Resource division among birds in North Finnish coniferous forest in autumn

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Densities, flock sizes and feeding stations of the bird species occurring in mixed flocks in old coniferous forests in northern Finland were recorded in October 1974. The combined density of all species was about one seventh and the tree biomass per unit area about one fifth of that in South Scandinavia. All species occurring in both regions, except *Parus montanus,* were scarcer in northern Finland. Preferences for tree species and parts of the trees were measured and compared with corresponding data from southern Scandinavia. In northern Finland the ground and the dwarf-scrub were used much more than in southern Scandinavia. *Parus cinctus* exploited these feeding stations to a large extent. The peripheral parts of the conifers were exploited remarkably little in Finland. Feeding niches seemed generally to be broader in North Finland than further south.

Introduction

The patterns of diversity and organization of bird communities have received much attention. The niche concept has been very useful in the elucidation of these problems (e.g. MACARTHUR 1972, CODY 1974, KARR 1974, TRAMER 1974).

During late autumn and winter, temperate coniferous forests are inhabited by a guild of species, which glean most of their food from the trees. In northern Finland (study area 66°N, 29°E) this guild consists of the Willow Tit *Parus montanus,* Crested Tit *Parus cristatus,* Siberian Tit *Parus cinctus,* Great Tit *Parus major,* Treecreeper *Certhia familiaris* and Siberian Jay *Perisoreus infaustus.*

In this paper we describe the division of resources among these different bird species in northern Finland. We compare the niches of the species and their exploitation of different feeding stations with those observed for the corresponding bird guild in South Swedish coniferous forests (ALERSTAM et al. 1974, ULFSTRAND 1975). The questions posed are: Do the species occurring in both northern Finland and southern Sweden occupy identical niches in both areas? Do niches have the same width in the two areas? Is the exploitation, by all species combined, distributed over different feeding stations in the same way in the two areas?

Methods and study areas

To obtain data on densities we used a line transect method proposed by EMLEN (1971). The detection points of the flocks were assigned to strips parallel to

the census line. We used the same strip widths as NILSSON (1974), i.e. 0—12.5 m, 12.5—25 m, 25—50 m and >50 m, from the census line. The density of each species was estimated from the strip(s) closest to the census line, where the numbers of detected birds divided by the area of the strip (strip width × length of census line) were higher than in strips farther from the census line. No differences in the conspicuousness of any species between spruce- and pine-dominated forests were apparent from the data, so all observations were lumped before estimating the strip width with assumed 100 per cent coverage. Our speed of progress through the forests was about 55 m/minute, excluding pauses to watch and follow flocks.

The feeding stations of the birds were recorded in the same way as described in ALERSTAM et al. (1974), although in Finland we collected up to 20 records (most often about 5) of each individual bird. Thus, the observations are not independent, which makes the interpretation of statistical tests difficult.

The forest composition was assessed in two ways. The numbers of trees and bushes more than 2 m high were counted in 12 areas of 20×20 m. Since it was difficult to find representative plots, the proportion of different tree species was also estimated subjectively. Our independent subjective estimates generally coincided.

We examined forest areas in northern Finland (65°30′—66°30′N, 25°30′—30°00′E) during 12 to 18 October 1974. Most of our line transect censuses were conducted in Oulanka National Park (66°20′N, 29°00′E). We selected forest areas for homogeneity and large size, and avoided human habitations and areas with young trees. It should be noted that most of the data refer to forests almost unaffected by man. Dead old trees and beard lichens were common in most localities.

Thin snow covered the ground locally, but there were always many snow-free patches and dwarf shrubs emerging above the snow.

Records of feeding stations were collected in South Swedish coniferous forests in October and the first days of November 1974. Other data from South Sweden (ALERSTAM et al. 1974, ULFSTRAND 1975) were also used for comparison.

Results

Abundances; Flock sizes

The numbers of individuals of each spe-

TABLE 1. Abundance of species in spruce- and pine-dominated coniferous forests. Numbers of individual recorded per hour presented as well as the calculated densities.

