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Recent changes in forest bird populations in northern Finland

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Recent decades have witnessed great changes in the densities of land birds in Finland. This study, based on habitat censuses made in northern Finland (Kainuu and Kuusamo) in 1943—1945 and 1970—1973, examines the relative importance of two components of population change: have the populations increased (decreased) within their previous habitats, or has the area of suitable habitats increased (decreased)? The results of the habitat censuses are compared with line transect data collected from northern Finland in 1942—77.

Changes in habitat area were probably responsible for population changes in certain species, such as *Perisoreus infaustus* and *Phoenicurus phoenicurus*, which have decreased with the clear-cutting of old pine forests. Within-habitat changes were more important in the majority of common species; thus *Parus cristatus* and *P. montanus* have decreased and *Turdus iliacus*, *Phylloscopus trochilus* and *Muscicapa striata* have increased. The within-habitat changes are suggested to be linked with changes in forest structure affecting winter resources (*Parus* spp.) or with habitat expansion resulting from increases in population due to increases in the amount of forest edge, in the bush layer of the forests, and in the extent of trees of young age classes.

As shown by a comparison between observations made during an excursion to Kuusamo in 1917 and the density estimates obtained in the line transect censuses in the 1970s, the bird fauna has changed considerably in Kuusamo during this century; population increases are more characteristic than decreases.

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1. Introduction

Line transect data have shown that the populations of Finnish land birds have undergone considerable changes during recent decades (JÄRVINEN & VÄISÄNEN 1977a, 1977b, 1977c, 1978a, 1978c, JÄRVINEN *et al.* 1977). Many of these changes can probably be traced to the effects of various human activities, such as forestry (JÄRVINEN *et al.* 1977). The changes can be split into two components, the relative importance of which has not been assessed: the populations may have increased (decreased) within their previous habitats or they may have been affected by changes in the area of suitable habitats. (A third possibility, which, for technical reasons, will be included in the latter alternative, is that the populations may have invaded new habitats or have disappeared from previously acceptable habitats.) Possibly, of course, the different components have had opposite and more or less counterbalancing effects, but they may also have acted in the same direction, one reinforcing the other.

The purpose of the present study was to gain insight into the factors responsible for the population changes among forest birds in Kainuu and Kuusamo, northern Finland, during recent decades. As the habitat censuses compared were made in two different areas, our paper also throws light on the problems involved in studying long-term changes in bird populations.

2. Material and methods

Our basic data come from two unpublished manuscripts. LEHTONEN (1946) censused forest birds in the area of

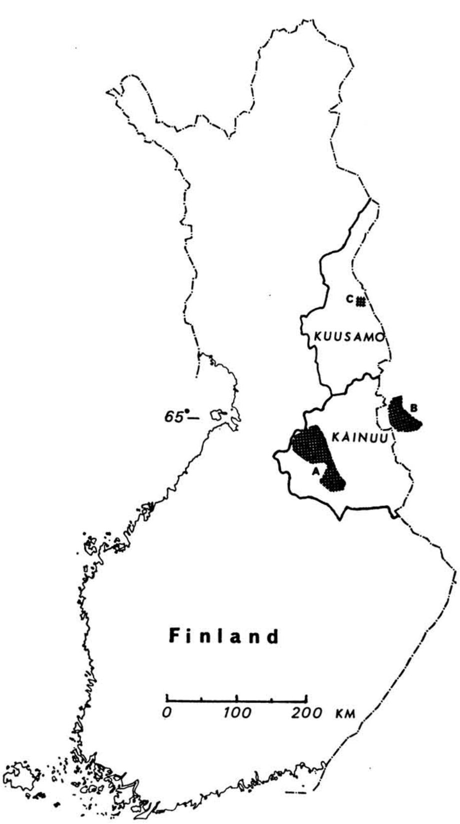

Fig. 1. The areas studied by Lehtonen (1946; area A studied in 1945, area B studied in 1943) and Mela (1975; area C). The biological provinces of Kainuu and Kuusamo are also shown.

