Ann. Zool. Fennici 24:281–294. 1987

Effects of forest management on birds breeding in northern Finland

Raimo Virkkala

Virkkala, R. 1987: Effects of forest management on birds breeding in northern Finland. — Ann. Zool. Fennici 24:281–294.

The effects of forest thinning and fragmentation on bird species were studied in northern Finland in 1982–1985. Based on line transect censuses bird communities of virgin and thinned pine forests, and contiguous and fragmented spruce forests were compared. There were no statistically significant differences in total bird densities in virgin and thinned pine forests, nor in uniform and fragmented spruce forests. The structure of bird communities was, however, different both in pine and spruce forests. The densities of the generalist species *Phylloscopus trochilus*, *Carduelis flammea* and *Turdus iliacus* and the marsh-nesting *Motacilla flava* were higher, and those of *Parus cinctus*, *Perisoreus infaustus* and *Phoenicurus phoenicurus* were lower in thinned forests than in virgin pine forests. Forest fragmentation had a positive effect on the densities of *Ph. trochilus*, *T. iliacus* and *C. flammea*, and a negative effect on the group of northern taiga species (*Tetrao urogallus*, *Picoides tridactylus*, *Parus cinctus*, *Perisoreus infaustus*, *Pinicola enucleator* and *Emberiza rustica*).

Line transect censuses had been carried out in the vicinity of the study area already in the 1940s and 1950s. Densities of the most common species in virgin forests were compared using the 1940–50 censuses and the present results. *Fringilla montifringilla* had increased fivefold from the 1940–50 period to the 1980s, but this was probably due to a collapse, caused by several cold winters, in the 1940s. Densities of species preferring old forests, such as *P. cinctus*, *Ph. phoenicurus* and *P. infaustus*, had remained nearly the same in the study area from the 1940–50s to the 1980s, although these species have drastically declined in the whole of northern Finland due to silvicultural practices. In my study area the densities probably remained almost unchanged as, even today, there are large, virgin forests left. The importance of these forests in the conservation of declining northern bird species is emphasized.

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

1. Introduction

Changes in the distribution and abundance of bird species in Finland have been well documented (e.g. von Haartman et al. 1963–72). Previously, the importance of climatic changes to the breeding bird fauna was emphasized (Kalela 1949, 1952, Merikallio 1951). Nowadays, human-caused — either direct or indirect (e.g. thorough environmental changes) — effects on bird populations have been considered to be a more important factor (von Haartman 1973, 1978, Järvinen & Väisänen 1979a, Helle & Järvinen 1986). The drastic changes that have occurred in the structure of Finnish forests during the recent decades have had a clear effect on the forest bird fauna breeding in Finland (see Helle & Järvinen 1986, Väisänen et al. 1986).

The increase in spruce in southern Finland has favoured bird species that prefer spruce-dominated forests (Järvinen et al. 1977a, Järvinen & Väisänen 1978a). Cuttings have caused forest fragmentation and regeneration, and cattle grazing in forests has ceased. These events have favoured species breeding in bushy forests and at forest edges (von Haartman 1973, 1978, Järvinen et al. 1977a, Järvinen & Väisänen 1979b). Ditching of open peatlands has increased the number of forest birds, especially habitat generalists (Järvinen et al. 1977a, Väisänen & Rauhala 1983).

The most important factor influencing forest birds in northern Finland has been the large-scale clear-cuttings, which began in the 1950s. As forest structure in northern Finland has changed during the last few decades the bird species of old forests have declined drastically and generalist species, which prefer young forests and edge areas, have increased (Järvinen et al. 1977a, Järvinen & Väisänen 1978b, 1979a, 1979b, Väisänen 1983, Väisänen & Rauhala 1983, Helle & Järvinen 1986, Väisänen et al. 1986). In particular, fragmentation of old forests caused by clear-cuttings has been supposed to have a negative effect on the species of old forests (Järvinen et al. 1977a, Järvinen 1981).

The influence of forestry on the northern Finnish bird community has been studied locally, especially in the area of Simo – Tervola, in southern Lapland (Väisänen & Rauhala 1983, Väisänen et al. 1986) and in Kuusamo, near the eastern border (Helle 1986a and references there). No detailed studies have been conducted in northern Lapland even though many northern forest (taiga) bird species (e.g. the Siberian tit *Parus cinctus*, the Siberian jay *Perosoreus infaustus* and the pine grosbeak *Pinocola enucleator*) are nowadays, in Finland, abundant only in the northern part of Lapland (Järvinen & Väisänen 1979a, Väisänen, pers. comm.). In this paper I examine how the fragmentation of uniform forest areas and the thinning of forests affect bird species in an area in northern Lapland.

2. Material and methods

2.1. Study area

The study area is located in northern Lapland, near Vuotso in Sodankylä (68° N, 27° E, Fig. 1). Phytogeographically it belongs to a slightly continental section of the north-boreal zone, where pine forest with reindeer lichen *Cladina* sp. is the dominating forest type (Ahti et al. 1968).

Ornithogeographically the study area is located in the north-boreal zone, where the dominant land bird species are *Phylloscopus trochilus, Fringilla montifringilla, Turdus iliacus* and *Motacilla flava* (Järvinen & Väisänen 1980). Vernacular names of bird species in this study are presented in Table 2.

2.2. Census methods

The line transect method (see Järvinen & Väisänen 1976) was used in estimating bird abundances in forests during the nesting period. This method is a one-visit census, in which the average efficiency in optimal conditions has been found to be about 67% in southern Finland (Tiainen et al. 1980) and about 87% in the mountain birch forests of Swedish Lapland (Järvinen et al. 1978) when compared with thorough mapping censuses (Anon. 1969), even though efficiencies in average conditions must be lower (e.g. Järvinen et al. 1978). There are great variations in efficiency between species and within the same species during different periods of the nesting season (Järvinen et al. 1977b, 1978, Järvinen 1978, Tiainen et al. 1980).

Censuses were carried out in 1982–85 between 9 June and 1 July. Individuals were counted if observed: (1) within 25 metres of the transect line (50 m wide main belt), or (2) outside the main belt, on the so-called supplementary belt. The main

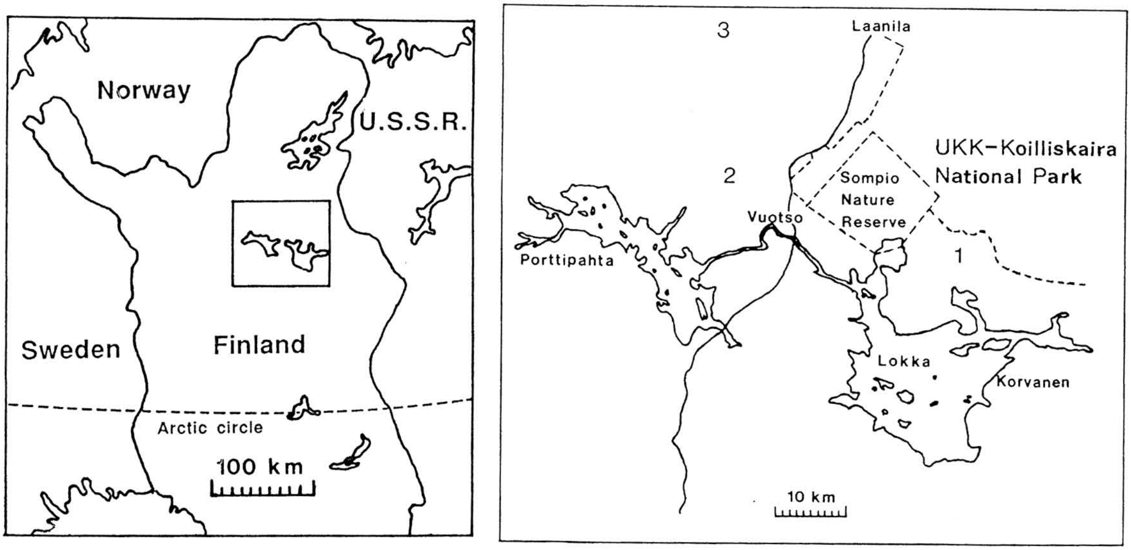

Fig. 1. Location of census areas. 1 = Stripe-cut forest areas, 2 = Tankajoki – Mäkärärova area, and 3 = Sotajoki area.