	Spruce-dominated forest		Pine-dominated forest	
	Ind./hr	Ind./km²	Ind./hr	Ind./km²
Parus montanus	4.1	17.3	2.5	10.5
Parus cristatus	0.7	3.0	0.9	4.6
Parus cinctus	1.3	4.7	1.0	3.0
Parus major	1.0	5.0	0.2	1.2
Certhia familiaris	0.3	1.4	—	—
Perisoreus infaustus	0.9	2.3	1.8	4.9
Total	8.4	33.7	6.5	24.2
Number of ind.	108		83	

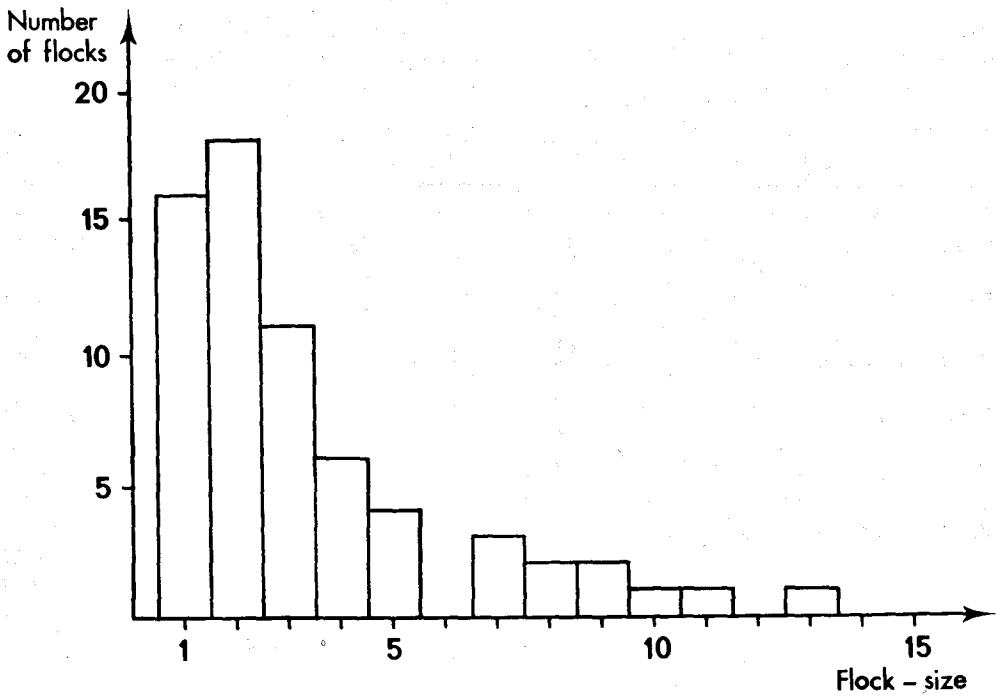


FIGURE 1. Frequency distribution of different flock-sizes.

cies recorded per hour as well as the calculated densities are presented in Table 1. Little difference was found between the two forest types in total abundance and abundance of different species. The Crested Tit and Siberian Jay

TABLE 2. Percentage distribution of feeding stations in spruce-dominated (A) and pine-dominated (B) coniferous forests.

	Spruce	Pine	Birch	Dwarf-scrub	Ground	Number of feeding stations
A						
Parus montanus	37	6	15	13	30	331
Parus cristatus	32	8	—	—	60	25
Parus cinctus	49	7	5	30	10	258
Parus major	21	66	8	1	5	88
Certhia familiaris	75	13	13	—	—	40
Perisoreus infaustus	75	17	3	5	—	73
B						
Parus montanus	10	77	2	8	2	146
Parus cristatus	38	47	—	—	16	133
Parus cinctus	21	31	0	28	20	135
Parus major	9	46	—	5	41	11
Perisoreus infaustus	6	84	5	5	—	55

TABLE 3. Percentage distribution of feeding stations in spruces, pines and birches in relation to that expected from random exploitation. A = spruce-dominated forest. B = pine-dominated forest.

		Spruce	Pine	Birch	Number of feeding stations	Probability of difference X^2-test. ns = no significance
A						
Parus montanus	Observed	64	10	26	189	$p<0.001$
	Expected	67	17	16		
Parus cristatus	Observed	80	20	—	10	
	Expected	66	24	11		
Parus cinctus	Observed	81	12	7	155	$p<0.001$
	Expected	67	22	11		
Parus major	Observed	22	70	8	83	$p<0.001$
	Expected	59	23	19		
Certhia familiaris	Observed	75	13	13	40	ns
	Expected	84	10	6		
Perisoreus infaustus	Observed	79	17	4	69	ns
	Expected	70	18	12		
B						
Parus montanus	Observed	12	86	2	131	ns
	Expected	13	82	5		
Parus cristatus	Observed	45	55	—	112	$p<0.001$
	Expected	13	82	5		
Parus cinctus	Observed	40	59	1	71	$p<0.001$
	Expected	18	78	5		
Parus major	Observed	17	83	—	6	
	Expected	16	83	2		
Perisoreus infaustus	Observed	7	89	5	52	ns
	Expected	16	81	3		

were probably more numerous in pine-dominated than spruce-dominated forests, whereas the reverse relationship held for the other species.

