristatus</i> L. ....	CrT	11.5	6.9	4.3
Great Tit, <i>Parus major</i> L. ....	GT	19.9	5.1	0.4
Treecreeper, <i>Certhia familiaris</i> L. ....	Tc	8.8	2.9	1.1
Coal Tit, <i>Parus ater</i> L. ....	CoT	8.9	–	0.4
Chiffchaff, <i>Phylloscopus collybita</i> Vieillot .....		7.7	0.5	–
Lesser Whitethroat, <i>Sylvia curruca</i> (L.) .....		12.6	0.3	–
Total .....			183.9	33.1
Diversity ( $\exp H'$ ) .....			5.72	3.22

1. Observed only in late April.

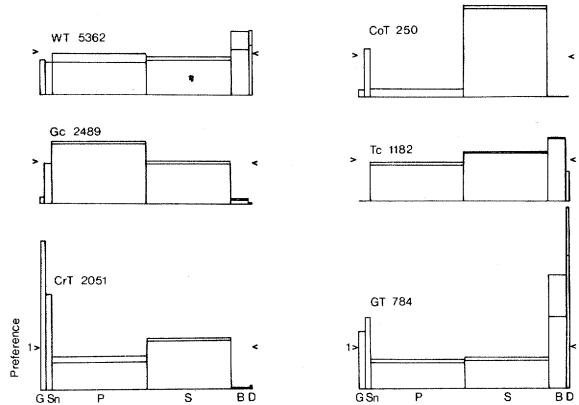


Fig. 2. The preference of foraging trees in winter. Explanations as in Fig. 1, except Sn = snow.

Chaffinch, to a much greater degree come from migratory periods, and the data about the Coal Tit were obtained from only few individuals.

### 3.3. Microsite utilization

Foraging height in trees and tree part were dependent; the more the species favoured trunk or branches, the lower it foraged (Figs 3, 4, also in pine and birch), which is an obvious consequence of the structure of trees. In spruce the average overlap in tree part use was 0.70 in summer, the average being lowered only slightly to 0.66 when foraging height was also taken into account. On the other hand, the average overlap in foraging height alone was much higher (0.84), and we may conclude that tree part was the more important dimension for segregation within trees (in other trees as well, Tab. 4). Among residents the Treecreeper and the Great Tit were the only species for which the independent observations did not indicate significant ( $\chi^2$ -test with  $p < 0.05$ ) seasonal change in tree part use. In winter all species except the two needle specialists, i.e. Goldcrest and Coal Tit, differed significantly in their foraging tree parts. In summer only the Brambling, with fewest observations, failed to show significant tree part use differences in comparison with the Chaffinch, Willow Tit

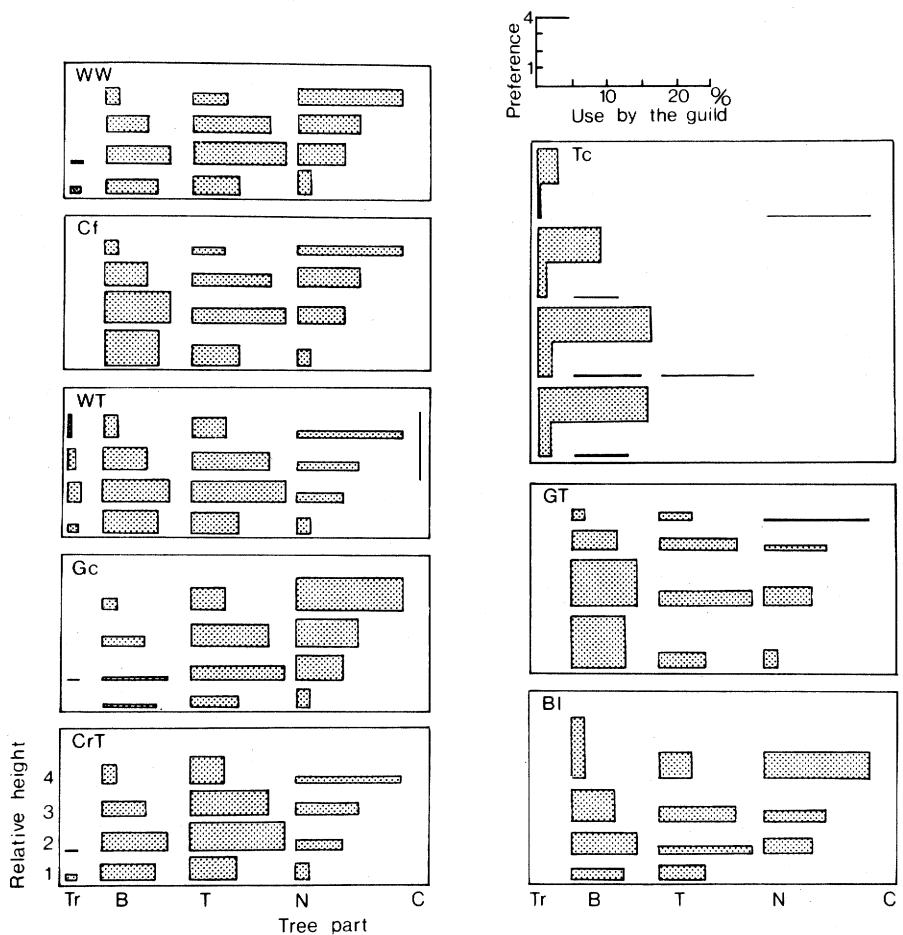
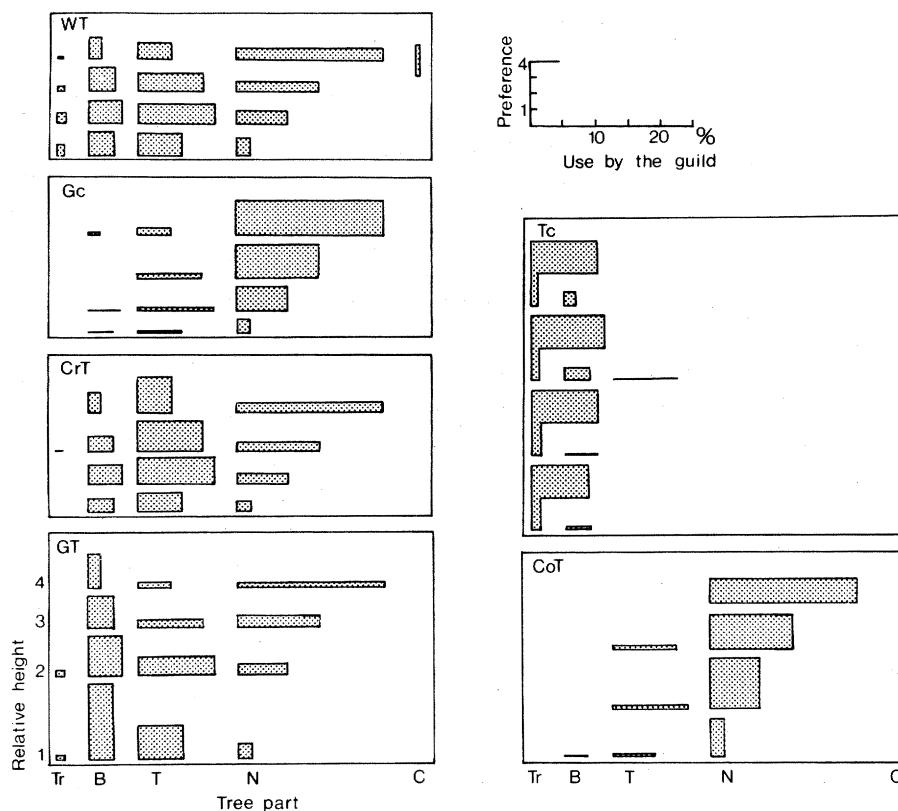