and supplementary belt together form the survey belt (Järvinen & Väisänen 1976). For different kinds of forests bird densities were calculated from both the main belt (MB) and the survey belt (SB) observations. All marsh-nesting species observed on the supplementary belt were excluded. Thus, for example, I did not consider waders other than *Numenius phaeopus*, *Tringa nebularia* and *Tringa erythropus*, which nest regularly in forests. *M. flava*, which is a typical marsh-nesting species, has been included in the survey belt data because it also occurs in open cut forests.

For every abundant species I statistically tested the ratio of main and supplementary belt observations by comparing the present data with the large data set of Järvinen & Väisänen (1983) from northern Finland in 1973–83. For the following species the difference was statistically significant (χ^2-test, $P<0.05$, $df=1$): *Ph. trochilus*, *T. iliacus*, *Phoenicurus phoenicurus*, *Carduelis flammea*, *Oenanthe oenanthe* and *M. flava*. In all these species the main belt percentage was lower in the present data than in that of Järvinen & Väisänen (1983). New species-specific correction coefficients were calculated for these species from the present data, following Järvinen (1976) and Järvinen & Väisänen (1983), in order to estimate the survey belt densities of these species. If the ratio of main and supplementary belt observations did not differ from each other in these two data sets, the correction coefficients (K) were taken from Järvinen & Väisänen (1983). Density-dependent correction coefficients (y) were used only for those species, whose species-specific correction coefficients (K) were taken from Järvinen & Väisänen (1983, see also 1977).

As the length of transects in a particular forest type differ (0.5–6.0 km), all the statistical tests of density differences are based on the number of pairs either on the main belt or on the survey belt (non-parametric tests). The expected number of pairs was calculated by applying the proportions of the line transect lengths of Table 1. When the expected number of pairs of a particular species in either of the two kinds of forests compared was less than five, Fisher's test (two-tailed) was used.

2.3. Census areas

Birds of old virgin forests were counted in Sompio Nature Reserve and in UKK-Koilliskaira National Park (Fig. 1). In the middle of Sompio Nature Reserve there is a mountain area (Nattastunturit) surrounded by barren, and in places rocky, pine forests. In the northern and western parts of Sompio Reserve there are more spruce-dominated, moist heath forests on the hillsides. I divided old, uniform forests into two classes: pine- and spruce-dominated (Table 1). In addition, birch-dominated virgin forests were censused in this area (see Virkkala 1985).

Pine-dominated heath forests of the area are very barren, with only a few individual birch trees (*Betula pubescens*) (Fig. 2). Bushes are nearly absent and the field layer is dominated by dwarf shrubs (*Vaccinium myrtillus*, *Calluna vulgaris*, *Empetrum nigrum*) and the ground layer by *Cladina*-lichens. In spruce-dominated forests there are more birches than in pine forests (Fig. 3). The bush layer consists of birches, spruces (*Picea abies*) and some willows (*Salix* spp.). In the field and ground layers the dominant species are *V. myrtillus*, *E. nigrum*, *Ledum palustre* and *Hylocomium splendens*. Both pine and spruce forests are over 200 years old. According to the Finnish forest type classification (Kalela 1961), spruce forests belong to the Hylocomium–Myrtillus (HMT) type and pine forests to the Empetrum–Myrtillus (EMT) or Myrtillus–Calluna–Cladina (MCClT) type.

Birds of fragmented forests were counted in a stripe-cut forest area southeast of the Sompio Nature Reserve (Fig. 1). In this area, uncut and clearcut forests alternate with each other in stripes. The width of each clearcut stripe was about 200 metres and that of a fully uncut stripe 100–120 metres. Virgin stripes were spruce-dominated forests (HMT). The cut stripes were covered by 0.5–1.5-metre-high birch, spruce and willow bushes and single trees (Fig. 4). Stripe-cuttings had been carried out in the late 1960s and they are clearly distinguishable in satellite photos (Punkari 1984: 79, 125). Line transects were performed along the virgin stripe, and therefore supplementary belt observations cannot be used (Table 1).

Birds in cut pine forests were counted in the following three areas: southeast of Sompio Nature Reserve, in the Tankajoki-Mäkärärova area, northeast of Vuotso and in the Sotajoki area, 30 km north of Vuotso (Fig. 1, Table 1). These census areas consisted mainly of two kinds of thinned forests: young forests (age about 50 years) and seed-tree forests. However, the difference between these forests was not clear, because in young forests some older trees had been left standing, and in seed-tree forests there were young pine trees in places as undergrowth, for which reason these forests were combined as a managed (thinned) pine forest type (Fig. 5). Managed pine forests belonged to the MCClT and EMT types, and there were more birches in them than in virgin pine forests, particularly in the bush layer. Nearly all dead (hole) trees had been removed. In places, the ground surface had been ploughed in order to improve forest regeneration. As a result, some dwarf shrub species like *Betula nana* and *Vaccinium uliginosum* were common in the field layer. Totally clear-cut areas were not censused.

Table 1. Distribution of line transect censuses in different forest types (length in km, main belt area in km^2 in parentheses).

Forest type	1982	1983	1984	1985	Total
Virgin pine forest	10.0 (0.5)	11.8 (0.6)	8.1 (0.4)	8.1 (0.4)	38.0 (1.9)
Managed pine forest	2.1 (0.1)	28.9 (1.4)	9.6 (0.5)	9.5 (0.5)	50.1 (2.5)
Uniform spruce forest	14.8 (0.7)	14.8 (0.7)	15.9 (0.8)	– –	45.5 (2.3)
Fragmented spruce forest	2.3 (0.1)	5.4 (0.3)	22.1 (1.1)	– –	29.8 (1.5)

Fig. 2. Virgin pine forest in Sompio Nature Reserve. All photos by the author.

Fig. 3. Virgin spruce-dominated forest in Sompio Nature Reserve.

2.4. Winter censuses

Winter densities of sedentary bird species were obtained from censuses made by skiing a total of 99 km in virgin forests and 45 km in managed pine forests in late winter (5–9 March 1983 and 23 February–2 March 1984). The census areas were situated around Vuotso, where line transect censuses were also carried out in summer. As in summer, the line transect method with a 50-m-wide main belt was used, which allows the representation of bird densities as pairs/km^2. Single birds or two birds of a species observed together were interpreted as "pairs", i.e., flocks of three or four individuals were interpreted as two pairs.

