

Seasonal Dynamics of Resource Partitioning Among Foliage-Gleaning Passerines in Northern Finland

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Summary. The five most abundant species were included in a year-round study with respect to six foraging niche dimensions. Approximately full multidimensional utilization functions were used for niche metrics. During summer foraging overlaps were invariably high, but in other seasons periodically lower. Foraging site breadth was lower in winter, when fewer sites are profitable for foraging than in summer. Feeding posture versatility, by contrast, was highest in winter. Seasonal foraging shifts were very prominent, as great in fact as between-species differences. Often seasonal trends were parallel in different species. Niche axes of macrohabitat-type (e.g. tree) were more open for foraging variation and axes of microhabitat-type (tree part) more rigid. Among the resident species seasonal variation in foraging was greatest in *Regulus regulus* and *Parus cristatus*, whereas the foraging behaviour was more stable for *P. montanus* (an abundant species with broad niche), perhaps owing to greater intraspecific competition. In these northern forests foliage-gleaners must be versatile generalists to cope with the unpredictable resources, and thus they overlap broadly in their general resource niches which are determined by their genetically fixed cost and benefit relations to each resource type. Anyhow, presumably during periodical food shortage, the actual resource uses adjusted by resource availability and competition may overlap narrowly.

Introduction

Insectivorous birds in boreal forests must be opportunistic in order to cope with the great temporal fluctuations in resource availability (Morse, 1971). Under food shortage each species should separate in foraging to reduce interspecific competition, while under food superabundance species could be able to use the same profitable foraging sites (see Baker and Baker, 1973; Smith et al., 1978). Seasonal changes in the foraging sites of foliage-gleaners (strictly speaking foliage-, twig- and branch-gleaners) have been demonstrated by Hartley (1953), Gibb (1954, 1960), Haftorn (1956) and Ulfstrand (1976, 1977). Betts (1955), Tinbergen (1960), Gibb and Betts (1963) and Laursen (1978) have recorded temporal fluctuations in the diet of foliage-gleaners.

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This study will analyze the short-term shifting pattern of resource utilization in the five most abundant foliage-gleaning species of northern Finland. Multidimensional niche metrics, which takes account for the dependencies between the six niche axes (see May, 1975; Alatalo and Alatalo, 1977), was used to get realistic estimates of the resource-utilization overlaps. The major questions for the study were:

1. How much do the foraging strategies of the different species change from month to month?
2. Which niche dimensions have the greatest seasonal shifts, and which are most rigid?
3. When are interspecific niche overlaps maximal and minimal, and what are the overlap levels at those times?

The answers hopefully will give insight into the process of competition in a strongly seasonal environment. Some relations between the niche concept, competition and optimal foraging theory will also be discussed.

Material and Methods

Field Work

The material was gathered in the predominantly coniferous forests near the city of Oulu (64° 57' N, 25° 48' E) in northern Finland, between March 1975 and March 1976 as well as in January–March 1978. During each month the same areas within the forest were visited, and a few short series of foraging observations (record each 15 s) were made for each bird individual encountered. In winter an average of 9.2 observations were made on each individual, and in summer somewhat less.

The six niche dimensions may be grouped as macrosites or macroaxes (habitat, tree, tree size) and microaxes (within-tree axes: height, tree part, feeding posture). Microaxes may be divided as microsite (height, tree part) and feeding posture (a measure of feeding technique). The categories for each axis were:

1. Habitat (pine forest, 22.0% of the forest (Alatalo, 1978); spruce f., 6.5%; mixed coniferous f., 9.6%; mixed f. (conifers and deciduous trees), 29.8%; young f., 16.9%; afforested swamp 15.2%).
2. Tree (pine; spruce; birch; other deciduous tree; ground; snow; air; other substrate). Pine *Pinus sylvestris*, spruce *Picea abies* and birch *Betula pubescens* are the only common tree species in these boreal forests.
3. Tree size (tall, over 5 m high; low)

4. Height (lowest quarter in tree; second q.; third q.; top q.).
5. Tree part (trunk; branch (diameter over 8 mm); twig (in deciduous trees includes leaves); needled twig; cone (or birch catkin)).
6. Feeding posture (horizontal; horizontal and longitudinally along twig; horizontal and transversely on twig; head upwards; head downwards; hanging upside down; sided (one side up); hovering).

Line transects (see Alatalo, 1978) were used to measure bird densities.