Flock sizes are shown in Fig. 1. Median and mean total flock sizes were 2 and 2.8, respectively. Flocks of seven or fewer birds contained on the average 1.3 species (n=58), while larger flocks contained 2.7 species (n=7).

Feeding stations

The distribution of feeding stations in different tree species, dwarf-scrub and on the ground (litter or moss) is shown in Table 2. The dwarf-scrub consisted of *Ledum palustre* and to some extent *Vaccinium* spp.

(A) Preference for tree species. The species composition of the forest was estimated at each observation site. If the birds chose tree species for feeding at random, the percentage distribution of feeding stations on different tree species should be equal to the weighted (by number of feeding stations) mean composition of tree species at the observation sites. The observed and expected distributions of feeding stations are compared in Table 3.

The data in this table may be utilized in two ways. (1) The expected distribu-

tions show the average tree species composition in the habitat of each bird species. Hence, in spruce-dominated forest, the Willow and Great Tits occurred in patches with a large proportion of birches. The Treecreeper was recorded at sites with a particularly large proportion of spruces. No such marked specific habitat differences were found in pine-dominated forest. (2) A comparison of the observed and expected frequencies of feeding stations reveals that, in spruce-dominated forest, the Willow Tit preferred birches, the Siberian Tit spruces, the Great Tit pines (but note the low number of records), while the Treecreeper and Siberian Jay exploited the tree species at random. Data for the Crested Tit are too few for safe conclusions. In pine-dominated forest the Crested and Siberian Tits preferred spruces, while the Willow Tit and Siberian Jay visited the trees at random. No conclusions can be reached for the Great Tit.

(B) Distribution of feeding stations in the trees. The distribution of feeding stations in different parts of the trees is shown in Table 4. The majority of the feeding stations in spruces were recorded at the trunk for the Treecreeper and the Siberian Tit, at the branches for the Willow Tit, at the twigs for the Crested Tit and at twigs-needles for the Siberian Jay. In pines, the majority of the feeding stations of the Treecreeper and the Crested and Siberian Tits were at the trunk, but the last-mentioned species also often occurred at other parts of the pines. The Willow and Great Tits mainly exploited the branches, while the twigs were often visited as well by the Siberian Jay. Generally, the twigs-needles of the pines were exploited to a very small extent; the Siberian Tit and Siberian Jay showed

TABLE 4. Percentage distribution of feeding stations in spruces, pines and birches.

	Trunk	Branch	Twigs	Twigs-needles	Number of feeding stations
Spruce					
Parus montanus	14	42	23	21	146
Parus cristatus	3	25	47	25	64
Parus cinctus	47	26	15	13	165
Parus major	33	28	6	33	18
Certhia familiaris	94	6	—	—	47
Perisoreus infaustus	—	36	21	43	58
Pine					
Parus montanus	36	40	21	4	169
Parus cristatus	67	12	17	4	69
Parus cinctus	29	23	25	24	80
Parus major	14	71	14	—	63
Certhia familiaris	100	—	—	—	17
Perisoreus infaustus	9	39	36	16	64
Birch					
Parus montanus	38	24	38		55
Parus cinctus	—	25	75		12
Parus major	29	71	—		7

TABLE 5. Exploitation at beard lichens. Percentages of numbers of feeding stations. The numbers of feeding stations are given in brackets.

	Spruce		Pine	
Parus montanus	8	(146)	4	(169)
Parus cristatus	—	(64)	55	(69)
Parus cinctus	2	(165)	19	(80)
Parus major	—	(18)	—	(63)
Certhia familiaris	—	(47)	—	(17)
Perisoreus infaustus	52	(58)	72	(64)

the highest rate of utilization of these parts. The few data of feeding stations in birches indicate that the Great Tit mainly visited the trunk and branches, the Willow Tit fed at the twigs as well, while the Siberian Tit mainly exploited the twigs.

From 50 to 85 % of the feeding stations at branches and twigs of the spruces and pines were at dead parts. There were no significant differences between bird species with respect to this exploitation of dead parts of the trees.

(C) Feeding stations at dwarf-scrub and on the ground. The Siberian Tit foraged to a very large extent in dwarf-scrub (Table 2), almost exclusively *Ledum palustre*. The Willow Tit also visited dwarf-scrub, but to a smaller extent. Litter and moss were exploited most by the Crested Tit, which did not feed at dwarf-scrub at all, and also by the Willow, Siberian and Great Tits.

(D) Feeding stations at beard lichens. Foraging in beard lichens was frequently seen in the Siberian Jay (Table 5) and also in the Crested and Siberian Tits in Pines. The Siberian Jay stores food mostly in beard lichens before the advent of winter (BLOMGREN 1964).