2.5. Old line transect censuses

Merikallio (1955, 1958) and his assistants, using the line transect method, counted birds in large areas of northern Finland during the 1940s and 1950s. In Forest Lapland he made censuses especially around Vuotso. These censuses were carried out in the vicinity of the present study area of the 1980s in the

Fig. 4. The edge of a virgin and clear-cut stripe in the stripe-cut forest area.

Fig. 5. Managed pine forest in Tankajoki – Mäkärärova area.

following areas: Vuotso, Laanila and Korvanen (Fig. 1) between 5 and 7 July 1946, and 18 and 20 June 1955. 22.1 km of transects were counted in 1946 and 22.7 km in 1955, in different kinds of forests. These censuses were gleaned from the original census data of Merikallio (kept in the Department of Zoology, University of Oulu). Large-scale clear-cuttings in northern Lapland started in the late 1950s, for which reason Merikallio's forest censuses were evidently made mainly in virgin forests. For example, in the Sodankylä area 64% of the forest area was over 120 years old according to the 1951–55 forest inventory, younger forests being situated mainly in the southern part of Sodankylä (Linnamies 1959).

3. Results

3.1. Virgin vs. managed pine forests

Total bird densities in virgin and managed pine forests did not differ significantly according to main belt observations (Table 2, χ^2-test). Survey belt densities in virgin and managed forests were almost equal (60 and 58 pairs/km^2, respectively). However, the year-to-year variation in densities must also be

Table 2. Densities of bird species (pairs/km²) in virgin and managed pine forests according to main belt (MB) and survey belt (SB) observations, the number of observations (*n*) on the main and survey belt and the proportion of each species (%) on the main belt. The statistical significance of density differences between these forests according to main and survey belt observations are presented.

Species	Virgin pine forest				Managed pine forest				Virgin	Managed	*P*	
	MB	*n*	SB	*n*	MB	*n*	SB	*n*	%	%	MB	SB
Rough-legged buzzard *Buteo lagopus*	–	–	–	–	–	–	0.02	2	–	–	–	–
Merlin *Falco columbarius*	–	–	0.1	2	–	–	–	–	–	–	–	–
Kestrel *F. tinnunculus*	–	–	–	–	–	–	0.02	1	–	–	–	–
Willow grouse *Lagopus lagopus*	1.6	3	2.1	8	1.6	4	0.8	4	3	3	n.s.	n.s.
Capercaillie *Tetrao urogallus*	–	–	–	–	–	–	0.3	1	–	–	–	–
Black grouse *T. tetrix*	–	–	–	–	–	–	0.1	1	–	–	–	–
Whimbrel *Numenius phaeopus*	1.6	3	0.3	18	1.6	4	0.8	16	3	3	n.s.	n.s.
Wood sandpiper *Tringa glareola*	–	–	–	–	0.4	1	0.1	1	–	1	–	–
Spotted redshank *T. erythropus*	–	–	0.1	1	–	–	0.3	4	–	–	–	n.s.
Greenshank *T. nebularia*	–	–	0.1	2	–	–	0.2	9	–	–	–	n.s.
Cuckoo *Cuculus canorus*	–	–	0.5	29	–	–	0.5	42	–	–	–	n.s.
Hawk owl *Surnia ulula*	0.5	1	0.1	1	0.8	2	0.6	6	1	2	–	n.s.
Three-toed woodpecker *Picoides tridactylus*	0.5	1	0.2	1	–	–	0.1	1	1	–	–	–
Black woodpecker *Dryocopus martius*	–	–	0.02	1	–	–	0.01	1	–	–	–	–
Tree pipit *Anthus trivialis*	0.5	1	1.6	20	0.8	2	2.0	33	1	2	–	n.s.
Yellow wagtail *Motacilla flava*	–	–	0.2	3	3.6	9	3.0	56	–	7	0.08	0.001
White wagtail *M. alba*	–	–	–	–	0.4	1	0.4	4	–	1	–	–
Waxwing *Bombycilla garrulus*	–	–	0.1	1	–	–	–	–	–	–	–	–
Siberian jay *Perisoreus infaustus*	2.6	5	2.3	10	0.4	1	0.2	1	5	1	n.s.	0.01
Hooded crow *Corvus corone*	–	–	–	–	–	–	0.02	1	–	–	–	–
Raven *C. corax*	–	–	0.1	6	–	–	0.01	1	–	–	–	n.s.
Dunnock *Prunella modularis*	–	–	0.1	1	–	–	–	–	–	–	–	–
Willow warbler *Phylloscopus trochilus*	4.2	8	7.1	135	10.4	26	11.7	294	7	21	0.05	0.001
Wood warbler *Ph. sibilatrix*	–	–	0.05	1	–	–	–	–	–	–	–	–
Arctic warbler *Ph. borealis*	–	–	0.1	1	–	–	–	–	–	–	–	–
Pied flycatcher *Ficedula hypoleuca*	0.5	1	0.4	5	0.4	1	0.4	6	1	1	–	n.s.
Spotted flycatcher *Muscicapa striata*	1.6	3	0.6	3	1.6	4	1.5	10	3	3	n.s.	n.s.
Wheatear *Oenanthe oenanthe*	2.6	5	2.1	30	1.2	3	1.7	31	5	2	n.s.	n.s.
Whinchat *Saxicola rubetra*	–	–	–	–	–	–	0.4	6	–	–	–	–
Redstart *Phoenicurus phoenicurus*	6.8	13	6.7	142	2.0	5	2.9	82	12	4	0.05	0.001
Bluethroat *Luscinia svecica*	–	–	–	–	0.4	1	0.7	9	–	1	–	n.s.
Redwing *Turdus iliacus*	2.1	4	1.9	34	4.8	12	5.4	125	4	10	n.s.	0.001
Song thrush *T. philomelos*	–	–	1.7	23	–	–	0.5	10	–	–	–	0.01
Fieldfare *T. pilaris*	–	–	–	–	–	–	0.1	1	–	–	–	–
Willow tit *Parus montanus*	–	–	–	–	0.4	1	0.2	1	–	1	–	–
Siberian tit *P. cinctus*	4.2	8	3.0	13	0.8	2	0.5	3	7	2	n.s.	0.01
Brambling *Fringilla montifringilla*	26.3	50	25.1	374	15.2	38	19.4	387	45	31	0.01	0.001
Siskin *Carduelis spinus*	–	–	0.05	1	–	–	–	–	–	–	–	–
Redpoll *C. flammea*	2.1	4	2.3	64	2.8	7	3.5	131	4	6	n.s.	0.01
Pine grosbeak *Pinicola enucleator*	–	–	0.4	2	–	–	–	–	–	–	–	–
Crossbill *Loxia* sp	–	–	0.4	13	–	–	0.1	6	–	–	–	0.05
Rustic bunting *Emberiza rustica*	–	–	0.2	1	–	–	–	–	–	–	–	–
Total	57.7	110	60.0	946	49.6	124	58.5	1287				

taken into account as the censuses of the managed forests were unequally distributed over the study years (for year-to-year variation see below). The biomass of breeding birds did not differ (virgin forests 5.57 kg/km² and managed forests 5.62 kg/km²). Species diversity in managed forests ($H'_{cor} \pm SD = 2.33 \pm 0.11$, correction for sample size and standard deviation according to Hutcheson (1970)) was not significantly different from that than in virgin pine forests ($H'_{cor} = 2.04 \pm 0.12$, $0.05 < P < 0.10$, *t*-test).