Fig. 3. The preference of tree parts and relative foraging heights (quarters) in tall spruce during summer. Tr = trunk, B = branch, T = twig, N = needled twig, C = cone. The breadth of the bar shows the relative use of the location by the whole guild, and height the preference of the location by the species (1 = species used the foraging site as frequently as the guild). The areas of bars are directly related to the proportional use of the location by the species.

Fig. 4. The preference of foraging locations in spruce during winter (for further details see Fig. 3).



and Crested Tit, respectively. Birds may be ranked with reference to diameter of tree part preferred, from trunk to twigs and needled twigs: Treecreeper; Great Tit + Chaffinch + Brambling; Willow Tit + Crested Tit + Willow Warbler; Goldcrest + Coal Tit. In winter needled twigs were used more often than in summer, especially by the Goldcrest.

### 3.4. Feeding posture

Feeding posture measures foraging technique and to some degree foraging site. For instance, birds may obtain food by hanging from the underside of twigs, whilst hovering birds are able to use the outermost tips of twigs. Far most of their foraging time birds were in a horizontal position (Tab. 2), with the exception of the trunk-gleaning Treecreeper. The Willow Tit and the Goldcrest changed significantly their feeding posture from summer to winter (independent observations,  $\chi^2$ -test,  $p < 0.05$ ). All species differed significantly in their feeding posture with exception of the Willow Tit versus Crested Tit, Brambling versus Chaffinch, and Goldcrest versus Coal Tit. The three summer visitors seldom used non-horizontal postures, but they hovered more often than tits. The two finches often walked longitudinally along branches or twigs. The Coal Tit, the smallest of the tits studied was very versatile in posture,

and the Great Tit was the least agile tit (see also Nilsson and Alerstam 1976, Perrins 1979). The Goldcrest very seldom hangs upside down (see also Palmgren 1932) but often hovers.

Feeding posture is dependent on tree part. While foraging on trunk, birds are most often vertically upwards. On branches and twigs horizontal position is strongly preferred, whereas on needled twigs posture versatility is high, as non-horizontal postures and hovering are frequently used. In winter tits and the Goldcrest more often used non-horizontal postures than in summer, which was partly a consequence of the general shift to needled twigs.

### 3.5. Niche overlap by components of diversity

The species diversity of the guild was almost twice as high in summer as in winter (Tab. 3). For the summer the within-habitat diversity, each habitat being weighted by its proportional use by birds, was on average 5.24. The standardized habitat overlap between species, each species weighted by its abundance, thus becomes  $(5.24-1)/(5.59-1) = 0.92$ . Through adding dimensions from macrosites to microaxes we obtain the average species diversity within the categories of the six-dimensional niche space. In summer the within-category diversity was higher than the foliage-gleaner species di-

Tab. 2. The relative proportions of different feeding postures in summer (S) and winter (W). For numbers of observations see Figs 1, 2.

	Season	Horizontal (longitudinally on twig)	Hanging			Hovering
			Upwards	Sided	Upside down	
Willow Warbler . . . . .	S	0.96 (0.03)	0.00	0.00	0.00	0.04
Chaffinch . . . . .	S	0.98 (0.14)	0.00	0.00	0.00	0.02
Willow Tit . . . . .	S	0.81 (0.02)	0.08	0.04	0.07	0.01
	W	0.75 (0.02)	0.14	0.03	0.07	0.00
Goldcrest . . . . .	S	0.88 (0.04)	0.03	0.05	0.01	0.03
	W	0.66 (0.04)	0.12	0.09	0.01	0.12
Crested Tit . . . . .	S	0.86 (0.02)	0.04	0.04	0.06	0.00
	W	0.82 (0.03)	0.09	0.04	0.05	0.00
Treecreeper . . . . .	S	0.00 (0.00)	0.97	0.02	0.01	—
	W	0.00 (0.00)	0.91	0.01	0.07	—
Great Tit . . . . .	S	0.93 (0.02)	0.02	0.02	0.02	0.01
	W	0.93 (0.01)	0.03	0.03	0.01	—
Coal Tit . . . . .	W	0.50 (0.01)	0.20	0.15	0.14	0.00
Brambling . . . . .	S	0.98 (0.11)	—	—	—	0.02
Guild . . . . .	S	0.90 (0.05)	0.04	0.02	0.02	0.03
	W	0.71 (0.03)	0.15	0.05	0.05	0.03