Latvajärvi — Vuokkiniemi — Vuonninen — Kursma in the U.S.S.R. during World War II between 12 June and 17 July 1943. He supplemented his counts by censuses made in the area of Vaala — Puolanka — Sotkamo — Jormasjärvi — Kajaani in Kainuu, Finland, between 2 and 19 June 1945 (see Fig. 1). The study area in the U.S.S.R. was characterized by virgin forests, while in Kainuu changes due to forestry were already observable in the 1940s. These data are compared with the censuses of MELA (1975), who studied forest birds in northern Kuusamo, mainly in the National Park of Oulanka, in 1967—1973 (Fig. 1). The forests in the National Park are virgin forests (SÖYRINKI *et al.* 1977).

The habitat censuses of LEHTONEN and MELA cannot be used to answer the basic questions posed in the Introduction, but must be compared with data indicating the general trends in Kainuu and Kuusamo. Such data were obtained from our (mainly unpublished) line transect counts made in the biological provinces of Kainuu and Kuusamo (Fig. 1). The line transect method has been described by JÄRVINEN & VÄISÄNEN (1976c) and the formulae used in estimating densities are given by JÄRVINEN & VÄISÄNEN (1977d). The line transect data were divided into three periods, 1942—1949, 1952—1963 and 1973—1977 (see JÄRVINEN & VÄISÄNEN 1977a, 1977b, 1977c, 1978a, JÄRVINEN *et al.* 1977).

Both LEHTONEN (1946) and MELA (1975) used the line transect method. Their main belts, which were the basis for the habitat data, were 60 m broad (normally, the main belt is 50 m). LEHTONEN divided his data into eleven habitats, because he wished to improve on the concepts of "ornithological coniferous forest" and "ornithological deciduous forest" introduced by SOVERI (1940). The forest types used by LEHTONEN are those of KUJALA (1936). The habitats and censuses were:

1. Barren pine forest (ClT, EcClT, CT). 63 pairs in 1.69 km².

2. Pine forest (EMT, VT), with 90—100 % pine and 0—10 % spruce or birch. 16 pairs in 0.36 km².

3—4. Coniferous forest (EMT and VT), with 45—90 % pine and 10—55 % spruce. 34 pairs in 0.38 km² (EMT) and 37 pairs in 0.43 km² (VT).

5—6. Spruce forest (HMT and MT), with 0—45 % pine (HMT) and 0—15 % birch (MT), the rest being spruce. 71 pairs in 0.81 km² (HMT) and 44 pairs in 0.43 km² (MT).

7—10. Mixed forest, with 15—80 % birch (if the main conifer was spruce, 20—85 %) or 10—60 % (main conifer pine, 40—90 %). 113 pairs in 1.07 km² (EMT), 100 pairs in 0.99 km² (VT), 42 pairs in 0.43 km² (HMT) and 124 pairs in 0.89 km² (MT).

11. Luxuriant, mesic forest (OMT and GDrMT). 41 pairs in 0.22 km².

In summary, the data of LEHTONEN comprise 685 pairs in 7.70 km².

MELA (1975) censused transects of altogether 722.6 km (67 % or 24.19 km² of the main belt in forest habitats). The forest habitats were classified into three broad types (the forest types given by SÖYRINKI *et al.* 1977):

1. Barren pine forest, including the true dry heath forest (Calluna-Cladina type) and the drier parts of heath forests of the Empetrum-Myrtillus type. 101 pairs in 9.18 km².

2. Mesic pine heath forest, with pine dominant (at least 2/3), and birch and spruce. This habitat includes the mesic parts of heath forests of the Empetrum-Myrtillus type and the true mesic heath forests of the Hylocomium-Myrtillus type or Ledum-Uliginosum type. 423 pairs in 10.08 km².

3. Spruce forest, with spruce dominant, but pine and birch also abundant. This habitat includes most heath

Table 1. The main parameters of the communities studied. L = Lehtonen (1946), M = Mela (1975), 1 = (relatively) barren pine forest, 2 = mesic conifer forest.

	L1	M1	L2	M2
Primary data				
Area (km²)	2.05	9.18	5.65	15.01
Pairs observed	79	101	606	956
Species observed	20	16	46	43
Community parameters				
Density (pairs/km²)	38.5	11.0	107.3	63.7
$H' \pm S.D.$	2.88±0.08	2.26±0.11	2.98±0.05	3.00±0.03

Table 2. Densities (pairs/km²) and frequencies (%, in parentheses) of breeding birds in the habitats studied. L = Lehtonen (1946), M = Mela (1975), 1 = (relatively) barren pine forest, 2 = mesic conifer forest.