The four most abundant species in virgin pine forests were *F. montifringilla*, *Ph. phoenicurus*, *P. cinctus* and *Ph. trochilus* and in managed forests *F.*

montifringilla, *Ph. trochilus*, *T. iliacus* and *M. flava*. *P. cinctus*, which was a dominant species (proportion 7%) in virgin pine forest (see also Virkkala 1985), was not among the ten most abundant species in managed forests. The frequency of the four most common species in both kinds of pine forests was about 70%.

F. montifringilla, *P. cinctus*, *Ph. phoenicurus* and *P. infaustus* had significantly higher densities in virgin forests than in managed forests, whereas *Ph. trochilus*, *T. iliacus*, *C. flammea* and *M. flava* had higher densities in managed forests either according to the main belt or survey belt data or both (χ^2-test or Fisher's test). Also *Loxia* sp. and *Turdus philomelos* had higher densities in virgin forests, but these species were not observed on the main belt.

3.2. Year-to-year variation in pine forests

Censuses of virgin pine forests were nearly evenly distributed over all the four study years, but over half of the censuses in managed pine forests (28.9/50.1 km, see Table 1) were made in 1983, so the annual variation of densities may have had an effect on the results. Consequently, in order to clarify the effects of year-to-year variation, I compared the annual densities of the most abundant species in virgin and managed pine forests by using survey belt observations.

Year-to-year variation did not have any effect on the observed density differences of *Ph. phoenicurus* and *T. iliacus* in virgin and managed pine forests. In all years, *Ph. phoenicurus* had a significantly higher density in virgin forests and *T. iliacus* in managed forests (χ^2-test). Also *Ph. trochilus* and *C. flammea* had higher annual densities in managed forests, but *Ph. trochilus* significantly so only in the years 1984 and 1985, and *C. flammea* in 1984. The density of *F. montifringilla* was significantly higher in old forests only in 1983, but the densities were slightly higher in managed forests in 1984 and 1985 (however not significantly, Table 3). The greater density of *F. montifringilla* in virgin pine forests in 1982–1985 was caused by the fact that the censuses of the managed forests were mostly made in 1983, when the density of *F. montifringilla* was particularly high in virgin forests. The densities of *F. montifringilla* vary greatly annually (e.g. Enemar et al. 1984), and the site fidelity of the species is weak (Mikkonen 1983). If year-to-year variation were taken into account in calculating the density of the bird fauna, the total bird densities of virgin and managed pine forests would be almost equal–according to survey belt 58.0 and 59.5 pairs/km^2, respectively. These values do not differ from the densities of bird fauna, which were obtained by pooling the data of different years (see Table 2).

Table 3. Annual densities (pairs/km^2) of *Fringilla montifringilla* in virgin and in managed pine forests according to survey belt observations, and the statistical significance of the density differences.

Year	Virgin pine forest		Managed pine forest		*P*
	p/km^2	*n*	p/km^2	*n*	
1982	28.3	107	25.1	21	n.s.
1983	30.4	141	16.3	191	0.001
1984	15.9	52	18.6	73	n.s.
1985	22.7	74	28.4	102	n.s.

3.3. Uniform vs. fragmented spruce forests

In stripe-cut fragmented spruce forests the main belt density of birds in 1982–84 (108 pairs/km^2) was significantly higher (χ^2-test, $P<0.05$) than in uniform spruce forests (83.4 p/km^2). Most of the censuses in fragmented forests were carried out in 1984 (22.1/29.8 km), whereas about 15 km of line transects were censused each year in the uniform spruce forests (Table 1). According to the more comparable censuses of 1984 the density of bird fauna in fragmented forests was 111 p/km^2 and in uniform forests 93 p/km^2 (Table 4, $P > 0.05$, χ^2-test). Species diversity in fragmented forests ($H'_{\mathrm{cor}} = 2.01 \pm 0.09$) was not significantly higher than that in uniform forests ($H'_{\mathrm{cor}} = 1.84 \pm 0.08$, $P > 0.05$, *t*-test). Biomass of bird pairs was 50% higher in uniform (19.05 kg/km^2) than in fragmented forests (13.16 kg/km^2). This difference was mainly due to a few individuals of a single species, *Tetrao urogallus*.

F. montifringilla, *Ph. trochilus*, *T. iliacus* and *T. philomelos* were the four most abundant species both in fragmented and in uniform forests (Table 4), comprising about 75% of the bird fauna. The censuses of 1982–83 were included only for such species, whose survey belt densities did not differ significantly (χ^2-test) in uniform forests between 1982–83 and 1984 (Table 4, part B). *Ph. trochilus*, *T. iliacus* and *C. flammea* had significantly higher densities in fragmented than in uniform forests. *T. philomelos*, *Ph. phoenicurus* and *Muscicapa striata* were also more common in fragmented forests, although not signifi-

Table 4. Densities and number of observations of bird species in uniform and in fragmented forests on the main (MB) and survey belt (SB), and proportion (%) of each bird species on the main belt. Supplementary belt observations could not be used in fragmented forests because a part of these observations came from the clear-cut stripe. Statistical tests are based on the differences in MB observations. Part A represents the results of censuses in 1984 only, but in part B some species from the data of 1982–83 are also included (see text).

Species	Uniform forest				Fragmented forest		Uniform	Fragmented	
	MB	*n*	SB	*n*	MB	*n*	%	%	*P*
A									
Buteo lagopus	–	–	–	–	0.9	1	–	–	–
Lagopus lagopus	–	–	1.4	2	–	–	–	–	–
Tetrao urogallus	2.5	2	2.8	3	0.9	1	3	1	–
Cuculus canorus	–	–	0.5	12	0.9	1	–	1	–
Picoides tridactylus	–	–	–	–	0.9	1	–	1	–
Anthus trivialis	1.3	1	1.9	12	–	–	1	–	–
Perisoreus infaustus	–	–	1.2	2	0.9	1	–	1	–
Corvus corax	–	–	0.03	1	–	–	–	–	–
Prunella modularis	–	–	0.2	1	–	–	–	–	–
Phylloscopus trochilus	10.1	8	10.8	93	23.5	26	11	21	0.05
Regulus regulus	–	–	0.8	2	–	–	–	–	–
Muscicapa striata	2.5	2	2.7	6	4.5	5	3	4	n.s.
Phoenicurus phoenicurus	3.8	3	2.6	25	5.4	6	4	5	n.s.
Turdus iliacus	3.8	3	7.6	44	13.6	15	4	12	0.05
T. philomelos	6.3	5	4.3	45	10.0	11	7	9	n.s.
Parus cinctus	3.8	3	2.9	5	1.8	2	4	2	n.s.
Fringilla montifringilla	50.3	40	41.6	233	38.9	43	54	35	n.s.
Carduelis spinus	–	–	1.5	13	–	–	–	–	–
C. flammea	2.5	2	1.1	19	7.2	8	3	7	n.s.
Pinicola enucleator	1.3	1	2.9	6	–	–	–	–	–
Loxia pytyopsittacus	2.5	2	1.4	19	1.8	2	3	2	–
Emberiza rustica	2.5	2	2.2	4	–	–	3	–	–
Total	93.2	74	90.4	547	111.2	123			
B									
Tetrao urogallus	2.6	6	3.2	10	1.3	2	3	–	n.s.
Perisoreus infaustus	0.9	2	1.8	9	0.7	1	1	–	–
Phylloscopus trochilus	10.5	24	10.0	277	23.5	35	13	–	0.01
Phoenicurus phoenicurus	2.6	6	2.3	64	6.0	9	3	–	n.s.
Parus cinctus	4.4	10	3.5	18	1.3	2	5	–	0.10
Fringilla montifringilla	47.0	107	42.5	682	42.3	63	56	–	n.s.
Carduelis flammea	1.3	3	1.6	76	6.7	10	2	–	0.01

cantly. The density of *P. cinctus* was lower in fragmented forests, and fragmentation seemed to have a slightly negative effect on *F. montifringilla* and *T. urogallus*, as well.