(E) Feeding behaviour. A large part of the feeding stations were recorded with the birds hanging at the branches, twigs or twigs-needles (Table 6). This applied to all species except the Great Tit.

Discussion

Abundances

The density of the Willow Tit in northern Finland during this study period was similar to that noted in southern Finland and Sweden in winter. The Crested Tit, Great Tit and Treecreeper occurred in much lower numbers in northern Finland than in southern Fennoscandia (KLOCKARS 1936, BERGROTH & BRUUN 1939, PALMGREN 1943, LEHTONEN 1948, NILSSON 1974, ALERSTAM et al. 1974). The combined density of all species in the guild in Lapland was about one sixth to one eighth of that found by the investigators cited above. Several species which are absent from northern Finland make up an important part of the bird guild in more southerly regions (cf. ALERSTAM et al. 1974). The Siberian Tit and Siberian

TABLE 6. Percentages of feeding stations at branches, twigs or twigs/needles with the birds hanging. Numbers of feeding stations are given in brackets.

	Spruce		Pine		Birch	
Parus montanus	25	(126)	29	(109)	32	(34)
Parus cristatus	47	(62)	70	(23)		
Parus cinctus	26	(188)	35	(57)	67	(12)
Parus major	—	(12)	2	(54)	—	(5)
Perisoreus infaustus	59	(58)	33	(58)		

Jay, on the other hand, are confined to northerly forests.

Why are birds so scarce in northern coniferous forests? It may be argued that there is less food in the north. The average height of the tree tops in the study areas in northern Finland was 17 m (range 14—23 m) but about 25 m in the South Swedish coniferous forest studied by NILSSON (1974). From these values we can calculate an index of tree volume. Using the regression on tree height (H) of diameter at breast height (D) provided by SPRING et al. (1974), we can calculate D, and take $D^2 \cdot H$ as an index of tree biomass. Calculated in this way, the biomass per tree in northern Finland is only 31 % of that in southern Sweden. In addition, tree density was 1140 per ha (>2 m high; 652>4 m high) in Finland but 43 % higher in Sweden. When these figures are combined, the tree biomass per unit area in northern Finland is found to be only about one fifth of that in southern Sweden. If the food available is calculated on the basis of tree biomass, it will be lower in North Finland than in southern Fennoscandia. This would explain the scarcity of birds in the northern forests, if winter food resources constitute the most important population-limiting factor. However, we have no data to check this speculation.

Segregation between the species

The characteristics of the habitats and feeding stations of each species can be summarized as follows:

Willow Tit: The most abundant species in both spruce- and pine-dominated forest, occurring predominantly in spruce-dominated forest. Birches were preferred to conifers for feeding. Foraged mainly at the branches of the spruces and pines. Occurred regularly both in dwarf-scrub and on the ground.

Crested Tit: More abundant in pine-dominated than spruce-dominated forest. Preferred spruces to pines. Birches were not visited. Fed at twigs and twigs-needles of the spruces and at beard lichens at the trunk of pines. Fed extensively on the ground, but not in dwarf-scrub.

Siberian Tit: More abundant in spruce-dominated than pine-dominated forest. Preferred spruces to pines. Foraged to a large extent at the trunks of spruces and pines and at the outer twigs of birches. Dwarf-scrub was heavily exploited. Occurred regularly on the ground also.

Great Tit: Occurred predominantly in spruce-dominated forest. Fed on the upper sides of branches and twigs (did not hang upside down while feeding). Occurred regularly on the ground.

Treecreeper: Occurred at very low densities in spruce-dominated forest. Foraged at the trunks.

Siberian Jay: More abundant in pine-dominated than spruce-dominated forest. Fed at beard lichens on branches, twigs and twigs-needles of the conifers. Fed at dwarf-scrub (berries) or on the ground to a minor degree or not at all.

In coniferous forests in South Sweden the bird species constellation is different from that in North Finland. In South Sweden, the Coal Tit, *Parus ater,* and the Goldcrest, *Regulus regulus,* make up an important part of the guild during autumn and winter (ALERSTAM et al. 1974, ULFSTRAND 1975), but these species are absent from northern Finland in winter. In contrast, the Siberian Tit and the Siberian Jay are found exclusively in the latter region. The Willow Tit, Crested Tit, Great Tit and Treecreeper are present in both areas.