Species	L1		M1		L2		M2	
Milvus migrans	—	—	—	—	0.2	(0.2)	—	—
Accipiter nisus	—	—	—	—	0.2	(0.2)	0.1	(0.1)
Buteo buteo	—	—	—	—	0.2	(0.2)	0.1	(0.2)
B. lagopus	0.5	(1.3)	—	—	—	—	—	—
Falco columbarius	—	—	—	—	0.2	(0.2)	—	—
Tetrao urogallus	—	—	—	—	—	—	0.4	(0.6)
Lyrurus tetrix	—	—	0.1	(1.0)	0.5	(0.5)	0.1	(0.1)
Lagopus lagopus	—	—	—	—	—	—	0.1	(0.1)
Tetrastes bonasia	—	—	0.5	(5.0)	0.2	(0.2)	2.4	(3.8)
Tringa nebularia	—	—	—	—	0.2	(0.2)	—	—
T. hypoleucos	—	—	—	—	0.2	(0.2)	—	—
Columba palumbus	—	—	—	—	0.2	(0.2)	—	—
Cuculus canorus	—	—	—	—	0.5	(0.5)	1.0	(1.6)
Aegolius funereus	—	—	—	—	—	—	0.1	(0.1)
Dryocopus martius	—	—	—	—	—	—	0.1	(0.2)
Dendrocopos major	3.9	(10.1)	—	—	3.5	(3.3)	0.3	(0.5)
Picoides tridactylus	0.5	(1.3)	—	—	0.4	(0.3)	0.1	(0.2)
Corvus corax	—	—	—	—	0.2	(0.2)	0.1	(0.1)
C. corone	—	—	—	—	0.5	(0.5)	0.1	(0.2)
Garrulus glandarius	—	—	—	—	0.2	(0.2)	—	—
Perisoreus infaustus	0.5	(1.3)	0.3	(3.0)	0.4	(0.3)	1.1	(1.8)
Parus major	—	—	—	—	0.4	(0.3)	0.3	(0.5)
P. cristatus	5.4	(13.9)	—	—	3.2	(3.0)	0.1	(0.2)
P. cinctus	1.5	(3.8)	—	—	—	—	0.7	(1.0)
P. montanus	2.0	(5.1)	0.3	(3.0)	11.5	(10.7)	1.0	(1.6)
Certhia familiaris	—	—	—	—	0.4	(0.3)	0.1	(0.2)
Troglodytes troglodytes	—	—	—	—	—	—	0.5	(0.8)
Erithacus rubecula	—	—	—	—	0.2	(0.2)	0.7	(1.0)
Tarsiger cyanurus	—	—	—	—	—	—	0.1	(0.1)
Phoenicurus phoenicurus	2.0	(5.1)	3.5	(31.7)	3.7	(3.5)	5.5	(8.7)
Turdus pilaris	—	—	—	—	1.2	(1.2)	0.2	(0.3)
T. iliacus	1.0	(2.5)	0.3	(3.0)	0.7	(0.7)	1.9	(2.9)
T. philomelos	0.5	(1.3)	0.2	(2.0)	3.2	(3.0)	1.9	(2.9)
T. viscivorus	1.5	(3.8)	0.3	(3.0)	0.5	(0.5)	0.5	(0.7)
Sylvia borin	—	—	—	—	0.5	(0.5)	—	—
S. communis	—	—	—	—	0.4	(0.3)	—	—
S. curruca	—	—	—	—	0.2	(0.2)	—	—
Phylloscopus trochilus	1.0	(2.5)	0.1	(1.0)	8.8	(8.3)	8.5	(13.3)
Ph. collybita	0.5	(1.3)	0.5	(5.0)	3.9	(3.6)	2.0	(3.1)
Ph. sibilatrix	—	—	—	—	0.2	(0.2)	—	—
Regulus regulus	—	—	—	—	0.7	(0.7)	1.4	(2.2)
Muscicapa striata	3.9	(10.1)	2.5	(22.8)	10.3	(9.6)	3.7	(5.8)
Ficedula hypoleuca	—	—	—	—	1.4	(1.3)	1.1	(1.8)
Prunella modularis	—	—	—	—	—	—	0.1	(0.1)
Anthus trivialis	2.4	(6.3)	0.3	(3.0)	7.3	(6.8)	4.7	(7.3)
Motacilla alba	—	—	—	—	—	—	0.1	(0.2)
Bombycilla garrulus	—	—	—	—	0.2	(0.2)	0.1	(0.1)
Carduelis spinus	—	—	0.2	(2.0)	5.8	(5.4)	2.3	(3.7)
C. flammea	2.9	(7.6)	—	—	1.9	(1.8)	2.7	(4.2)
Pyrrhula pyrrhula	—	—	0.1	(1.0)	1.6	(1.5)	1.1	(1.8)
Pinicola enucleator	—	—	—	—	0.2	(0.2)	—	—
Loxia curvirostra	2.0	(5.1)	0.5	(5.0)	4.6	(4.3)	1.9	(2.9)
Fringilla coelebs	3.4	(8.9)	—	—	20.5	(19.1)	3.9	(6.2)
F. montifringilla	0.5	(1.3)	1.0	(8.9)	2.1	(2.0)	10.4	(16.3)
Emberiza citrinella	2.9	(7.6)	—	—	2.7	(2.5)	—	—
E. rustica	—	—	—	—	1.4	(1.3)	0.2	(0.3)