3.4. Ecological groups

Next I divided the bird species into ecological groups in cut and virgin forests by adopting the classification of Haapanen (1965) and Alatalo (1978) (Table 5). The data of pine forests are based on the years 1982–85 and those of spruce forests on the year 1984, so that comparison is possible only within pine and spruce forests. The clearest difference between cut (managed pine and fragmented spruce forest) and virgin forests, as regards feeding technique, was the larger amount of ground insectivorous birds in cut forests (χ^2-test, $P < 0.05$). There were more hole-nesters in virgin than in managed pine forests ($P < 0.01$), whereas no difference was found between uniform and fragmented spruce forests. In virgin pine forests (compared with managed forests) there were significantly more birds which nest in trees ($P < 0.01$) and both in virgin pine forests and in uniform spruce forests (compared with fragmented forests) less birds, which nest on the ground or in bushes ($P < 0.01$).

Table 5. Percentage distribution of breeding birds based on feeding, migratory and nesting status in uniform and fragmented spruce forests according to 1984 censuses, and in virgin and managed pine forests according to 1982–85 censuses.

	Uniform spruce forest (n=74)	Fragmented spruce forest (n=123)	Virgin pine forest (n=110)	Managed pine forest (n=124)
Feeding groups				
Foliage insectivores	68.9	58.5	64.5	54.8
Ground insectivores	12.2	21.1	9.1	22.6
Flycatchers	6.8	9.0	15.5	8.1
Seed eaters	6.8	8.1	3.6	5.7
Others	5.3	3.3	7.3	8.8
Migratory status				
Sedentary	6.8	3.3	14.5	6.5
Wandering	6.8	8.9	5.5	7.3
Migratory	86.4	87.8	80.0	86.2
Nesting				
In tree holes	10.8	11.4	24.5	12.1
In trees	58.1	39.0	50.0	31.5
On ground/in shrubs	31.1	49.6	25.5	56.4

3.5. Sedentary birds in winter

The densities of foliage-feeding bird species in winter and summer of 1983 and 1984 are presented in Table 6. Winter densities of *Parus cinctus* and *Perisoreus infaustus* correspond well to their densities in summer. The total winter density (4.5 p/km^2, n = 22) in old forests was about three times as high as in managed pine forests (1.7 p/km^2, n = 4; difference $0.05<P<0.10$, χ^2-test).

Table 6. Densities of sedentary species (pairs/km^2) of the foliage-gleaning guild in virgin forests and managed pine forests in winter and summer of 1983 and 1984.

Species	Year	Virgin forest		Managed forest	
		Winter	Summer	Winter	Summer
Parus cinctus	1983	3.0	3.8	0.9	1.0
	1984	2.7	3.9		
Parus montanus	1983	0.4	–	0.4	0.5
	1984	0.4	–		
Perisoreus infaustus	1983	1.3	1.4	0.4	0.5
	1984	1.2	1.4		

3.6. Comparison with Merikallio's censuses in the 1940s and 1950s

Densities of the most abundant bird species in virgin forests around Vuotso, according to main belt observations in 1946 and in 1955 and in the 1980s, are presented in Table 7. The densities of the 1980s have been calculated in two ways: (1) by pooling the whole data of virgin old forests (114.6 km), and (2) first by combining spruce- and birch-dominated forests and then calculating mean densities for these and for pine forests. The habitat distribution in Merikallio's censuses can, however, differ from that of the 1980s, and so affect the results. For example, Merikallio probably counted more pine forests than I did. Merikallio's data are based only on two years, therefore, year-to-year variation in densities may restrict generalization of the results.

Table 7. Densities of the most common bird species in virgin forest around Vuotso, according to main belt observations in the 1940s and 50s and in the 1980s. Densities of species in the 1980s have been obtained by calculating the mean density of birch-spruce and pine forests. In parentheses are the pooled data of the 1980s, on which the statistical tests (χ^2-test or Fisher's test) are based.

Species	1940s and 50s		1980s		
	p/km^2	n	p/km^2	n	P
Fringilla montifringilla	7.6	17	37.6 (38.4)	220	0.001
Phylloscopus trochilus	11.6	26	9.8 (10.8)	62	n.s.
Phoenicurus phoenicurus	3.6	8	4.3 (3.5)	20	n.s.
Parus cinctus	6.2	14	4.2 (4.2)	24	n.s.
Turdus iliacus	5.4	12	3.8 (4.2)	24	n.s.
Carduelis flammea	2.7	6	2.5 (2.4)	14	n.s.
Perisoreus infaustus	2.2	5	1.4 (1.2)	7	n.s.
Anthus trivialis	2.2	5	1.1 (1.0)	6	n.s.

Differences in bird densities of virgin forests seem not to be great between the 1940–50s and the 1980s, with the exception of *F. montifringilla*. The density of *F. montifringilla* has increased fivefold. The late census time of 1946 and the exceptionally cold spring of 1955 (Järvinen & Väisänen 1979a) have possibly resulted in the low density of these years. Moreover, in the 1940s the population of *F. montifringilla* had collapsed, probably as a result of several cold winters (Merikallio 1951). Otherwise its population has remained almost stable in northern Finland during a longer period (1910–29 as compared with 1973–77, Järvinen & Väisänen 1979a).

4. Discussion

4.1. Local vs. regional factors

Factors affecting bird communities have different emphasis depending on whether they are considered on a local or regional level (Wiens 1981, 1983). On a local scale the populations are affected more stochastically by environmental changes and such factors as conditions during migration and fluctuations in food resources (Helle & Järvinen 1986). Regionally such factors do not have as marked an effect on populations, and thus the observed changes of local populations may not necessarily be generalized to the regional level.

Changes of northern Finnish bird fauna have earlier been examined regionally by comparing densities of the 1940s and 1950s with densities of the 1970s (Järvinen & Väisänen 1979a, 1979b, Väisänen 1983, Väisänen et al. 1986). The clear declines and increases of many species have been assumed to be due to the effects of forest management on the structure of forests (Järvinen & Väisänen 1978b, 1979a, 1979b, Väisänen 1983, Helle & Järvinen 1986). For example, the populations of *P. cinctus*, *Ph. phoenicurus* and *P. infaustus* have declined and those of *Ph. trochilus*, *T. iliacus* and *M. flava* have increased significantly. The increase of *F. montifringilla* has not been supposed to be associated with any change in the forest structure (Järvinen & Väisänen 1979a). In the present study, the observed changes in local populations due to forestry correspond in most species well to the verified regional changes of species. Also Helle & Järvinen (1986) have found that the effects of regeneration and splitting of forests on bird populations in Kuusamo corresponded well in almost all species (20 out of 22) with the population changes in the whole of northern Finland.