Niche Metrics

The multidimensional niche metrics employed will be described and discussed more fully in another paper (Alatalo, in preparation). Niche overlaps between two species (C) were measured by the simple measure of proportional overlap, which is the sum of the minimum relative frequencies over all categories (e.g. Hurlbert, 1978 Eq.1):

$$C = \sum \min(p_{xi}, p_{yi}),$$

where p_{xi} is the relative frequency of observations for species x in the category i , and p_{yi} the corresponding frequency for species y . Niche breadth (B) was measured by the antilogarithmic Shannon's entropy ($\text{Exp}H'$). Original values were standardized by dividing them by the $\text{Exp}H'$ -breadths of the pooled annual data for the whole guild. Niche breadth 1.00 indicates that the species used the dimension(s) as broadly as the whole guild during the whole year.

May (1975) stressed that when more than one resource dimension is involved, there is in general no substitute for measuring the species' full multidimensional utilization functions. This means that each possible combination of one-dimensional categories has to be used as a separate category when counting multidimensional niche overlaps or breadths (see also Alatalo and Alatalo, 1977). Products or averages of one-dimensional overlaps are very rough approximations of niche overlap in multidimensional niche space. Basically this is due to the fact that niche axes seldom are totally independent (assumption for product) or dependent (for average), but for the product measure there are other reasons as well.

However, it was not feasible to use full multidimensional utilization functions when calculating niche overlap or breadth for all six dimensions simultaneously, since the number of observations would have to be enormous to represent all 6168 separate categories. We can overcome this difficulty by employing full multidimensional utilization functions only between those niche dimensions which are most dependent (Alatalo and Alatalo, 1979). In this case it is reasonable to include 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 independence between these three matrices was constructed, and full multidimensional calculus was employed on this new matrix. To put it another way, I used full multidimensional utilization functions except that: (1) each species was assumed to use the same tree of same size in a similar fashion (with respect to tree part, height and feeding posture) in all habitats, and (2) feeding posture was assumed to be dependent on tree part only. Both assumptions are realistic, and I conclude to have used approximately full six-dimensional utilization functions.

Results

Seasonal Resource Utilization Distributions

Tree part and tree were the most important niche axes to segregate the foraging of the different species (Fig. 3). Therefore I will present the resource use distributions only for tree (Fig. 1) and tree