versity in the forest as a whole in winter. This illustrates the much greater diffuse niche overlap (which is not the same as competition) in summer, as foliage-gleaners are at that time likely to meet a larger number of other species of the same guild in any foraging site than would be met during winter in the whole forest. The increase in species diversity per foraging site is due to the presence of several migratory species in summer. The average six-dimensional niche overlap between species (standardized overlap) was also lower in winter than in summer, which was due to the sharper niche segregation within trees.

Interaction components of diversity measure the dependency of resource axes in showing niche differences (Alatalo and Alatalo 1977, 1979a). For the sake of brevity I shall not present these interactions, which almost exclusively were positive, indicating some redundancy between niche axes. Redundancy means that same

niche segregation is shown by either axis; e.g. if species A forages on needled twigs in the top quarter of tree and species B on branches in the lowest quarter, then tree part and foraging height are redundant. In particular redundancy was strong between tree part and feeding posture, between tree part and foraging height, and between habitat and tree size.

### 3.6. Resource use overlaps between each species and the guild

The six-dimensional niche overlap between each species and the remaining guild, on average, was lower in winter than in summer (Tab. 4). The decreased overlap in winter was due to a sharper niche separation of species with respect to microaxes. The lowest overlaps for any dimension were found for tree part. The average tree and feeding posture overlaps were also below 0.80, but the latter was strongly dependent on tree part as a niche axis. In winter tree part alone gave 77% of the differences shown by all six dimensions together, but in summer the corresponding proportion was only 56%. The two most important axes, tree and tree part, between themselves accounted for 87% of all differences in winter and 77% in summer.

In summer the six-dimensional guild overlap of different species varied between 0.52 and 0.72, excluding the Treecreeper which is almost completely segregated from other species in tree part use. To some degree, different dimensions were important in niche segregation of different species. For instance in winter the Crested Tit most strongly segregated in terms of tree selection, and the Willow Tit in tree part.

Tab. 3. Hierarchical components of species diversity; the average diversities ( $\text{ExpH}'$ ) within categories of the multidimensional matrix, and corresponding standardized niche overlaps (L).

Number of dimensions	Dimension added	Summer		Winter	
		$\text{ExpH}'$	L	$\text{ExpH}'$	L
Diversity in the whole forest		5.59		3.14	
1 . . . . .	Habitat	5.24	0.92	3.05	0.96
2 . . . . .	Tree	4.71	0.81	2.86	0.87
3 . . . . .	Tree size	4.66	0.80	2.84	0.86
4 . . . . .	Height	4.48	0.76	2.70	0.79
5 . . . . .	Tree part	3.99	0.65	2.25	0.59
6 . . . . .	Feeding posture	3.76	0.60	2.16	0.54



summer (0.63). The Great Tit to a certain extent overlaps with these species, whereas the Goldcrest has a more distinct niche after having shifted to the needled twigs. In winter the variation in species-pair overlaps was greater than in summer, but this does not hold if only the species regularly spending the winter in the forests are considered. The Coal Tit is clearly segregated judging from the few individuals encountered.

### 3.8. Seasonal change of species composition versus foraging shifts

In winter the average six-dimensional species-pair overlap (0.26) was lower than in summer (0.38), and a similar trend was shown by the overlap components of species diversity, which weight each species according to its abundance (Tab. 3). Now I will inspect whether the wintertime decrease in foraging overlaps is a consequence of the changing species composition, or do residents actively lower their mutual overlap by shifting their foraging.

Considering all the nine species, the foraging overlap on average is far lower among residents in summer than among summer visitors or between residents and summer visitors (case A, Tab. 6). The values emphasize the great role of changing species composition for producing narrow foraging overlap in winter, summer visitors overlapping extensively with other species. However, the more distinct segregation between residents is solely due to the trunk-specialized Treecreeper.

Excluding the Treecreeper, considering foliage-gleaners in a more strict sense, the picture is quite different (case B, Tab. 6). The average overlap between residents is equally high than that between summer visitors. In case C only the regular foliage-gleaners of the forest are included. The overlap in summer was highest among the three residents (see also Fig. 5). In winter the overlap between the Goldcrest and the two tits decreased as the