4.2. Changes in virgin forest bird populations

Neither densities of species preferring old forests nor those of species benefitting from forest management had changed clearly in virgin habitats around Vuotso during the past 30–40 years. Väisänen et al. (1986) compared bird density changes in a virgin forest area of about 1 km^2 from the beginning of this century (1915) with the 1980s. The study area surroundings were uncut in the beginning of the century, but by the 1980s had been cut leaving the area an island of old forest. Of the old forest species, *P. cinctus* had totally disappeared and *Ph. phoenicurus* decreased radically, whereas *Ph. trochilus*, *T. iliacus* and the chaffinch *Fringilla coelebs* had increased. In this case, cuttings that had taken place in the surroundings caused changes in the bird community on an area that had remained intact. However, the densities in 1915 were based on tentative estimates rather than on quantitative censuses, compared with the 1980s (line transect census, see Väisänen et al. 1986), which may in some species limit the accuracy of the results.

Helle (1986b) and Helle & Mönkkönen (1985) studied bird population changes in Kuusamo, 200 km south of my study area, from the beginning of the 1970s to the 1980s. Their study area in virgin, conifer forests of the Oulanka National Park was surrounded by forest regeneration areas. They found out that many species had similar trends in Oulanka during this ten-year-period compared with those in the whole of northern Finland from the 1940s to the 1970s (e.g. the hazel hen *Bonasa bonasia*, the robin *Erithacus rubecula*, *Ph. phoenicurus* and *Emberiza rustica*). However, the significant decreases in two species (*Ph. trochilus* and *T. iliacus*) were contrary to the trend found in northern Finland, and the reason for this could not be explained. Helle (1986b) stressed that the somewhat large Oulanka Forest (70 km^2) had not managed to preserve its "original" bird faunal characteristics, but the bird community resembled that of any managed forest. The situation around Vuotso seems quite different: the populations of species that have decreased in northern Finland (e.g. *P. cinctus*, *Ph. phoenicurus* and *P. infaustus*) have remained quite stable in the virgin forests, at least no clear declines have taken place. The bird community of virgin forests also clearly differs from that of managed forests (see next section). There are still large virgin forest areas of some hundreds of square kilometers in UKK-Koilliskaira National Park, in Sompio Nature Reserve and north of the

Porttipahta artificial lake (as yet, however) around Vuotso, so it is not surprising that the effects of cuttings in the area have not reached the bird fauna of old forests.

4.3. Virgin vs. managed pine forests

There were no clear differences in the total bird density, species diversity and total biomass between virgin and managed pine forests. In Kuusamo the bird density was even higher in managed than in virgin forests (75 vs. 54 pairs/km^2, Helle 1986b). However, the structure of the bird community in Vuotso was different in the virgin, compared with the managed pine forests: species of old forests (*P. cinctus*, *Ph. phoenicurus* and *P. infaustus*) had declined and *Ph. trochilus*, *T. iliacus*, *C. flammea* and *M. flava* had increased in managed pine forests. The density of sedentary species was significantly higher in virgin forests than in managed forests, both in Kuusamo (Helle 1986b) and in Vuotso ($P<0.05$, χ^2-test). Haapanen (1965) found in southern Finland that the bird density of virgin and managed barren forests did not differ, but the density of hole-nesting species in managed forests was only about half of that in virgin forests, as also is the case in this study. The situation was quite different in southern Sweden, where the total bird density was three times as high in virgin as in managed forests, but the hole-nesters made up about the same proportion in both forests (Nilsson 1979). However, the reason for the difference may be that forest management of natural mixed forests in southern Sweden eliminates a high proportion of the deciduous tree species present. This is not so in northern taiga forests, where management even increases the abundance of deciduous trees (S. G. Nilsson, pers. comm.).

A lack of nesting holes was probably one factor causing lower densities of *Ph. phoenicurus* and *P. cinctus* in managed forests. Near Vuotso there is a young pine-growing forest area, in which there are nest-boxes (about 70 in an area of 1 km^2) suitable for *P. cinctus* (but not for *Ph. phoenicurus*). However, in the years 1983–85 only 1–2 of the boxes were yearly occupied by *P. cinctus* (mean density 1.3 pairs/km^2, or one-third of its density in virgin forests). Because the winter density of *P. cinctus* is low in managed pine forests, it is possible also that a shortage of feeding resources in winter restricts tits nesting in these forests. Jansson et al. (1981) observed that for *Parus montanus* and the crested tit *Parus cristatus* food abundance was crucial for winter survival, and also limited the size of the breeding population in spring. Tits diminish the amount of their important food — spiders — even by about 50% during the winter (Jansson & von Brömssen 1981).

The lower density of *P. infaustus* in managed, compared with virgin pine forests, can also be due to scarcer food resources in winter, although the diet of the species is versatile (besides spiders and tree insects also berries and small mammals, according to von Haartman et al. 1963–72). The complicated social behaviour of *P. infaustus* can play some role in the absence of the species in managed forests. The brood stays together throughout the year and fledglings of the previous year may still be in the territory in spring (Blomgren 1971, von Haartman et al. 1963–72, Lindgren 1975, own observations). If Siberian jays disappear from managed forests, recolonization may be uncertain, because juvenile jays seem not to disperse widely (adult birds are totally sedentary, see Lindgren 1975).

The higher densities of *Ph. trochilus*, *T. iliacus* and *C. flammea* in managed, compared with virgin pine forests, were probably due to a larger amount of deciduous trees and bushes. *Ph. trochilus* prefers deciduous forests (Kuusisto 1941, Tiainen 1981, Tiainen et al. 1983), and the seeds of *B. pubescens* and *B. nana* are the main food of *C. flammea* (Peiponen 1962). *M. flava* nests in managed pine forests as these forests are open and have become swampy and bushy from ploughing.

Anthus trivialis has increased in southern Finland due to forest cuttings and habitat changes (Järvinen & Väisänen 1978a, Haila et al. 1980), but declined in northern Finland (Väisänen 1983, Helle & Järvinen 1986, Väisänen et al. 1986). *A. trivialis* accepts the sparse North Finnish forests as its breeding habitat (see Tables 2 and 4) but does not breed in the dense South Finnish forests (Helle & Järvinen 1986). Consequently, it seems not to benefit from the large clearcuts (Helle & Järvinen 1986) or forest thinning (this study, see Table 2) in northern Finland.

4.4. Uniform vs. fragmented spruce forests

The fragmentation of formerly continuous forests is related to the theory of island biogeography by MacArthur and Wilson (1967) (see, e.g., Whitcomb et al. 1981, Haila 1986, Haila et al. 1987). In habitat islands the situation is not so unambiguous as in true islands because many generalist species can survive in habitats created by forestry, between the fragments of virgin forests. Two important factors affect the bird community of fragmented forests: edge effect and the minimum area requirements of species.