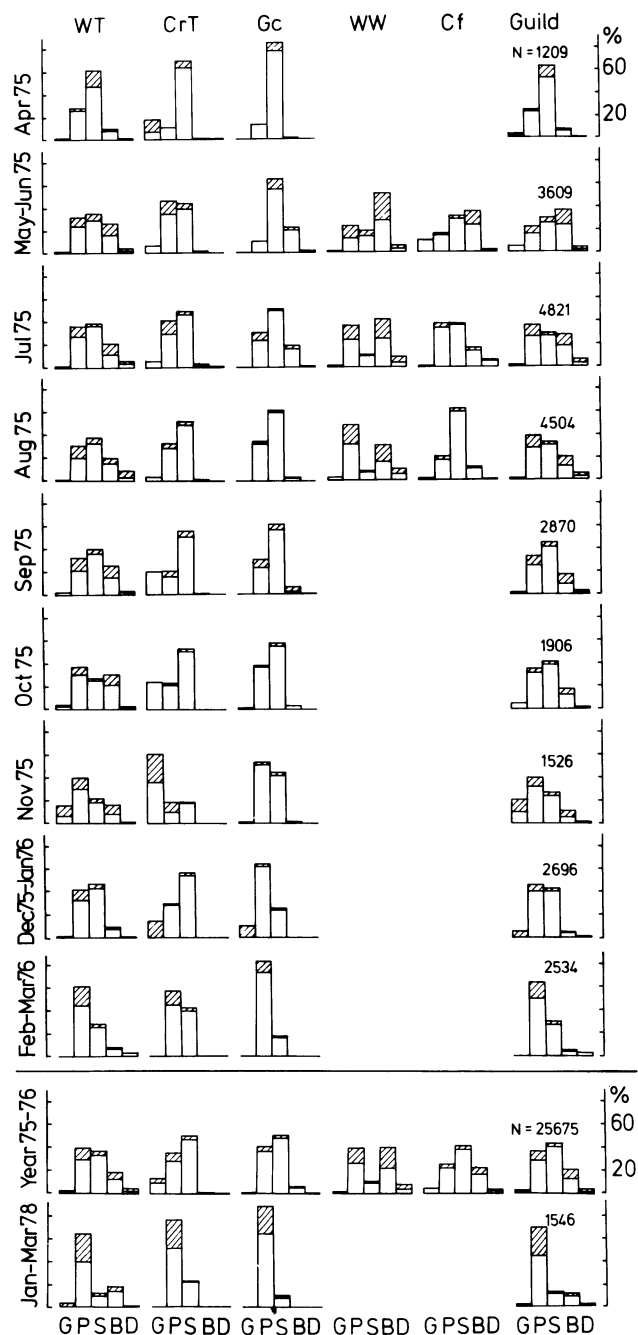


Fig. 1. Monthly use of trees. Bird species: *WT*, Willow Tit; *CrT*, Crested Tit; *Gc*, Goldcrest; *WW*, Willow Warbler; *Cf*, Chaffinch. Tree categories: *G*, ground (includes air and other rarely used substrates, hatched=snow); *P*, pine (for trees hatched=low tree); *S*, spruce; *B*, birch; *D*, other deciduous tree. Numbers of observations given above the distribution for the guild

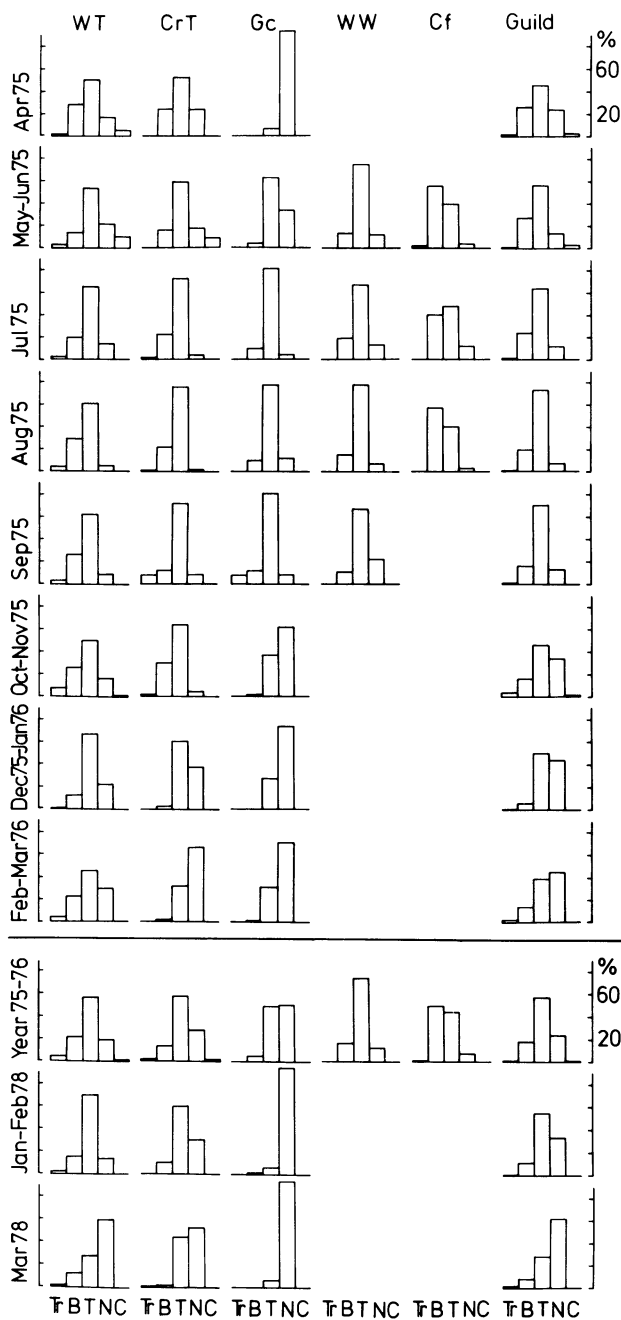


Fig. 2. Monthly use of tree parts in tall pines. Tree parts: *Tr*, trunk; *B*, branch; *T*, twig; *N*, needled twig; *C*, cone. For species abbreviations see Fig. 1

part in pine (Fig. 2). The Willow Tit *Parus montanus* was most generalized with respect to foraging sites. The Crested Tit *P. cristatus* was specialized on twigs of coniferous trees, and the Goldcrest *Regulus regulus* on needled twigs of conifers. Among the two summer visitors, the Willow Warbler *Phylloscopus trochilus* used deciduous trees and pines and preferred low trees much more than did the other species. The Chaffinch *Fringilla coelebs* preferred spruce and used branches relatively often.