forests of the Hylocomium-Myrtillus type and herb-rich mesic heath forests, herb-rich mesic forests and herb-rich damp forests. 533 pairs in 4.93 km².

Certain points of method should be noted. First, the numbers reported by Lehtonen (1946) may have been somewhat low, owing to his long census period (covering the first half of July, when birds sing less frequently than in June), and the fact that during the census work he wrote detailed descriptions of forest structure. On the other hand, MELA (1975) seems to have made his censuses quite rapidly, which will certainly have resulted in low estimates.

3. Results

As LEHTONEN (1946) and MELA (1975) classified habitats very differently, we made a new classification based on the bird data (see e.g. JÄRVINEN & VÄISÄNEN 1976a, 1976b, 1977d). Briefly, we compared the frequencies of species in the different habitats, and combined two samples if the frequencies were sufficiently similar (for criteria, see JÄRVINEN & VÄISÄNEN 1976b, 1978b).

The three forest habitats of MELA were related as follows: The spruce forest was very close to the mesic pine heath forest, and the two samples were combined. The third sample, the barren pine forest, was clearly different. We thus obtained a two-habitat classification: barren pine forest (M1) and mesic conifer forest (M2).

We then classified the habitats of LEHTONEN as L1 and L2 to match M1 and M2 as closely as possible. No direct numerical comparison could, however, be made, because within-habitat changes would then have been arbitrarily minimized. The eleven habitats of LEHTONEN were classified stepwise, the most similar habitats being combined first; the calculations were then repeated with the combined samples instead of the original ones, and again the most similar samples were combined. The resulting classification can be interpreted as follows: L1 is barren or relatively barren pine forest (two samples, habitats 1—2 of LEHTONEN), while L2 is mesic conifer forest.

Table 1 shows the main parameters of the bird communities occupying the four habitats. Table 2 shows the species composition of the communities.

It is clear from Table 1 that the more southern habitats studied by LEHTONEN were more productive than those studied by MELA. The difference was particularly great for the barren pine forest. Diversity, H' (see JÄRVINEN & VÄISÄNEN 1977d for formulae), differs clearly between habitats 1 and 2 ($P < 0.05$ for L and $P < 0.001$ for M), the pine forest being less diverse. A highly significant difference also exists between the diversity values for L1 and M1 ($P < 0.001$).

The differences between habitats L and M (Table 2) may be due to three different causes: differences in habitat quality in the study areas, geographical factors, and long-term population changes. As we have line transect data from Kainuu and Kuusamo, the two relevant biological provinces in Finland (Fig. 1), it is possible to correct for the biases in the data. Table 3 gives data for forest species with frequencies exceeding 2 % in both Kainuu and Kuusamo in at least one of the three study periods (1942—49, 1952—63 and 1973—77) and which had at least 10 pairs in at least one of the habitats studied.

Table 3. Densities (pairs/km^2) of certain species in the biological provinces of Kainuu and Kuusamo in three periods. The estimates are based on our line transects.