Do the species that occur in both South Swedish and North Finnish coniferous forest occupy different niches in the two areas? The feeding habits of these species in South Sweden have been described by ALERSTAM et al. (1974) and ULFSTRAND (1975). The percentage distributions of feeding stations in spruces and pines are compared between the two different regions in Table 7. The evenness (H'/H' max. PIELOU 1969) values of the exploitation of different feeding stations are also presented in the table. A high value for this index

TABLE 7. Percentages distribution of feeding stations in the Willow Tit, Crested Tit, Great Tit and Treecreeper in North Finland and South Sweden. Data from S. Sweden Feb —74 are from ALERSTAM et al. 1974.

	Trunk	Branch	Twigs	Twigs-needles	Evenness H'/H' max	Number of feeding stations	Region and date
Spruce							
Parus montanus	14	42	23	21	0.94	146	N Finland Oct —74
	2	28	5	65	0.62	43	S Sweden Oct—Nov —74
	7	67	23	3	0.65	30	S Sweden Feb —74
Parus cristatus	3	25	47	25	0.83	64	N Finland Oct —74
	—	18	7	75	0.65	44	S Sweden Oct—Nov —74
	3	61	19	17	0.74	36	S Sweden Feb —74
Parus major	33	28	6	33	0.91	18	N Finland Oct —74
	—	71	3	26	0.64	31	S Sweden Oct—Nov —74
Certhia familiaris	94	6	—	—		47	N Finland Oct —74
	88	13	—	—		24	S Sweden Oct—Nov —74
	93	7	—	—		43	S Sweden Feb —74
Pine							
Parus montanus	36	40	21	4	0.86	169	N Finland Oct —74
	14	46	28	12	0.90	65	S Sweden Oct—Nov —74
	15	58	24	3	0.76	71	S Sweden Feb —74
Parus cristatus	67	12	17	4	0.69	69	N Finland Oct —74
	10	21	30	39	0.93	61	S Sweden Oct—Nov —74
	12	62	23	3	0.72	92	S Sweden Feb —74
Parus major	14	71	14	—	0.72	63	N Finland Oct —74
	43	37	9	11	0.86	35	S Sweden Oct—Nov —74
Certhia familiaris	100	—	—	—		17	N Finland Oct —74
	80	20	—	—		41	S Sweden Oct—Nov —74
	96	4	—	—		28	S Sweden Feb —74

combined with many recorded categories of feeding stations indicates a broad niche. The following differences between the feeding habits in the two regions emerge: (1) Feeding in dwarf-scrub or on the ground is more frequent in the Willow and Crested Tits in northern Finland. (2) The proportion of feeding station records of birds hanging at the branches, twigs and twigs-needles is higher in northern Finland, especially for the Crested Tit but also for the Willow Tit. In autumn 1974, this proportion was 53 % in North Finland and 10 % in South Sweden for the Crested Tit, and 28 % and 23 %, respectively, for the Willow Tit. (3) The Crested Tit was demonstrated to prefer pines to spruces in southern Sweden, but the reverse situation was found in Finland. However, the preference for pines in southern Scandinavia is not a constant feature. HAFTORN (1954) and NILSSON (unpubl.) have recorded temporary preferences for spruces. (4) The Willow and Crested Tits in North Finland foraged relatively more often at the trunks of the conifers. (5) The birds in northern Finland generally seem to be less "specialized", in terms of exploitation of different feeding stations, than in South Sweden. This is particularly evident from the data on evenness of feeding stations in spruces (Table 7,

Fig. 2). It should be added that the Siberian Tit and Siberian Jay were "generalists" also as was demonstrated by their exploitation of many categories of feeding stations and their correspondingly high evenness values (Fig. 2). The Goldcrest and the Coal Tit, on the other hand, exploit few categories of feeding stations on the mainland of southern Sweden (ALERSTAM et al. 1974) and their evenness values are low (Fig. 2).

Although the feeding habits of each species in northern Finland possessed certain specific properties, extensive overlapping of their feeding niches occurred. The even distributions of the feeding stations of most species in northern Finland suggests relaxed interspecific competition as compared with conditions in South Swedish coniferous forests. LACK (1971) speculated that the Crested and Siberian Tits are potential competitors (judging from their similar beak shapes) and that they replace each other geographically. The present data show that the feeding niches of the two species do not overlap to any remarkable extent. In fact, the niches occupied