During late winter 1975, in April, all the three resident species preferred spruce to other trees. The summer visitors in particular

visited birches in early summer, and so did also the Goldcrest, which at other times foraged only in conifers. All the three residents during summer moved to the inner parts of conifers from the needled twigs, and the shift was most prominent for the Goldcrest (more pronounced in pine than in spruce). Especially in autumn, the Crested Tit visited the ground fairly often. In some days during early winter insects (e.g. *Collembola*) were available on the snow, and the tits and the Goldcrest readily switched to this source. In the winters of 1976 and 1978 eggs of Lachnidae (*Cinara*, *Schizolachnus*) were abundant on pine needles, and Goldcrests almost exclusively foraged on needles of pine. The Crested and Willow Tits had the same shift, but to a lesser degree. The profitability of pine needles is shown by the fact that 50 needled tips (10 cm long) of pine had 83 insect eggs and 11 insects or spiders, whereas 50 spruce tips had only 6 insect eggs and 13 imagines. Tits did not use needled twigs much in midwinters. Lachnid eggs were small (0.35 mg wet weight), and tits should have gathered 110 eggs per minute during a six hour day to fulfill their energy needs (for estimation, see Alatalo, 1978). Gibb (1960) estimated that tits have to eat 24 insects per minute in winter, and thus the above number may be too high to be profitable, even though these eggs were typically found in clusters of four. Later in March the days are much longer and birds can use twice as much time for feeding, and these small items may be more profitably exploited. In particular this is true if the food stores on the branches and twigs have become depleted.

Seasonal Changes in Foraging Overlap

The average overlaps in the six-dimensional resource utilization of species were high in summer 1975 and in late winters 1975–1976 and 1978 (Fig. 3). The foraging overlap was lowest in April 1975 (late winter) and in late autumn 1978. Summer visitors are included for the averages. The overlaps between the three residents were also high in summer. The decrease in foraging overlaps in non-breeding seasons was due mostly to the shift of Goldcrests to the needled twigs in winter. But in late parts of winters 1975–1976 and 1978 tits also moved their foraging to pine needles, where lachnid eggs provided a relatively abundant food resource. In spruce, contrary to pine, the foraging overlaps between species were all the winter lower than in summer (Fig. 4).

Among macroaxes tree was the most effective in segregating foraging sites of different species, and among microaxes it was the tree part (Fig. 3). Seasonal trend for macrosite overlap was closely determined by tree overlap, and that for microaxes overlap by tree part overlap. Together these two axes accounted for 91% (r^2) of the seasonal variation in the six-dimensional foraging overlap, and they alone contributed 78% of all the six-dimensional niche differences. The tree part (and microaxes) overlap, having the highest values in summer months, varied seasonally more than tree (and macroaxes) overlap. Tree overlap did not have any seasonal trends between summer and winter, but habitat overlap was slightly higher during winter than in summer.

The Goldcrest occasionally escaped the foraging overlap with tits almost totally, the minimum overlaps being 25% (0.14) of maximum (0.57) with the Crested Tit and 51% (min.=0.26; max.=0.51) with the Willow Tit. For the Crested Tit and the Willow Tit, which are the most similar species in this guild (Alatalo, in preparation; Ulfstrand, 1977), the minimum monthly six-dimensional overlap 0.38 was 62% of the maximum (0.61). General resource niches of species can be illustrated by the pooled annual