	Kainuu			Kuusamo		
	1942–49	1952–63	1973–77	1942–49	1952–63	1973–77
	(12.0 km)	(47.9 km)	(98.8 km)	(45.5 km)	(24.0 km)	(90.0 km)
Perisoreus infaustus	1.8	0.3	0.5	1.7	0.6	1.1
Parus cristatus	5.8	2.2	0.7	1.8	0.6	–
P. montanus	5.8	2.9	3.6	4.3	–	1.1
Phoenicurus phoenicurus	3.6	3.1	1.9	6.5	5.4	2.2
Turdus iliacus	1.4	1.7	8.1	1.7	2.0	6.8
Phylloscopus trochilus	5.8	14.3	23.3	9.5	12.7	20.3
Muscicapa striata	5.0	4.0	6.4	3.4	4.5	8.2
Anthus trivialis	4.2	9.4	6.4	7.3	10.8	5.7
Carduelis spinus	2.5	0.6	4.6	1.1	–	2.4
Fringilla coelebs	8.9	14.6	16.9	6.4	7.9	4.6
F. montifringilla	0.9	11.2	4.9	5.6	20.4	9.6
All land birds	87.8	108.1	143.6	84.4	101.7	105.7

Table 4. Ratios showing the average densities of certain species in Kainuu as compared with those observed in Kuusamo. See text.

Perisoreus infaustus	0.765	*Muscicapa striata*	0.956
Parus cristatus	3.625	*Anthus trivalis*	0.840
P. montanus	2.278	*Carduelis spinus*	2.200
Phoenicurus phoenicurus	0.610	*Fringilla coelebs*	2.138
Turdus iliacus	1.067	*F. montifringilla*	0.478
Phylloscopus trochilus	1.021	Total density	1.163

The geographical difference between the two biological provinces was now expressed as follows. We computed the average density of each species in Kainuu and Kuusamo during the study period; for example, the average density of *Perisoreus infaustus* in Kainuu was $(1.8 + 0.3 + 0.5)/3 = 0.87$ pairs/km^2. We then calculated a ratio, dividing the average density in Kainuu by that in Kuusamo (Table 4). For example, the density of *P. infaustus* was about 31 % higher in Kuusamo than in Kainuu during the study period; this difference in favour of M1 and M2 in a comparison of the habitats presumably means that *P. infaustus* is more abundant in the more northern Kuusamo than in Kainuu. The ratios in Table 4 were then used to correct the densities in the habitats, but corrections were also made for the difference in habitat quality between the two study areas.

There are two possible ways to correct the bias due to the difference in habitat quality. If the habitats studied had been of the same quality, we should have expected that the ratio of the densities of species in L1 and M1 (or L2 and M2) would equal the ratio of their densities in Kainuu and Kuusamo, 1.163 (Table 4). However, the actual ratios were higher, $38.5/11.0 = 3.50$ (L1:M1) and $107.3/63.7 = 1.68$ (L2:M2). Thus, in relation to the averages for the respective areas (Table 3), the habitats studied by LEHTONEN in the 1940s were of higher quality than the habitats studied by MELA in the early 1970s. (Notice that habitat quality is here defined on the basis of bird density.) On the assumption that differences in habitat quality have similar effects on all species, corrections can now be made for these differences by multiplying the densities of M1 and M2 by $3.50/1.163 = 3.01$ and $1.68/1.163 = 1.44$, respectively. This correction, theoretically at least, eliminates the differences due to habitat quality, while the ratios given in Table 4 eliminate the differences due to geography. These two corrections were applied to the densities observed in M1 and M2, and the results are given in Table 5, where they are compared with the original densities in L1 and L2. Any remaining difference between the densities of the corresponding habitats should indicate a long-term trend within the habitats. The general trend in Kuusamo (deduced from a comparison of periods 1942—49 and 1973—77; data in Table 3) is also given in Table 5. The trends in Kuusamo and Kainuu were similar ($r = 0.775$, $P < 0.01$, between the percentage changes in the two provinces). This high correlation suggests that our comparison between the data of LEHTONEN and MELA is valid.

Table 5. The corrected densities of M1 and M2 compared with the actual densities observed in L1 and L2. The estimates for the general trends (%) in Kuusamo are based on our line transect data. See text and Table 3.