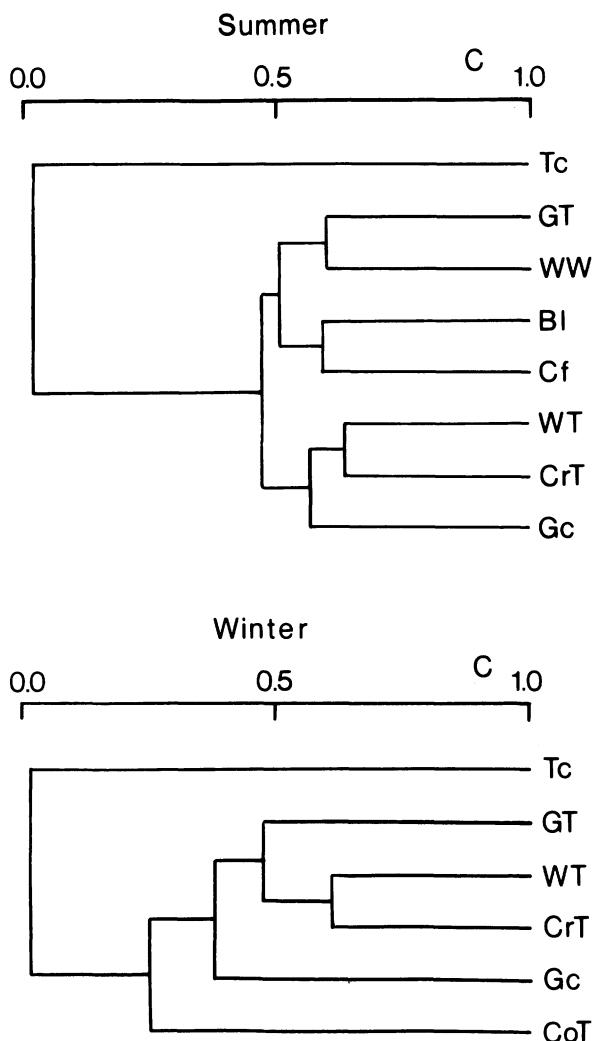


Fig. 5. Dendograms on six-dimensional niche overlaps (C) by the UPGMA-method (Sokal and Sneath 1963).

Tab. 6. Average six-dimensional species-pair overlaps (C) in summer and winter for selected species groups.

	A. All nine species		B. Foliage-gleaners (Tc excluded)		C. Regular foliage-gleaners (residents: WT, CrT, Gc; summer visitors: WW, Cf, GT)	
	Overlap	Number of species	Overlap	Number of species	Overlap	Number of species
<b>SUMMER</b>						
Summer visitors exclusively .....	0.513	3	0.513	3	0.547	3
Residents exclusively .....	0.317	5	0.508	4	0.583	3
Overlaps between residents and summer visitors .....	0.405	5,3	0.503	4,3	0.486	3,3
All species .....	0.385	8	0.506	7	0.517	6
<b>WINTER</b>						
Residents exclusively .....	0.281	5	0.452	4	0.503	3
Residents and the Coal Tit .....	0.256	6	0.375	5	-	



Tab. 8. Correlations ( $r$ ) between the species-pair overlaps for each niche axis and the weight relations of species (larger to smaller). Treecreeper not included (summer,  $n = 21$ ; winter,  $n = 10$ ; significance levels not indicated because of the difficulty in determining the number of independent observations).

Niche axes	Summer	Winter
<b>One-dimensional</b>		
Habitat .....	-0.07	0.03
Tree .....	-0.09	0.04
Tree size .....	-0.02	-0.26
Height .....	-0.09	-0.84
Tree part .....	-0.73	-0.48
Feeding posture .....	0.00	-0.58
<b>Three-dimensional</b>		
Macroaxes (habitat, tree, tree size) .....	-0.16	0.04
Microaxes (height, tree part, posture) .....	-0.73	-0.50
Six-dimensional .....	-0.43	-0.39

parts, if at the same time they gain the benefit of reduced interspecific competition.

Since more energy-consuming foraging methods may be acceptable among smaller than larger birds (Norberg 1977), a negative correlation is to be expected between the size of birds and their posture versatility. In winter (again excluding the Treecreeper) this was confirmed ( $r = -0.90$ ,  $p < 0.01$ ) but in summer the negative correlation was not significant ( $r = -0.49$ ,  $p > 0.10$ ). In summer a small species, the Willow Warbler, was very stereotypic with respect to feeding posture. Factors other than size (e.g. leg structure; Palmgren 1932, Oosterhaus 1962) of course also determine the feeding posture among foliage-gleaners.

To summarize, body size, tree part selection and feeding posture were closely interrelated in foliage-gleaners. The trunk-gleaning Treecreeper requires a quite different morphology. Body size was not related to the use of macrosite-dimensions, but among tits a thin beak has been shown to be associated with the use of conifers and a broader beak with deciduous trees (Snow 1954, Betts 1955, Haftorn 1956, Partridge 1976).

#### 4.2. Complementarity of niche axes

Complementarity of niche axes means that high niche breadth or niche overlap in one axis will be compensated for by low values for another axis (Cody 1974, Schoener 1974). In most cases the niche overlaps given by different axes (Tab. 4) correlated positively (24 of the 30 cases), and none of the 6 negative correlations was significant ( $p > 0.05$ ). The correlation between the overlap for macroaxes and microaxes was positive, but not significantly (summer:  $r = 0.32$ , winter:  $r = 0.58$ ).

For niche breadth (Tab. 7) negative correlations between axes were more common (12 of the 30 cases), particularly for feeding posture in winter. The only significant negative correlation was between tree and feeding posture ( $r = -0.96$ ,  $p < 0.05$ ). The negative correlations for feeding posture arose in winter, since the Goldcrest and the Coal Tit had very high posture breadths, but low niche breadths for all foraging site dimensions. In general, when considering niche shape in three-dimensional space determined by macrosite, microsite and feeding posture (Tab. 7), most species had fairly similar breadths for all three axes indicating rounded niche shapes (cf. Hanski and Koskela 1977). As an exception elongated shapes appear to exist in the Coal Tit and the Goldcrest in winter, when they are specialized with respect to the foraging site, but use the needled twigs with versatile postures. However, the interpretation is complicated by the fact that all species scored higher posture breadths on needled twigs.