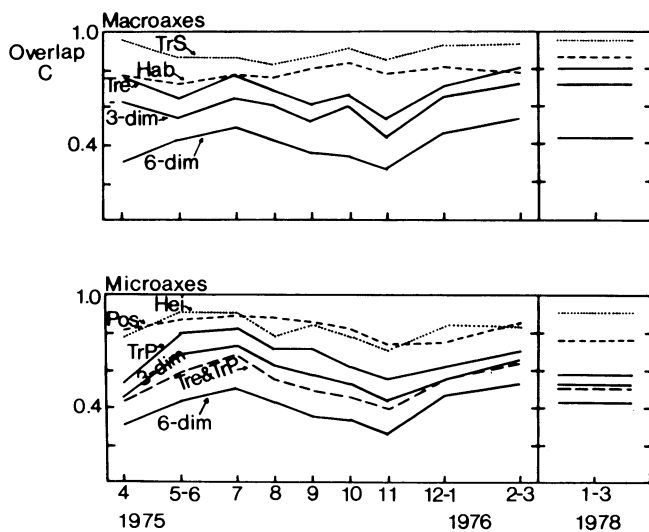


Fig. 3. Monthly average overlaps (*C*) between species for each dimension and for some combinations (both figures include the six-dimensional average overlaps). Abbreviations: *Hab*, habitat; *Tre*, tree; *TrS*, tree size; *Hei*, height; *TrP*, tree part; *Pos*, posture

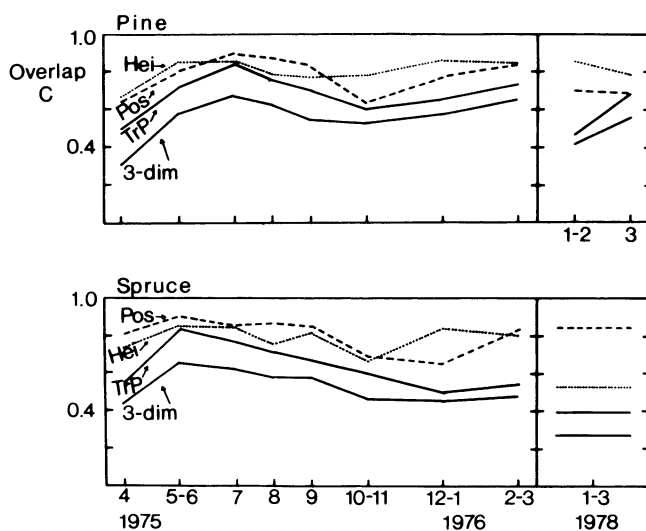


Fig. 4. Monthly average resource use overlaps (*C*) between bird species in tall pine and in tall spruce. For the abbreviations of dimensions see Fig. 3

data, and overlaps between them (0.56, 0.54 and 0.66, respectively) were equal or slightly higher than the maximum monthly resource use overlaps.

Seasonal Variation in Niche Breadth

Resource space available for birds is narrower in winter, and for macrosites the niche breadth of the whole guild was high in summer, and low in winter (Fig. 5). Macrosite breadth of the guild was also high in November as a consequence of the frequent use of ground and snow, the less typical foraging sites, by the two tits. For microsites within trees the seasonal trend is not equally well defined. Highest breadth was attained in April 1975,