Species	L1	M1	L2	M2	Trend in Kuusamo
Perisoreus infaustus	0.5	0.7	0.4	1.2	−35
Parus cristatus	5.4	–	3.2	0.5	−100
P. montanus	2.0	2.1	11.5	3.3	−74
Phoenicurus phoenicurus	2.0	6.4	3.7	4.8	−66
Turdus iliacus	1.0	1.0	0.7	2.9	+300
Phylloscopus trochilus	1.0	0.3	8.8	13.1	+114
Muscicapa striata	3.9	7.2	10.3	5.1	+141
Anthus trivialis	2.4	0.8	7.3	5.7	−22
Carduelis spinus	–	1.3	5.8	8.6	+118
Fringilla coelebs	3.4	–	20.5	12.0	−28
F. montifringilla	0.5	1.4	2.1	7.2	+71

Table 6. The densities of certain species in the study habitats, expressed as percentages of their average densities in Kainuu in 1942–49 (L1, L2) or in Kuusamo in 1973–77 (M1, M2). *Parus cristatus* was not observed in the line transects in Kuusamo in 1973–77, so the corresponding entries are shown by dots.

Species	L1	M1	L2	M2
Perisoreus infaustus	28	27	22	100
Parus cristatus	93	...	55	...
P. montanus	34	27	198	90
Phoenicurus phoenicurus	56	159	103	250
Turdus iliacus	71	4	50	28
Phylloscopus trochilus	17	0	152	42
Muscicapa striata	78	30	206	45
Anthus trivialis	57	5	174	82
Carduelis spinus	0	8	232	96
Fringilla coelebs	38	0	230	85
F. montifringilla	61	10	233	108

Another method for assessing the effect of habitat quality does not require the assumption that all species are similarly affected by changes in this variable. By comparing the densities of the different species in the habitats studied and in Kainuu or Kuusamo in 1942—49 or 1973—77, respectively (Table 6), it may be inferred that certain species were probably over- or underrepresented in our study habitats in comparison with the corresponding habitat in the other area (Kainuu or Kuusamo). However, the figures given in Table 6 are affected by the variety of the habitats in Kainuu and Kuusamo. Table 6 was therefore not used as a basis for corrections, but simply to check our conclusions regarding each species.

Below, we compare the estimates given in Table 5 for within-habitat and general trends. If the two trends are similar, the within-habitat trend is presumably of major importance in determining the general pattern. If the two trends differ, the area of suitable habitats has probably changed or the density of the species has changed in habitats other than those considered here. In the following we shall assume that the latter possibility may be neglected, as the habitats studied include the most important forest habitats of the study area and because the species studied were characteristically forest species.

Perisoreus infaustus. The within-habitat trend shows a clear increase, but the species may have been overrepresented in M2 as compared with L2 (Table 6). As the general trend has been a decrease in the whole province, we conclude that the area of suitable habitats has probably decreased.

Parus cristatus. The within-habitat decrease is similar to the general trend in the province. Thus there is no need to invoke a change in the area of suitable habitats.

P. montanus. The species may have been overrepresented in L2 (Table 6). As a result, the clear decrease in Kuusamo is probably due to a moderate decrease within M2 and a moderate reduction in the area of suitable habitats. Alternatively, the whole trend may be due to a decrease in numbers within M2.

Phoenicurus phoenicurus. There appears to have been a clear increase within the habitats, but the trend can hardly be real: we should expect this species to be overrepresented in habitats of poor quality, as is confirmed by the data in Table 6. Hence, it seems probable that the general trend — a clear decrease — is due to a reduction in the area of suitable habitats.

Turdus iliacus. The increase within habitats L2 and M2 is similar to the general increase in the populations, which suggests that any increase in the area of suitable habitats will have been of minor importance. As the species was clearly underrepresented in M1 and M2 as compared with L1 and L2, it seems unlikely that any change occurred in the area of suitable habitats, the whole trend probably being due to within-habitat changes. (The underrepresentation may have been due to a population increase between the main census years of MELA, 1970—73, and our last period in line transect data, 1973—77).

Phylloscopus trochilus. Habitats L1 and M1 are not important for this species. The increase within L2 and M2 has been considerable, but less than that observed in the whole province. This suggests that the area of available habitats has increased, but the species may also have been underrepresented in M2 (Table 6). If so, the trend is wholly due to within-habitat changes.