It is no surprise to find positive correlations (Cody's 1974 supplementary relationships) in overlaps or breadths between niche axes, as axes often are dependent on each other, and in this study even the categorization was dependent in certain respects (e.g. habitat and tree). I made a more careful test of complementarity between overlaps for tree use and overlap within trees, measured by the maximum tree part overlap in spruce, pine or birch (Fig. 6). There was a slight, but

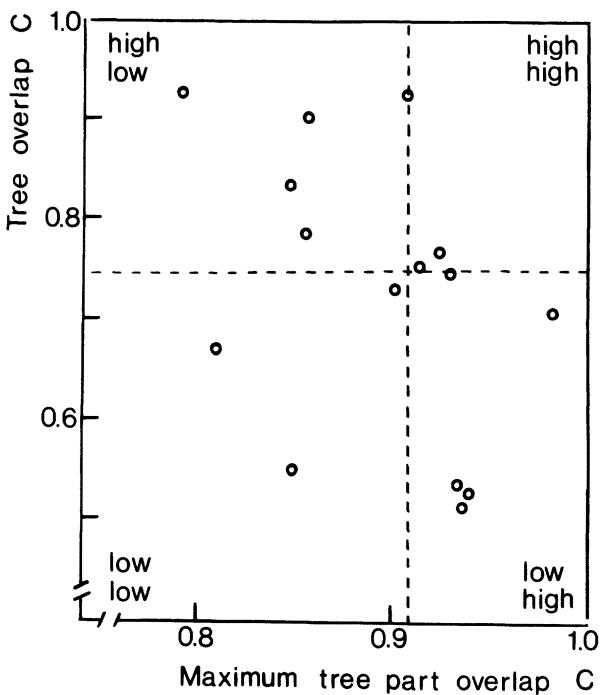


Fig. 6. Complementarity of foraging overlaps in summer (Tc and Bl excluded). Maximum tree part overlap in spruce, pine or birch against the overlap in foraging tree. Broken lines give the median overlaps for both niche axes.

non-significant, negative correlation ( $r = -0.41$ ,  $p > 0.05$ ) between overlaps. But correlation analysis is not exactly suitable for testing complementarity, as low overlap in one axis may be coupled with low or high overlap in the other axis, while only the high overlap in one axis should be complemented by low overlap in the other axis (cf. Schoener 1968). I divided the figure with median lines into four parts. Two of the observations fall into the corner of high overlaps for both dimensions, but they are situated very near the cross of the median lines. In other corners the points are more spread out. Perhaps this pattern indicates some maximum tolerable overlap with respect to these two dimensions together, i.e. complementarity.

Pairwise correlations do not indicate much complementarity (if any) between niche axes in this guild. However, there is complementarity in the general sense that several niche axes interact to give the actual overlaps between niches; to some degree different axes were involved in segregation of niches of different species (Tab. 4). Excluding the Treecreeper, species-pair overlaps were fairly constant in summer as illustrated by Fig. 5. Cody (1968) showed the constancy of overall niche separation in multidimensional niche space for grassland birds, different axes being important in different communities. In the present study each regular member of the foliage-gleaning guild had a relatively constant multidimensional niche separation; overlap with the guild 0.53–0.72 in summer and 0.43–0.62 in winter (Tab. 4).

Regular spacing of species in a one-dimensional niche space (see Schoener 1974, Pianka 1976 or the model of May and MacArthur 1972) would result to some overlap between the nearest neighbours, whereas overlaps between other pairs should be much smaller or negligible. In the multidimensional niche space of the foliage-gleaners, such low overlaps did not exist, and this most probably was due to the complementary relations of niche axes. In one-dimensional niche space equal species-pair overlaps can be obtained only assuming very odd niche shapes. There may be a limit to the maximum niche overlap set by interspecific competition, but, on the other hand, nor do extremely low overlaps exist within this foliage-gleaning guild.

#### 4.3. Which axes and how many?

Guild members differed most strongly with respect to tree part. Moermond (1979b) suggested that optimal choice of patch types (structural microhabitats) is influenced by the locomotion costs associated with foraging in each patch type. Selection should act to enhance adaptation for site-specific foraging. Different tree parts require different adaptations (e.g. in terms of body size and feeding posture) for the most effective exploitation of food on them, and genetic differences between species are likely to become established for tree part utilization. The same tree part at different heights is

much less likely to require height-specific adaptations, and differences in foraging height generally were only a consequence of differences in tree part selection.

Among macroaxes tree was the most important, and after tree part it was the second axis in niche separation. The importance of tree within macrosite dimensions is readily understood, since in this case habitat was not much more than the indicator of the tree species present. Tree size, on the other hand, was a dimension with little heterogeneity (low or high tree) and thus afforded little room for segregation. Habitat overlap would have been reduced if the two habitat specialists, Chiffchaff and Lesser Whitethroat, had been included in the analysis (they were too scarce to get representative data). Contrary to foliage-gleaners, macroaxes (habitat and tree) were found to be most important in foraging site segregation for woodpeckers by Alatalo (1978a). Woodpeckers generally are specialists on trunks, and thus cannot be segregated by microaxes as easily as foliage-gleaners.

The question of how many axes are involved in segregating foraging site niches is a difficult one, since all axes so far considered more or less segregate species further even after the five other dimensions have been taken into account. In summer tree part as the most important axis explained only 56% of the six-dimensional niche differences, emphasizing the multidimensionality of niche separation within the guild. However, the two most important axes, tree part and tree, explained 77% of the six-dimensional foraging differences in summer and up to 87% in winter. MacArthur (1965), Levins (1968) and Schoener (1974) argued that if the number of species goes up the number of important dimensions should also increase. In fact, when comparing winter and summer, this seems to be true; in winter tree part alone explained as much of the differences as tree part and tree together in summer. Furthermore, in a guild of only three flycatching species, in the same forest and basically with the same niche dimensions studied, the most important niche axis (macrosubstrate = tree in this study) explained 80% of the multidimensional foraging site differences (Alatalo and Alatalo 1979b).

#### 4.4. Competition in winter and summer

Land bird populations in the temperate and cold regions are often assumed to be food limited in winter and to have a relative superfluity of food in summer, which suggests that species should be well segregated in resource use in winter to avoid interspecific competition. In summer competitive release might occur, allowing higher foraging overlaps between species. Besides this study, greater niche separation in winter has been reported for many temperate zone bird species (for references see Alatalo 1980). Thus the hypothesis of the need for distinct niches during food shortage seems to be supported. Within resident foliage-gleaners, niche overlap was lowered by the shift of the Goldcrest from

twigs to needled twigs during winter. Interestingly, the increased segregation in winter is achieved in microsites, tree part in particular. In winter all the four regular species form mixed-species flocks, and they may be enabled to do so by tree part segregation.