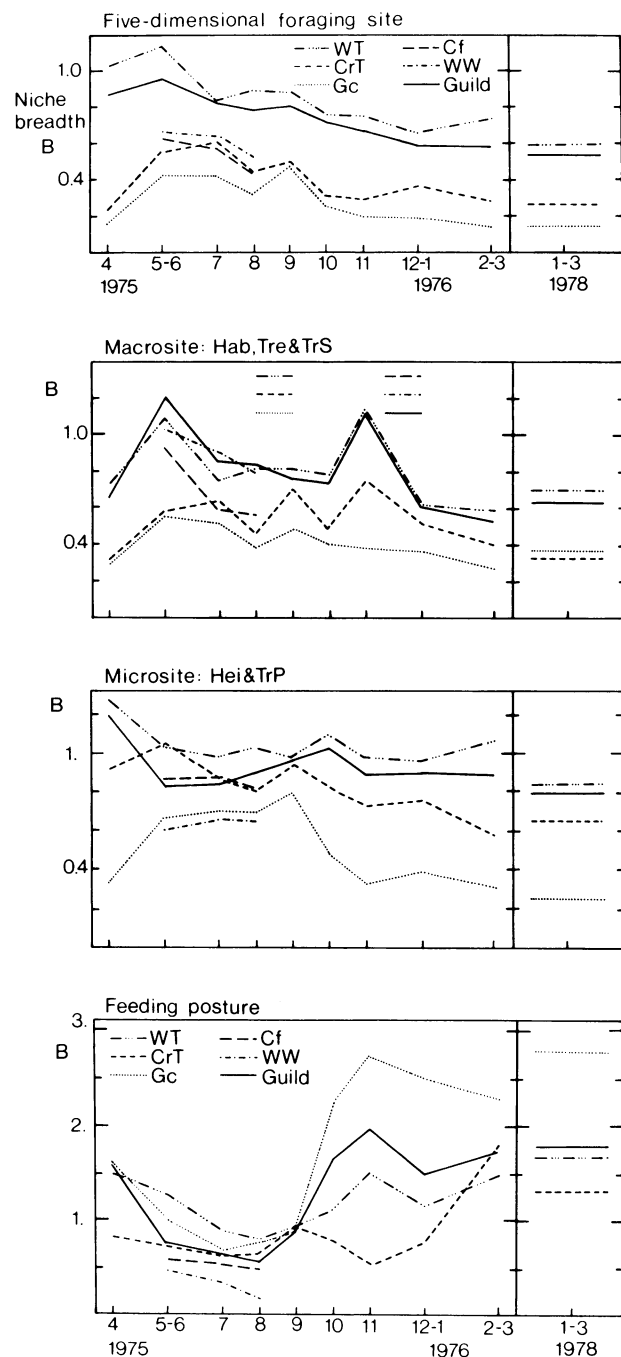


Fig. 5. Niche breadths (*B*) for each species and the whole guild along some combinations of niche dimensions. Bird species abbreviations as in Fig. 1

when the exploitation of cones by the Willow Tit increased the variety of resources used by the guild. The Goldcrest greatly narrowed its microsite breadth in winter when moving to the needed twigs exclusively. The five-dimensional foraging site volume of the guild was largest in summer and narrower in winter, April 1975 being an exception. The Willow Tit showed the same trend, but the Goldcrest and the Crested Tit had narrow foraging site niches in April as well.

The Willow Tit is highly generalized in terms of foraging site; it used all the foraging sites of the guild, and in more even propor-

tions than the guild. The other species are specialized on some part of the foraging site niche of the Willow Tit (included niches of Miller, 1967).

During the summer peak in foraging overlap (Fig. 3), specific foraging site volumes were high as can be expected. Yet, in winter, foraging site breadths tended to be low whether the overlap was low or high. During high overlaps in winter all species specialized on needed twigs of pine, and the guild niche breadth was narrow.

The seasonal trend of feeding posture versatility was reversed in relation to the foraging site volume, versatility being highest in winter. This is mostly a consequence of the increased use of needed twigs, where versatile postures are needed, although posture versatility was increased 20% during winter on needed twigs as well (Alatalo, in preparation). In winter fewer foraging sites are available, but they might be used more efficiently than in summer, as indicated by the versatile postures.

Magnitudes of Seasonal Shifts

The magnitude of seasonal foraging shifts was estimated for each species using components of diversity (Alatalo and Alatalo, 1977 and in press). The seasonal variation in foraging is the difference between the niche breadth of the pooled annual data and the average monthly niche breadth divided by the niche breadth of the annual data. On the average the use of trees varied most (Table 1), and the foraging tree could be changed almost totally from time to time (Fig. 1). For habitat, which is strongly dependent with tree species, the seasonal variation was somewhat greater than for tree part or feeding posture, which are also interrelated.

To get an impression of the magnitude of seasonal foraging shifts I compared the between-month variation averaged over species to the between-species variation averaged over months (Table 1; both measured with components of diversity using $\text{Exp}H'$). For the six-dimensional niche the seasonal shifts in foraging within a year on the average were as large, or even slightly higher, as the between species differences for each month.

Table 1. The between-month and the between-species components of niche breadth to compare the seasonal changes in foraging within species with overall foraging differences between species. Between-month component averaged over species and the between-species component averaged over months

Niche axes	Between-month component	Between-species component	Between-month Between-species
Habitat	0.089	0.063	1.41
Tree and tree size	0.156	0.143	1.09
Tree	0.148	0.142	1.04
Tree size	0.050	0.058	0.86
Height and tree part	0.113	0.138	0.82
Height	0.042	0.040	1.05
Tree part	0.079	0.161	0.49
Feeding posture	0.068	0.108	0.63
All six dimensions	0.332	0.290	1.14

Among the two most important axes in niche separation, tree part produced somewhat more segregation than tree. However, the seasonal foraging shifts were much more prominent for foraging tree. For further comparison I united the two axes of minor importance (tree size and height in tree) with tree or tree part with which they were strongly related. Altogether the relation between seasonal variation in foraging and resource use separation of species was the greater the more the axes were of macrohabitat-type. This might mean that microaxes in some way are more fixed and macroaxes more open for seasonal foraging variation. It is instructive to consider the relation between the two types of variation as it is in this way that we eliminate the differences in the heterogeneity of each axis with respect to foraging.