Due to the edge effect, total bird density is higher at the edge between the forest and the open than in the middle of the forest or open. Different bird species react in different ways to the vicinity of an edge (Vickholm 1983, Helle 1986a). The edge effect has been observed to increase the density of a forest bird community to the distance of about 50 m from the edge, compared with the forest interior (Haila et al. 1980, Hansson 1983, Helle 1983, Vickholm 1983). According to studies carried out in different parts of Finland the density of a forest bird community has been observed to be 20–40% higher at the edges than in the interior of the forest (Haila et al. 1980, Helle 1983, Vickholm 1983), which is supported by my data, in which the total bird density in fragmented forests of the stripe-cut area was about 20% higher than that of the uniform forest area. The edge effect may largely be due to increased coverage of bushes (Helle 1983) or greater foliage volume at the edges (Hansson 1983). The increased bird density found in this study may be connected with the greater amount of deciduous trees and bushes at the edge, compared with the uniform forest areas (own field obs.). Probably due to this reason, *Ph. trochilus*, *T. iliacus* and *C. flammea* are more numerous in fragmented than in uniform forests. *Ph. trochilus* and *T. iliacus* have been observed to prefer forest edges also in Kuusamo (Helle 1983, 1984) and in Ahvenanmaa (Haila et al. 1980), and *Ph. trochilus* (but not *T. iliacus*) in Lammi (Vickholm 1983).

Minimum area requirements are another factor affecting the occurrence of species in forest fragments. The fragmentation of old forests in this study is very small-scale on the scale of northern Finland: stripes of virgin forest were 1.0–2.5 km long (10–30 ha) and the distance between virgin stripes was only 200 metres. Even so, the density of the group of northern taiga species (Haila 1985), namely *T. urogallus*, *Picoides tridactylus*, *Parus cinctus*, *Perisoreus infaustus*, *Pinicola enucleator*, and *E. rustica*, was significantly lower in fragmented than in uniform forests ($P<0.05$, χ^2-test). Most of these species are sedentary and their minimum area requirements may possibly restrict their occurrence in fragmented forests. For example, *P. cinctus* has a very large breeding territory, about 15 hectares (Haftorn 1973, Virkkala 1985 and unpubl., see also A. Järvinen 1982). In fragmented forests *P. cinctus* probably suffers from a shortage of feeding resources in winter, as also in managed pine forests. Tits have to be in motion more in fragmented than in uniform forests in winter, which can be energetically disadvantageous for them on short and cold winter days.

In a study area situated in southern Finland *Ph. phoenicurus* showed clear preference for large forest fragments (in contrast to this study), which was supposed to be due to a lack of nest holes in the small fragments (Haila et al. 1987). In the stripe-cut forests of this study there were plenty of suitable nesting holes in virgin stripes, and clear-cut stripes had increased the openness of the forest, which can be advantageous for a flycatcher such as *Ph. phoenicurus*, because also the density of another flycatcher, *M. striata*, was also higher in fragmented forests.

5. Conclusions

The total density of birds in managed (thinned) pine forests seemed not to differ from that of virgin pine forests. Cuttings had been carried out mainly 15–20 years before the beginning of this study, so that young deciduous trees and bushes had already regenerated in these forests. The results might have been different if censuses had been carried immediately after cuttings, for particularly generalist species preferring deciduous trees had increased (the same argument holds true for stripe-cut forests). The negative effect of forest thinning on species of old forests (*P. cinctus*, *Ph. phoenicurus*, *P. infaustus*) was clear.

The edge effect, owing to fragmentation of forests, may increase the total density of bird fauna in southern Finland (see, however, Vickholm 1983), where the clear-cut areas are usually small. Clear-felled areas in northen Finland are usually large and, furthermore, bird densities in clear-cut areas and young forests, for example in Kuusamo, are lower than in virgin forests (Helle 1985, 1986a). Consequently, forest fragmentation cannot increase the total bird densities (see also Helle 1983). Instead, the effect of large clear-cuttings can be greater on species which suffer from forest fragmentation.

It has been hypothesized that northern taiga species are susceptible to forest fragmentation, which has strengthened their decline during the last few decades (Järvinen et al. 1977a, Järvinen 1981). My results support this suggestion. It also seems that forest splitting and thinning have parallel effects on the northern taiga species (e.g. *P. cinctus*). These species can become endangered in the long run, so that conservation of large, virgin forest areas is well founded.

Acknowledgements. I am greatful to Y. Haila, P. Helle, O. Järvinen, S. G. Nilsson and J. Tiainen for reading the manuscript. The study was financially supported by grants from Emil Aaltonen Foundation, Finnish Cultural Foundation, Jenny and Antti Wihuri Foundation and Suomen Biologian Seura Vanamo.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in north western Europe. — Ann. Bot. Fennici 5:169–211.

Alatalo, R.V. 1978: Bird community energetics in a boreal coniferous forest. — Holarct. Ecol. 1:367–376.

Anon. 1969: Recommendations for an international standard for mapping method in bird census work. — Bird Study 16:249–254.

Blomgren, A. 1971: Siberian Jay. — British Birds 64:25–28.

Enemar, A., Nilsson, L. & Sjöstrand, B. 1984: The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. — Ann. Zool. Fennici 21:321–338.

Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — Ann. Zool. Fennici 2: 153–196.

von Haartman, L. 1973: Changes in the breeding bird fauna of North Europe. — In: Breeding biology of birds. National Academy of Sciences, Washington D.C., pp. 448–481.

—"— 1978: Changes in the bird fauna in Finland and their causes. — Fennia 150:25–32.

von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin I-II. —1092 pp. Otava, Helsinki.

Haftorn, S. 1973: Lapmeisa Parus cinctus i hekketiden (Summary: A study of the Siberian Tit Parus cinctus during the breeding season) — Sterna 12:91–155.

Haila, Y. 1985: Birds as a tool in reserve planning. — Ornis Fennica 62:96–100.

—"— 1986: North European land birds in forest fragments: evidence for area effects? — In: Verner, J., Morrison, M. L. and Ralph, C. J. (eds), Modeling habitat relationships of terrestrial vertebrates: 315–319. — Univ. of Wisconsin Press, Madison.

Haila, Y., Järvinen, O. & Väisänen, R. A. 1980: Effects of changing forest structure on long-term trends in bird populations in SW Finland. — Ornis Scand. 11:12–22.

Haila, Y., Hanski, I. K. and Raivio, S. 1987: Forest fragmentation and breeding bird distribution in coniferous taiga, southern Finland. — Ornis Fennica, 64:90–106.

Hansson, L. 1983: Bird numbers across edges between mature conifer forest and clearcuts in Central Sweden. — Ornis Scand. 14:97–103.

Helle, P. 1983: Bird communities in open ground - climax forest edges in Northeastern Finland. — Oulanka Reports 3:39–46.

—"— 1984: Effect of habitat area on breeding bird communities in Northeastern Finland. — Ann. Zool. Fennici 21: 421–425.

—"— 1985: Effects of forest regeneration on the structure of bird communities in northern Finland. — Holarct. Ecol. 8:120–132.

—"— 1986a: Effects of succession and fragmentation on bird communities and invertebrates in boreal forests. — Acta Univ. Oul. A 178. 1986. Biol. 26.

—"— 1986b: Bird community dynamics in a boreal forest reserve: the importance of regional trends. — Ann. Zool. Fennici 23:157–166.

Helle, P. & Järvinen, O. 1986: Populations trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — Oikos 46:107–115.