A reviewer suggested an alternative, non-competitive, hypothesis: in result of the food shortage in winter birds have to concentrate on sites where they are best adapted to forage, species having different optimal sites because of the morphological differences. In summer it would be an optimal strategy to use superabundant insect populations even if they happen to occur in less ideal places. Yet birds should use these less ideal places also in winter if food availability there is high enough to compensate for the suboptimal foraging adaptations. The argument above is reasonable only if food is less evenly distributed over different sites in winter than in summer, quite irrespective of absolute food availability per se. On the other hand, the inclusion of interspecific competitive effects, makes it less likely that the use of less ideal places is optimal, if food availability decreases. In winter absolute food levels in relation to consumption are low, and the consumption of food by other species has a greater effect in depleting food resources than in summer.

#### 4.5. Residents versus migrants

Among foliage-gleaners, residents were more similar to each other with respect to foraging behaviour than guild members were on average. All residents have to cope with the restricting winter conditions. Residents are small, use versatile feeding postures and exploit needled twigs. Summer visitors, to an important degree, exploit resources seldom used by residents, except the Willow Tit, such as deciduous trees and low trees. They include the clumsy and heavy Chaffinch and Brambling, which morphologically are typical seed-eaters, but which eat arthropods in trees in summer, when the food probably is relatively plentiful in these northern forests. The capability of using versatile feeding postures associated with small body size seems to be an important adaptation for winter, so as to enable the birds to use scarce resources effectively (to get food from under the twigs or from the outermost twigs). The average weight of residents was 9 g and that of summer visitors 18 g.

#### 4.6. Niche breadth

Niche width with respect to foraging sites decreased in winter, when resource space is reduced and fewer sites provide food for birds. On the other hand posture versatilities were high for residents and increased in winter. In general, in an uncertain environment, a broad niche is optimal (Levins 1968), but the actual resource use width depends also on the variety of resources available. This reduces the applicability of the traditional optimal foraging models in seasonal comparisons (see Smith et

al. 1978). Birds should become less specialized in their choice of food when food is scarce (Emlen 1966, MacArthur and Pianka 1966), and increased posture versatility in winter might indicate the more generalized use of food within patches.

Increased interspecific competition in winter should cause niche breadth to shrink since each species will retire into its exclusive niche (Baker and Baker 1973); for example the Goldcrest narrowed its tree part use. Yet posture versatility did not decrease with the supposed increase in interspecific competition. Feeding posture is related to diet as a niche axis, both being microaxes within foraging sites. The compression hypothesis for non-evolutionary interactions states that when species number is increased, species should decrease the number of habitat types but increase the number of prey types utilized (MacArthur and Pianka 1966, MacArthur and Wilson 1967, Schoener et al. 1979). Similarly we might hypothesize that if competition pressure varies seasonally it is more economical to shift foraging sites than diet (or feeding posture) within foraging sites. When suitable prey is encountered within a patch, there is no reason to disregard it even though interspecific competition would be severe. However, my data does not provide an appropriate test of this hypothesis, since the number of patch types available was reduced during winter.

Abundance has been shown to correlate positively with niche breadth (Levins 1968, McNaughton and Wolf 1970, Hanski and Koskela 1977). For the four regular species in winter, there was a clear positive correlation between numerical dominance and the six-dimensional niche width ( $r = 0.98, p < 0.05$ ). In summer the relation was weaker ( $r = 0.43, p > 0.10$ ); the Willow Warbler was abundant although, its niche width was intermediate. Besides, the Great Tit and the Crested Tit were less abundant than expected on the basis of their niche width. According to Cody (1974) species are common because they are generalists and use a wide variety of the habitats or resources, or because they are specialists on an abundant resource. At Oulu population abundance and degree of generalization seem to be related in residents, but the summertime situation was obscured by the fact that populations, presumably are limited by winter conditions, and the abundance of summer visitors and residents, respectively, therefore are not strictly comparable.

#### 4.7. How much overlap?

This is one of the most basic questions in niche studies, but comparison between different studies with respect to overlap levels is difficult. It is often not known how much of the real foraging differences have been revealed, furthermore, different niche metrics give different absolute values. In this study the species-pair overlaps for foliage-gleaners (Treecreeper and irregular species excluded) were far above zero, ranging between

0.35 and 0.63. In the same forest multidimensional resource use overlaps among three flycatching species were of the same magnitude (0.36–0.59; Alatalo and Alatalo 1979b).

These estimates are based primarily on foraging site, and actual foraging niche overlaps should be lower, if species make use of different foods within each foraging site. For insectivorous birds that forage in similar ways, the mean size of prey increases with body size (Betts 1955, Hespeneide 1975, Wilson 1975). The weight of the foliage-gleaners in my study area varied between 5.7 and 22.2 g (Tab. 1), which indicates that food preferences should be different. A step towards attaining realistic foraging niche overlap values would be to combine multidimensional foraging site information and the diet. However, diets have to be known separately for, at least, the most important foraging sites, since foraging site and diet certainly correlate heavily (see Betts 1955, Laursen 1978).

Interestingly, the greatest foraging overlaps were found for the Willow Tit and the Crested Tit (0.63 in summer, 0.61 in winter), which are also most similar in size and structure. It is not likely that these two species would have very different cost-benefit functions for each prey type, as would be necessary for them to be able to segregate in diet in the same patch. Furthermore insectivores of temperate regions should be opportunists (plastic, see Morse 1971) to deal with the marked fluctuations in kinds and sites of resources. Thus they cannot afford to specialize too much in diet, and it can be assumed that for species similar in size and structure foraging site differentiation should be more important than diet differences in avoiding interspecific competition. Periodically, the foraging site overlaps of these birds were considerably lower than the general wintertime or summertime overlaps considered here (Alatalo 1980).