Among residents seasonal shifts in foraging were much more pronounced for the Goldcrest (between-month component = 0.43) and the Crested Tit (0.44) than for the Willow Tit (0.29). The monthly six-dimensional resource use breadths of the former two species represented slightly less than 60% of their annual resource use breadth, but for the Willow Tit they represented over 70%. During the summer the Chaffinch was more opportunistic (0.30) than the Willow Warbler (0.20).

Parallel Foraging Shifts in Different Species

Different species often appeared to change their resource use in a parallel way from month to month (Figs. 1, 2). The conclusion is justified by positive correlations between residents in their proportional use of tall pines (Willow Tit–Crested Tit, $r=0.61$, $p<0.10$; WT–Goldcrest, $r=0.84$, $p<0.05$; CrT–Gc, $r=0.50$, $p>0.10$) and in the use of needed twigs in tall pines (WT–CrT, $r=0.73$, $p<0.05$; WT–Gc, $r=0.54$, $p>0.10$; CrT–Gc, $r=0.68$, $p<0.05$). Other species explained 25–71% of the seasonal trends in the use of pine, emphasizing the parallelism in the seasonal foraging shifts.

Discussion

Niche Concept and Seasonal Resource Utilization

As a result of natural selection, animals optimize (more or less) their resource use to maximize their fitness, this being the framework for the optimal foraging theory (e.g. Pyke et al., 1977). The resource use of an animal at a single point in time is determined on the one hand by its genetically fixed cost and benefit relations to each resource type, and on the other hand by the availability of each resource type. Strictly speaking the matter is not this simple. For instance, the effects of predation or nutritional requirements have to be taken into account at the same time (e.g. Pyke et al., 1977). Moreover cost and benefit relations may be affected by learning (Partridge, 1976). The genetically fixed cost and benefit relations might be thought of as the *general resource niche*, whereas the resource utilization in any single period might be described as the *actual resource use*, which is adjusted by food availability.

The presumed effects of interspecific competition are threefold. Firstly, it has been one of the major forces in the evolution of the genetically fixed resource niche of each population (see Roughgarden, 1976). Secondly, interspecific competition may be preventing the invasions of new species into a local guild (see MacArthur, 1972). Thirdly, competition may still be operating within the guild, if the genetically fixed niche differences do not provide enough segregation between species.

The concept of general resource niche is comparable to Hutchinson's (1957; see also Miller, 1967) fundamental niche, which is the pre-interactive, pre-competitive or virtual niche (see Vandermeer, 1972; Pianka, 1976), but relative cost and benefit functions are substituted for the probability of survival. The realized niche or the post-competitive and post-interactive niche is less comparable with the actual resource use, which measures resource utilization, and which takes account of the availability of resources (current competition partially determines the resource availability).

The separate consideration of the general resource niche and the actual resource use is instructive for species with opportunistic foraging behaviour in a variable resource space. The general resource niche may be approximated by the pooled annual foraging observations, although these do not reflect exactly the relative cost-benefit relations of each resource type. Obviously such observations show a pattern affected by the resource availability during the whole year, but when considering overlaps between general resource niches of species this may nevertheless be quite instructive, since resource types become weighted by their general availability (cf. Schoener, 1974; Hurlbert, 1978). The annual pooled resource use is to some degree also affected by current competition, but periodically the food available for foliage-gleaners appears to be superabundant and in this way eliminates the current competition (besides this study see Hartley, 1953; Wiens, 1977; Rabenold, 1978, 1979).

With respect to the general resource niche of different species some differences in the niche boundaries were found; the Crested Tit was the only species never to use deciduous trees, all species but tits avoided the trunk, and the Willow Tit was the only species to use birch seeds during winter 1978. However relative differences in the preferences for different foraging sites by each species seem to be more important in niche segregation. The actual (monthly) resource uses of species varied to a large degree, presumably as a consequence of differences in the availability of resources. The conclusion is justified by the parallel seasonal trends in the foraging sites of different species.