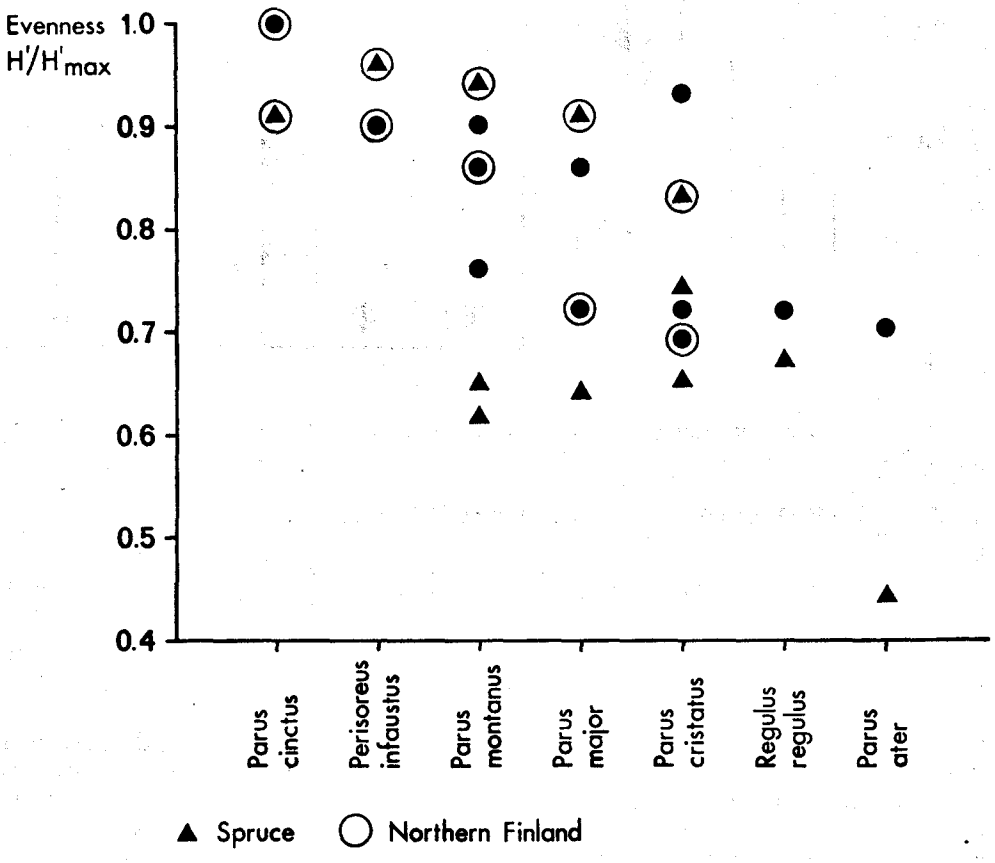


FIGURE 2. Niche width, measured as evenness of exploitation of feeding stations within the trees. Primary data from Tables 4, 7 and ALERSTAM et al. 1974.