#### 4.8. Comment on multidimensional niche metrics

Multidimensional foraging overlaps most often have been estimated by averaging one-dimensional overlaps (summation) or by multiplying one-dimensional overlaps (product measure), the former being based on the assumption of complete dependency and the latter of independency between niche axes. In this case, considering the average non-circular overlap with the guild (Tab. 4), the summation overlap would be 0.82 in summer and 0.76 in winter and the product 0.29 and 0.18. The approximately full multidimensional calculus instead gave intermediate overlaps 0.52 and 0.40, respectively. For niche breadths (Tab. 7) the summation measure is 0.87 in summer and 0.89 in winter, product is 0.41 and 0.44, whereas the approximately true six-dimensional width is 0.50 and 0.51.

For niche overlap neither way of one-dimensional projections provided estimates that are near the true multidimensional overlaps. Theoretically it would be

possible to obtain lower multidimensional overlaps than the product overlap (May 1975, Alatalo and Alatalo 1977), but in practice this may be rare. Hanski (1978) found that the multidimensional niche width was well approximated by the summation measure, but in this case products gave a better result. Altogether these comparisons underline the importance of using as full multidimensional utilization functions as possible for niche metrics.

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#### References

- Alatalo, R. H. 1978a. Resource partitioning in Finnish woodpeckers. – *Ornis Fennica* 55: 49–59.
- and Alatalo, R. V. 1979a. Estimation of genetic variation by the components of gene diversity. – *Aquilo Ser. Zool.* 20: 111–117.
- Alatalo, R. V. 1978b. Bird community energetics in a boreal coniferous forest. – *Holarct. Ecol.* 1: 367–376.
- 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. – *Oecologia (Berl.)* 45: 190–196.
- and Alatalo, R. H. 1977. Components of diversity: multivariate analysis with interaction. – *Ecology* 58: 900–906.
- and Alatalo, R. H. 1979b. Resource partitioning among a flycatcher guild in Finland. – *Oikos* 33: 46–54.
- and Alatalo, R. H. 1979c. On the measurement of niche overlap. – *Aquilo Ser. Zool.* 20: 26–32.
- Alerstam, T., Nilsson, S. G. and Ulfstrand, S. 1974. Niche organization during winter in woodland birds in southern Sweden and the island of Gotland. – *Oikos* 25: 321–330.
- Baker, M. C. and Baker, A. E. M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. – *Ecol. Monogr.* 43: 193–212.
- Betts, M. M. 1955. The food of titmice in oak woodland. – *J. Anim. Ecol.* 24: 282–323.
- Cohen, J. E. 1979. Food webs and niche space. – Princeton Univ. Press, Princeton.
- Cody, M. L. 1968. On the methods of resource division in grassland bird communities. – *Am. Nat.* 102: 107–147.
- 1974. Competition and the structure of bird communities. – Princeton Univ. Press, Princeton.
- Colwell, R. K. and Futuyma, D. S. 1971. On the measurement of niche breadth and overlap. – *Ecology* 52: 567–576.
- Croxall, J. P. 1977. Feeding behaviour and ecology of New Guinean rainforest insectivorous passerines. – *Ibis* 119: 113–146.
- Emlen, J. M. 1966. The role of time and energy in food preference. – *Am. Nat.* 100: 611–617.
- Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. – *Ecol. Monogr.* 46: 257–291.
- Gibb, J. A. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. – *Ibis* 96: 513–543.
- 1960. Populations of tits and goldcrests and their food supply in pine plantations. – *Ibis* 102: 163–208.
- and Betts, M. M. 1963. Food and food supply of nestling tits (Paridae) in Breckland pine. – *J. Anim. Ecol.* 32: 489–533.