Competition in the Seasonal Environment

The foliage-gleaners in northern Finland broadly overlapped with respect to their general resource niches, with the average overlap for residents being 0.59 (using pooled annual data) in the six-dimensional resource space. Much lower temporary overlaps in the actual resource use were recorded, the corresponding average for minimum monthly foraging overlaps being 0.26. During food shortage these foliage-gleaners are likely to compete with each other, owing to the overlap in their general resource niches. Competition could be avoided by the withdrawal of each species to its exclusive part of the niche space. However, in their variable environment these birds are likely to be often far below the carrying capacity of the environment, enjoying thus relative superfluity of food with little interspecific competition. This is obvious if bird populations are limited by the period when the food resources are lowest, and for insectivorous birds the difference between the minimum and the maximum food availability is multifold. The periodically weakened interspecific competition is illustrated by temporally higher overlaps in actual resource use between species and by the parallelism of foraging shifts of different species.

Temperate-zone bird populations are assumed to be food limited in winter and to have a relative superfluity of food in summer (Lack, 1954, 1971; Gibb, 1960; Fretwell, 1972; Wilson, 1976; Rabenold, 1978, 1979). Niche separation of temperate-zone birds

has been reported to be greater in winter than in summer (Gibb, 1954; Betts, 1955 according to Baker and Baker, 1973; Haftorn, 1956; Newton, 1967; Stallcup, 1968; Baker and Baker, 1973; Opdam, 1975). On the other hand in summer diffuse competition is intensified as migrants increase the species number in the guild, and Ulfstrand (1977) reported greater overlap in winter than in summer. Studies in other areas and of other animal groups as well support the hypothesis of lower resource use overlap during food shortage (see Smith et al., 1978 for review; also Feinsinger, 1976).

In northern Finland the foraging overlaps for the pooled winter observations were somewhat lower than those for pooled summer observations (Alatalo, in preparation). Now considering resource use overlaps during short time periods in summer, they are found to be relatively high all the time. In winter the population levels of birds could be nearer the carrying capacity, but in a variable unpredictable environment, relative superabundance of food at this time may still be rather common (e.g. during beechmast in England, Hartley, 1953). As a case in point, periodically during winter of 1976 and 1978, foraging overlaps were found that were as high as those of summer, for all the resident birds concentrated their foraging on pine needles with abundant lachnid eggs.

Then what is the lowest that the foraging overlap between two species can be and both still coexist? The Willow Tit and the Crested Tit are the most similar species in this guild (see also Ulfstrand, 1977). It is unlikely that these similar sized species of same genus would differentiate drastically in diet in the same foraging site (cf. Hespenheide, 1975). Thus foraging site dimensions should reveal a considerable proportion of the niche differences between these two species. At the lowest their foraging overlap in the six-dimensional niche space with approximately full multidimensional calculus was 0.38, much above zero, but much lower than the overlap of annual foraging observations (0.66). Foraging overlaps measured for data pooled with respect to time tend to overestimate actual resource use overlaps, and even shorter time periods than one month, might have given still lower overlaps.

Foraging Shifts

Seasonal foraging shifts were quite large; monthly differences in the foraging sites of each species being as large as the foraging site differences between species in each month. Foliage-gleaners in temperate areas are generalists and plastic, changing foraging sites readily, and often in a parallel way in order to cope with the variable resource availability. The seasonal variation in foraging was more prominent for the Goldcrest and the Crested Tit than for the Willow Tit, which had a much broader niche. The Willow Tit is more abundant than the Goldcrest or the Crested Tit (Alatalo, 1978), and perhaps intraspecific competition in flocks is keener for the Willow Tit than for the other species causing greater stability in the species-level foraging.

In general niche axes of macrohabitat-type seemed to be more open for foraging variation and axes of microhabitat-type more rigid, in relation to the amount by which these axes give between-species niche separation. The use of microaxes (tree part and feeding posture) was correlated with body size of birds, and therefore they seem to be more genetically fixed than macroaxes (Alatalo, in preparation). Thus the same bird could change foraging tree more easily than tree part in the same tree.

Acknowledgements. I am very grateful to Risto H. Alatalo, Chris Perrins, Seppo Sulkava and Staffan Ulfstrand for valuable com-

ments on the manuscript. Jorma Kyrki kindly identified the lachnids. The study was supported by grants from the Emil Aaltonen Foundation. Part of the work was accomplished at the Department of Zoology, Uppsala University (visit supported by the Letterstedtska Föreningen) and at the Edward Grey Institute of Field Ornithology, Oxford University (visit supported by the British Council).

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Received in February 1980