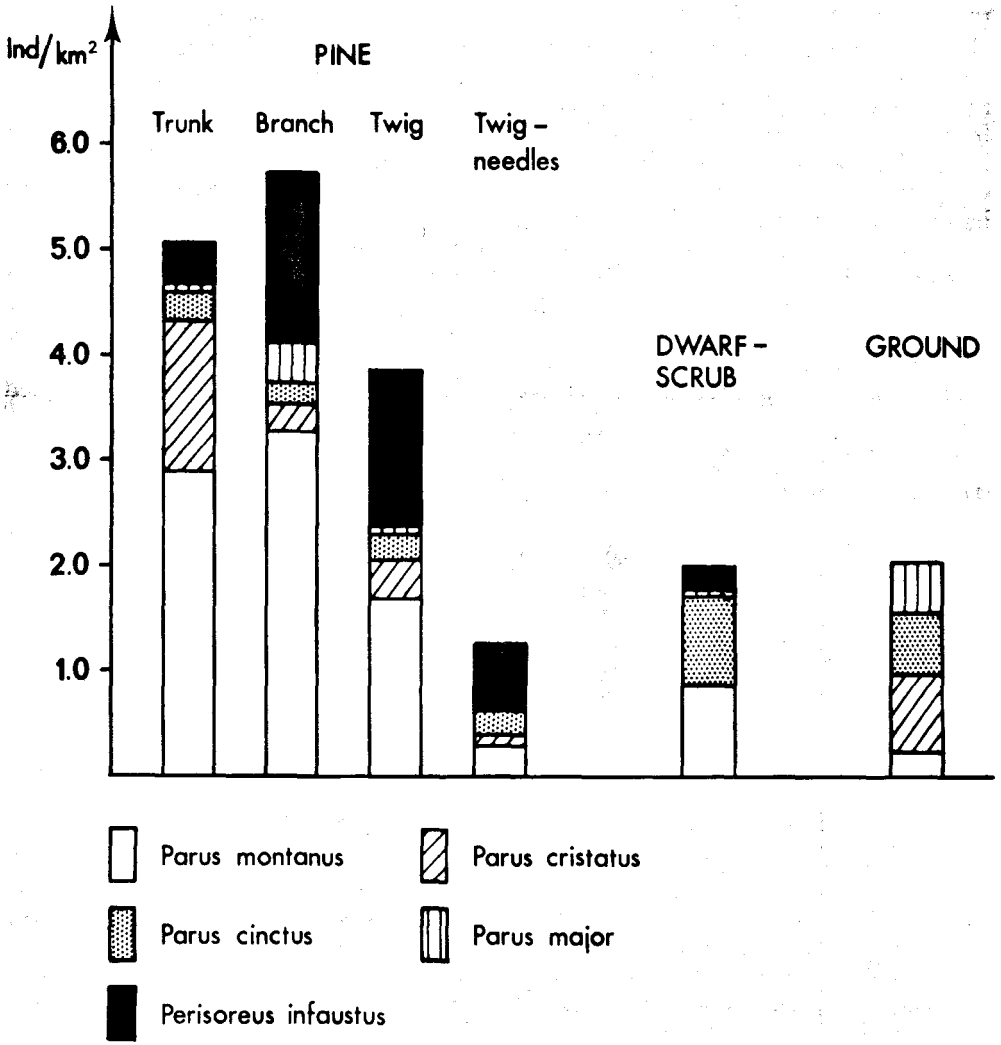
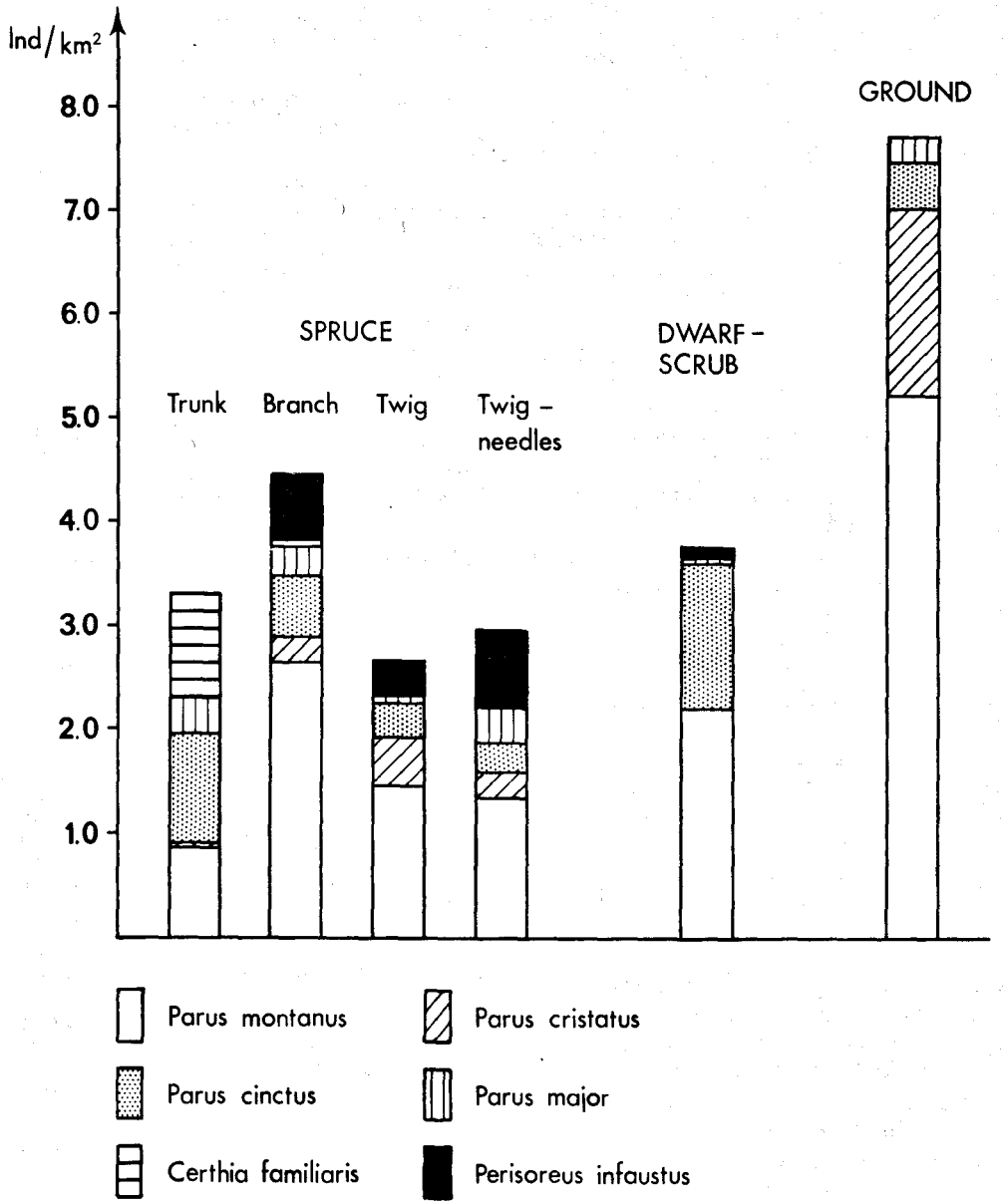