- Haartman, L. von, Hildén, O., Linkola, P., Suomalainen, P. and Tenovuo, R. 1963–72. Pohjolan linnut värikuvin. – Otava, Helsinki.
- Haftorn, S. 1956. Contribution to the food biology of tits especially about storing of surplus food. Part IV. – Kgl. Norske Vid. Selsk. Skr. 4: 1–54.
- Hanski, I. 1978. Some comments on the measurement of niche metrics. – Ecology 59: 168–174.
- and Koskela, H. 1977. Niche relations of dung-inhabiting beetles. – Oecologia (Berl.) 28: 203–231.
- Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. – J. Anim. Ecol. 22: 263–288.
- Herrera, C. M. 1978a. Niche-shift in the genus *Parus* in southern Spain. – Ibis 120: 236–240.
- 1978b. Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. – J. Anim. Ecol. 47: 871–890.
  - 1979. Ecological aspects of heterospecific flocks formation in a Mediterranean passerine bird community. – Oikos 33: 85–96.
- Hespenheide, H. A. 1975. Prey characteristics and predator niche width. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Belknap Press, Cambridge, Mass., pp. 158–180.
- 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.
- Järvinen, O. and Väistönen, R. A. 1979. Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. – Oikos 33: 261–271.
- Karr, J. R. and James, F. C. 1975. Eco-morphological configurations and convergent evolution in species and communities. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Belknap Press, Cambridge, Mass., pp. 258–291.
- Laursen, K. 1978. Interspecific relationships between some insectivorous passerine species, illustrated by their diet during spring migration. – Ornis Scand. 9: 178–192.
- Levins, R. 1968. Evolution in changing environments. – Princeton Univ. Press, Princeton.
- Ludescher, F.-B. 1973. Sumpfmeise *Parus p. palustris* L. und Weidenmeise *P. montanus salicarius* Br. als sympatrische Zwillingssarten. – J. Orn. 114: 3–56.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. – Ecology 39: 599–619.
- 1965. Patterns of species diversity. – Biol. Rev. 40: 510–533.
  - and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. – Am. Nat. 101: 377–385.
  - and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.
  - and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press, Princeton.
- May, R. M. 1975. Some notes on estimating the competition matrix,  $\alpha$ . – Ecology 56: 737–741.
- and MacArthur, R. H. 1972. Niche overlap as a function of environmental variability. – Proc. Natl. Acad. Sci., USA 69: 1109–1113.
- McNaughton, S. J. and Wolf, L. L. 1970. Dominance and the niche in ecological systems. – Science 167: 131–139.
- Miller, R. S. 1967. Pattern and process in competition. – Adv. Ecol. Res. 4: 1–74.
- Moermond, T. C. 1979a. Habitat constraints on the behaviour, morphology, and community structure of *Anolis* lizards. – Ecology 60: 152–164.
- 1979b. The influence of habitat structure on *Anolis* foraging behaviour. – Behaviour 70: 147–167.
- Morse, D. H. 1967. Competitive relationships between *Parula* warblers and other species during the breeding season. – Auk 84: 490–502.
- 1970. Ecological aspects of some mixed-species foraging flocks of birds. – Ecol. Monogr. 40: 119–168.
  - 1971. The insectivorous bird as an adaptive strategy. – Annu. Rev. Ecol. Syst. 2: 177–200.
  - 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. – Ibis 120: 298–312.
- Nilsson, S. G. and Ålerstam, T. 1976. Resource division among birds in North Finnish coniferous forest in autumn. – Ornis Fennica 53: 15–27.
- Norberg, R. Å. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. – J. Anim. Ecol. 46: 511–529.
- Oosterhaus, S. M. B. 1962. Adaptive modification of the leg structure of some North American warblers. – Amer. Midl. Nat. 68: 475–486.
- Palmgren, P. 1932. Zur Biologie von *Regulus r. regulus* (L.) und *Parus atricapillus borealis* Selys. Eine Vergleichende Ökologische Untersuchung. – Acta Zool. Fenn. 14: 1–113.
- Partridge, L. 1976. Some aspects of the morphology of blue tits *Parus caeruleus* and coal tits *P. ater* in relation to their behaviour. – J. Zool., London 170: 121–133.
- Pearson, D. L. 1977. Ecological relationships of small antbirds in Amazonian bird communities. – Auk 94: 283–292.
- Perrins, C. M. 1979. British tits. – Collins, London.
- Pianka, E. R. 1976. Competition and niche theory. – In: May, R. M. (ed.), Theoretical ecology: principles and applications. Blackwell, Oxford, pp. 114–141.
- Rabenold, K. N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. – Ecol. Monogr. 48: 397–424.
- Ricklefs, R. E. and Cox, G. W. 1977. Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. – Oikos 29: 60–66.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray grackle. – Ecol. Monogr. 37: 317–350.
- Roughgarden, J. 1976. Resource partitioning among competing species – a coevolutionary approach. – Theor. Pop. Biol. 9: 388–424.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. – Ecology 49: 704–726.
- 1974. Resource partitioning in ecological communities. – Science 185: 27–39.
  - Huey, R. B. and Pianka, E. R. 1979. A biogeographic extension of the compression hypothesis: competitors in narrow sympatry. – Am. Nat. 113: 295–298.
- Smith, J. N. M., Grant, P. R., Grant, B. R., Abbott, I. J. and Abbott, L. K. 1978. Seasonal variation in feeding habits of Darwin's ground finches. – Ecology 49: 831–843.
- Snow, D. W. 1949. Jämförande studier över våra mesarters näringssökande. – Vår Fågelvärld 8: 159–169.
- 1954. The habitats of Eurasian tits *Parus* spp. – Ibis 96: 565–585.
- Sokal, R. and Sneath, P. 1963. Principles of numerical taxonomy. – Freeman, San Francisco.
- Ulfstrand, S. 1962. On the nonbreeding ecology and migratory movements of the great tit *Parus major* and the blue tit *Parus caeruleus* in southern Sweden. – Vår Fågelvärld suppl. 3: 1–145.

- 1976. Feeding niches of some passerine birds in a south Swedish coniferous plantation in winter and summer. – *Ornis Scand.* 7: 21–27.
  - 1977. Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. – *Oecologia (Berl.)* 27: 23–45.
  - and Nilsson, S. G. 1976. Quantitative composition and foraging niches of a passerine bird guild in pine plantations in Denmark during winter. – *Ornis Scand.* 7: 171–178.
  - Wilson, D. S. 1975. The adequacy of body size as a niche difference. – *Am. Nat.* 109: 769–784.
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## Also . . .

Jordano, P. 1982. Migrant birds are the main seed dispersers of blackberries in southern Spain. – *Oikos* 38: 183–193.

Between-habitat variation in fruit production and bird attributes enhancing seed ingestion and removal were studied to describe the avian seed-dispersal system of blackberries (*Rubus ulmifolius*, Rosaceae) in southern Spain.

Migrant birds were largely responsible for seed dispersal. Among 20 passerine species recorded feeding on fruits, five removed the bulk of seeds: *Sylvia atricapilla* (29.6% of 897 visits recorded), *Erythacus rubecula* (15.2%), *S. borin* (14.7%), *S. melanocephala* (10.1%) and *Turdus merula* (7.7%). During an average day ≈ 32400 seeds left a parent clone through the activity of these species.

Seed production was density-dependent, being maximum in high-density situations. Seed removal (i.e., fruit consumption) from individual clones was dependent on crop size, habitat occupied and ripening phenology. Clones ripening a small crop later in the season and/or in low-density habitats had a lower fraction of the crop consumed than did those producing huge crops in high density habitats and/or synchronously with autumn bird migration.

The small, passerine birds presumably contributed to the bulk of seed dispersal because they (1) feed on *Rubus* fruits extensively, (2) showed high visit rates and removed a very high fraction of the seed crop from parent clones, (3) did not damage the seeds nor drop them beneath the parent clone and (4) performed species-specific flights to apparently safe sites for the plant, thus enhancing its colonizing ability.

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