Helle, P. & Mönkkönen, M. 1985: Oulangan kansallispuiston metsälinnustosta erityisesti 15 viime vuoden aikana (Summary: On the forest bird fauna of the Oulanka National Park, northern Finland). — Aureola 10:21–30

Hutcheson, K. 1970: A test for comparing diversities based on the Shannon formula. — J. Theor. Biol. 29:151–154.

Jansson, C. & Brömssen, A. von 1981: Winter decline of spiders and insects in spruce Picea abies and its relation to predation by birds. — Holarct. Ecol. 4:82–93.

Jansson, C., Ekman, J. & Brömssen, A. von 1981: Winter mortality and food supply in tits Parus spp. — Oikos 37:313–322.

Järvinen, A. 1982: Ecology of the Siberian Tit Parus cinctus in NW Finnish Lapland. — Ornis Scand. 13:47–55.

Järvinen, O. 1976: Estimating relative densities of breeding birds by the line transect method. II. Comparison between two methods. — Ornis Scand. 7:43–48.

—"— 1978: Species-specific census efficiency in line transects. — Ornis Scand. 9:164–167.

—"— 1981: Dynamics of North European bird communities. — Acta XVII Congr. Int. Ornithol. (Berlin 1978), pp. 770–776.

Järvinen, O. & Väisänen, R. A. 1976: Finnish line transect censuses. — Ornis Fennica 53:115–118.

—"— 1977: Constants and formulae for analysing line transect data. — Mimeogr., 10 pp., Helsinki.

—"— 1978a: Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. — J. Ornithol. 119:441–449.

—"— 1978b: Recent changes in forest bird populations in northern Finland. — Ann. Zool. Fennici 15:279–289.

—"— 1979a: Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. — Oikos 33: 261–271.

—"— 1979b: Changes in bird populations as criteria of environmental changes. — Holarct. Ecol. 2:75–80.

—"— 1980: Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. — Ann. Zool. Fennici 17:67–85.

Järvinen, O. & Väisänen, R. A. 1983: Correction coefficients for transect censuses of breeding birds. — Ornis Fennica 60:97–104.

Järvinen, O. , Kuusela, K. and Väisänen, R. A. 1977a: Metsien rakenteen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana (Summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975). — Silva Fennica 11:284–294 .

Järvinen, O., Väisänen, R. A. and Haila, Y. 1977b: Bird census results in different years, stages of the breeding season and times of the day. — Ornis Fennica 54:108–118.

Järvinen, O., Väisänen, R. A. and Enemar, A. 1978: Efficiency of the line transect method in mountain birch forest. — Ornis Fennica 55:16–23.

Kalela, A. 1961: Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. — Arch. Soc. Vanamo 16 Suppl.:65–83

Kalela, O. 1949: Changes in geographic ranges in the avifauna of northern and central Europe in relation to recent changes in climate. — Bird-Banding 20:77–103.

—"— 1952: Changes in the geographic distribution of Finnish birds and mammals in relation to recent changes in climate. — Fennia 75:38–51.

Kuusisto, P. 1941: Studien über die ökologie und Tagesrhytmik von Phylloscopus trochilus acredula (L.) mit besonder Berücksichtigung der Brutbiologie. — Acta Zool. Fennica 31:1–120.

Lindgren, F. 1975: Iakttagelser rörande lavskrikan (Perisoreus infaustus) - huvudsakligen dess häckningsbiologi. — Flora och Fauna 70:198–210 .

Linnamies, O. 1959: Valtion metsät sekä niiden käytön ja hoidon yleissuunitelma: vuosien 1951–55 inventoinnin tuloksia (Summary: The state forests of Finland and a general management plan for them based upon an inventory made in 1951–1955). — Acta Forestalia Fennica 68:1–226 .

MacArthur, R. H. and Wilson, E. O. 1967: The theory of island biogeography. — Princeton Univ. Press, Princeton.

Merikallio, E. 1951: Der Einfluss der letzten Wärmeperiode (1930-49) auf die Vogelfauna Nordfinnlands. — Proc. X Int. Ornithol. Congr. (Uppsala, 1950), pp. 484–493.

—"— 1955: Suomen lintujen levinneisyys ja lukumäärä. — Otava, Helsinki.

—"— 1958: Finnish birds. Their distribution and numbers. — Fauna Fennica 5:1–181.

Mikkonen, A. 1983: Breeding site tenacity of the Chaffinch Fringilla coelebs and the Brambling F. montifringilla in northern Finland. — Ornis Scand. 14:36–47.

Nilsson, S. G. 1979: Effect of forest management on the breeding bird community in Southern Sweden. — Biol. Conserv. 16:135–143.

Peiponen, V. 1962: Über Brutbiologie, Nahrung und geographische Verbreitung des Birkenzeisigs (Carduelis flammea). — Ornis Fennica 39:37–60.

Punkari, M. 1984: Suomi avaruudesta. —176 pp., Tähtitieteellinen yhdistys Ursa, Helsinki.

Tiainen, J. 1981: Habitat preferences by breeding forest passerines in an area in S Finland. — Proc. Second Nordic Congr. Ornithol. 1979:38–42.

Tiainen, J., Martin, J.-L., Pakkala, T., Piiroinen, J., Solonen, T., Vickholm, M. and Virolainen, E. 1980: Efficiency of the line transect and point count methods in a South Finnish forest area. — Proc. VI Int. Con. Bird Census work, Göttingen, 1979, pp. 107–113.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. and Virolainen, E. 1983: The habitat and spatial relations of breeding Phylloscopus warblers and the Goldcrest Regulus regulus in southern Finland. — Ann. Zool. Fennici 20: 1–12.

Vickholm, M. 1983: Avointen reunojen vaikutus metsälinnustoon. — M. Sc. thesis, Dept. Zoology, Univ. Helsinki, 180 pp.

Virkkala, R. 1985: Lapintiaisen (Parus cinctus) ekologiasta hakatulla ja luonnontilaisella metsäalueella Metsä-Lapissa. — M. Sc. thesis, Dept. Zoology, Univ. Helsinki, 121 pp.

Väisänen, R. A. 1983: Pohjois-Suomen maalinnuston kannanmuutokset viime vuosikymmeninä (Summary: Long-term population changes of the most abundant north Finnish land birds during the past 40 years). — Aureola 8:58–65 .

Väisänen, R. A. & Rauhala, P. 1983: Succession of land bird communities on large areas of peatland drained for forestry. — Ann. Zool. Fennici 20:115–127.

Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local populations in boreal forests? — Ornis Scand. 17: 282–292.

Whitcomb, R. F., Lynch, J. F., Klimkiewicz, M. K., Robbins, C. S., Whitcomb, B. L. & Bystrak, D. 1981: Effect of forest fragmentation of the eastern deciduous forest. — In: Burgess, R. L. & Sharpe, D. M. (eds), Forest island dynamics in man-dominated landscapes: 124–205. Ecological Studies 41, New York.

Wiens, J. A. 1981: Scale problems in avian censusing. — Stud. Avian Biol. 6: 513–521.

—"— 1983: Avian community ecology: an iconoclastic view. — In: Brush, A. H. and Clark, G. A. (eds), Perspectives in ornithology: 355–403. Cambridge Univ. Press, Cambridge.

Received 28.V.1987
Printed 23.XII.1987