FIGURE 3. Occurrence of the bird species on different feeding stations. A. spruce-dominated forest. B. pine-dominated forest. Data derived from Tables 1—4.

by the Willow Tit and the Siberian Tit showed greater similarity.

It should be pointed out that the present data refer to autumn conditions, with more than eight hours of daylight and temperatures at about 0°C; little snow occurred, the dwarf-scrub and the ground being left open to exploitation at many places, and there was practically no snow in the coniferous trees. The situation may be very different during the winter. SNOW (1952) found that the Willow and Siberian Tits behaved markedly differently during midwinter in Swedish Lapland. The Siberian Tit stayed for a comparatively



long period of time in each tree, while the Willow Tit visited a tree only for a brief period and flew off a long distance to the next tree. No such difference was noted in this study; in fact the two species associated freely in mixed flocks. SNOW (op. cit.) recorded Great Tits only in the close vicinity of human

habitations during midwinter, while we regularly observed this species several kilometres from any houses.

Total exploitation of feeding stations

The exploitation of the conifers, dwarf-scrub and ground in spruce-dominated and pine-dominated forests is shown in Fig. 3. The relations between total exploitation of trunks, branches and twigs are similar in North Finland and South Sweden (ALERSTAM et al. 1974). The exploitation rate in Lapland is, however, only about 15 % of that in Sweden (cf. the low density of birds in northern Finland as compared with southern Sweden, p. 20).

The utilization rate of twigs-needles is extremely low, amounting to only a few percentage units of that in South Sweden. In the latter region, twigs-needles is the feeding station frequented most often. Mainly the Coal Tit and Goldcrest forage in these parts of the trees. In spite of the absence of these two species from northern Finland, no niche expansion of the Willow, Crested or Great Tits into the peripheral parts of the trees has occurred, nor does the Siberian Tit visit the twigs-needles to any large extent. The Siberian Jay, a large bird compared with the other species, often foraged at these parts of the trees, but almost certainly used food quite different from that of the much smaller Coal Tit and Goldcrest.

The low utilization rate of the twigs-needles in North Finland may be related to the fact that the species present are unable to exploit these parts at an economic rate (SCHOENER 1971). Later in winter, snow will prevent the birds from feeding in these parts of the trees. The habit of hanging during feeding may be an adaptation to exploiting the snow-free lower sides of twigs and branches. Similarly, the intense utilization of the tree trunks by the tits in northern Finland may be related to their lack of snow-cover during the winter and/or the scarcity of Treecreepers.

One may assume that it would be advantageous for the birds during the autumn to concentrate their feeding to those parts of the environment that will be blocked later by snow. This strategy would "save" food that may be used later on during the winter. Such an explanation can be advanced for the high exploitation rate of dwarf-scrub and the ground during the study period.

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Selostus: Lintujen keskinäisestä ravintovarojen käytöstä Pohjois-Suomen havumetsissä syksyllä

Lokakuussa 1974 tutkittiin sekaparvissa liikkuvien lintujen runsautta, parvikokoa ja ruokailup aikkoja Pohjois-Suomen vanhoissa havumetsissä. Kaikkien lajien kokonaistiheys oli noin seitsemäsosa ja puiden biomassa pinta-alayksikköä kohden viidesosa vastaavista arvoista Etelä-Skandinaviassa. Kaikki molemmilla alueilla esiintyvät lajit, hömötiaista lukuun ottamatta, olivat harvallkuisempia Pohjois-Suomessa. Eri puulajien ja puiden osien suosinta ruokailupaikkoina mitattiin ja tuloksia verrattiin Etelä-Skandinaviasta koottuihin aineistoihin. Edellisellä alueella linnut ruokailivat paljon enemmän maassa ja varvikossa kuin jälkimmäisellä. Lapintiainen käytti näitä ruokailupaikkoja laajassa mitassa. Sen sijaan havupuiden oksiston ulko-osia linnut käyttivät Suomessa huomattavan vähän. Kaiken kaikkiaan "ruokailulokerot" olivat Pohjois-Suomessa väljemmät kuin etelämpänä.