Muscicapa striata. The within-habitat trends are opposite, but this may be due to overrepresentation in L2 (Table 6). It thus seems that the trend is due to clear within-habitat increases.

Anthus trivialis. The decrease observed within the habitats accords well with the general trend. However, the species may have been considerably underrepresented in M1 and M2. Thus the pattern is obscure; either the populations within the habitats or the suitable area or both have decreased.

Carduelis spinus. As the species has pronounced annual fluctuations, the within-habitat trend seems sufficiently similar to the general trend and there is no need to postulate any increase in the habitat area.

Fringilla coelebs. The within-habitat decrease seems sharper than the general trend, perhaps because the species was underrepresented in M1 and M2 (Table 6). We conclude that the within-habitat trends are the major component of the decrease of the species in Kuusamo.

F. montifringilla. This species also has significant annual fluctuations. So it seems that within-habitat changes are responsible for the general increase. That the main cause is within-habitat increase is further supported by the fact that the species was not overrepresented in M1 and M2, but rather the opposite, especially in M1. It cannot be excluded that there has been a simultaneous decrease in the area of available habitats, but an alternative explanation may be the annual fluctuations.

We emphasize that the above analysis is based on a considerable number of assumptions, most of which cannot be tested. Further, the results depend on several corrections applied to the primary data. In consequence, the directions of the changes are much more important than their magnitudes. The following summary of the changes is thus useful:

	Within-habitat change	Change of habitat area
Perisoreus infaustus	0 or +	—
Parus cristatus	—	0
P. montanus	—	0 or —
Phoenicurus phoenicurus	0	—
Turdus iliacus	+	0
Phylloscopus trochilus	+	0 or +
Muscicapa striata	+	0
Anthus trivialis	0 or —	0 or —
Carduelis spinus	+	0
Fringilla coelebs	—	0
F. montifringilla	+	0 or —

4. Discussion

A. Population changes related to forest structure

Our data suggest that considerable changes have occurred in the breeding populations of common forest birds in northern Finland, or more accurately in Kuusamo, during recent decades. A comparison of our line transect data with the censuses of LEHTONEN (1946) and MELA (1975) made it possible to evaluate the importance of the within-habitat changes in populations in relation to other changes, which may be of two kinds: changes in the area of suitable habitats or changes within habitats other than those studied by LEHTONEN and MELA. Our data suggest that in most of the common species densities have been affected by within-habitat changes; decreases in the available areas seem to have been important only for *Perisoreus infaustus* and *Phoenicurus phoenicurus* and possibly for *Parus montanus*, *Anthus trivialis* and *Fringilla montifringilla*, while the changes may have enlarged the habitats of *Phylloscopus trochilus*.

These changes can be related to changes in the structure of the forests in NE Finland. In recent decades (from the early 1950s to about 1970) forest management has caused two major changes in this area: first, the mean volume of the growing stock has decreased considerably (by about 20 %), implying that the older forests have been extensively clear-cut, and second, in NE Finland it is chiefly the pine forests that have been cut (for data, see KUUSELA 1972, 1977). In recent decades, the older pine forests have certainly diminished in area more than any other major forest habitat in NE Finland. This observation fits well with our finding that certain species have decreased because of decreases in the area of suitable habitats. MERIKALLIO (1921), who made an excursion in Kuusamo in 1917, stressed the importance of the pine forests for *Phoenicurus phoenicurus*, *Anthus trivialis* and *Fringilla montifringilla*. *Perisoreus infaustus* and *Parus montanus* occurred in considerable numbers in mesic pine forests (MELA 1975) included in habitat M2, though the highest densities were reached in the spruce forests.

The inference is that the species whose populations appear to have declined (at least partially) because of shortage of suitable habitats are all birds more or less associated with pine forests. However, it was also necessary to ascertain whether any species typical of old pine forests had increased considerably in Kuusamo in recent times.

We examined the original records of MELA (1975) from the three forest types and included all species with a frequency of at least 3.0 % in at least one of the habitats. Of the five species that have apparently decreased in density in Kuusamo owing to the cutting of old pine forests, each was more than marginally represented in pine forests (density in one of the pine forest types more than 40 % of that in the spruce-dominated forest). The other species fulfilling the same condition were *Turdus iliacus*, *T. viscivorus*, *Muscicapa striata* and *Carduelis flammea*. In recent decades, as seen from Table 3, *T. iliacus* and *M. striata* have increased in Kuusamo, but it is probable that these species are favoured by open forests and edges created by forest cuttings (e.g. VON HAARTMAN *et al.* 1963—1972, JÄRVINEN *et al.* 1977), so this result is not unexpected. Further, no data seem to suggest that *C. flammea* is associated with old pine forests, and it is thus understandable that the population has been stable from the 1940s to the 1970s (unpublished line transect data).

The only species mentioned in the above list which seems really to be associated with old pine forest is *T. viscivorus*, and in recent decades the species has decreased in Kuusamo by about 75 % (unpublished line transect data; see also JÄRVINEN *et al.* 1977).

As a further test of the importance of changes in forest structure for bird populations we studied the descriptions given by MERIKALLIO (1921) on the habitat preferences of various species in Kuusamo. These descriptions suggest that old pine forests are important for the following species (in addition to those already mentioned): *Tetrao urogallus*, *Apus apus*, *Dryocopus martius*, *Parus cinctus*, *Bombycilla garrulus* and *Fringilla coelebs*. These species have always had quite low densities in Kuusamo, according to the line transect data (unpublished). *P. cinctus* had 2.2. pairs/km^2 in the 1940s, although only 0.1 pair/km^2 in the 1970s (cf. also JÄRVINEN *et al.* 1977, JÄRVINEN & VÄISÄNEN 1977a, 1977c). Of the other species, *T. urogallus* and *D. martius* have certainly decreased considerably (unpublished line transect data and JÄRVINEN *et al.* 1977), while the other three species are somewhat difficult cases: *A. apus* also inhabits human settlements, *B. garrulus* has wild annual fluctuations, and *F. coelebs* occurs mainly in river valleys in Kuusamo (MERIKALLIO 1921).

The within-habitat changes observed in the commonest species (p. 285) may have many causes. They may also be affected by changes in the area of suitable habitats if the populations are regulated by winter resources (see FRETWELL 1972). For example, the recent within-habitat decrease of *Parus cristatus* in Kuusamo (Table 5) may have been due to the decrease of old pine forests, because these are important for the species outside the breeding season: In October 1974, the density of *P. cristatus* in Kuusamo was higher in pine-dominated than in spruce-dominated forest (NILSSON & ALERSTAM 1976). As these workers also observed numerous *P. montanus* in pine-dominated forests, the within-habitat decrease of that species may also be due to the cutting of old pine forests (see also JÄRVINEN *et al.* 1977). It should be noticed that NILSSON & ALERSTAM (1976) frequently observed *Perisoreus infaustus* in pine-dominated forests.

As the other species showing within-habitat changes are migrants, it is not possible to explain these changes by studying the winter resources available in Kuusamo.

We have elsewhere (JÄRVINEN *et al.* 1977) pointed out that many species benefit from the edges and the bushy growth created by forestry; these changes seem to be an important cause of many population increases observed in the Finnish land bird fauna in recent decades. Because the area studied by MELA (1975) lies mainly within the borders of Oulanka National Park, where forests have not been cut at all, it seems that the within-habitat changes observed in *Turdus iliacus*, *Phylloscopus trochilus*, *Muscicapa striata*, *Carduelis spinus* and *Fringilla coelebs* must be due to habitat expansion over larger areas. *F. coelebs* provides an instructive example in this connection. The species is ubiquitous in southern Finland and the populations have increased somewhat in recent decades, a major cause probably being increases in the extent of forest edges. In Kuusamo, the species has decreased which at first seems paradoxical; but there the species is a habitat specialist, occurring mainly in river valleys (MERIKALLIO 1921), and so it is quite understandable that changes due to forestry have had different effects on the populations of this species in different parts of Finland! As regards *C. spinus*, the wide annual fluctuations of the species cause certain difficulties, but the increase seems too great to have been due to chance. It should also be noted that in northern Finland the proportion of spruce, the tree species favoured by *C. spinus* in summer, has decreased slightly in recent decades, though in southern Finland the trend has been in the opposite direction (e.g. JÄRVINEN *et al.* 1977). So it seems that the habitat expansion postulated in this case refers to wide regions, such as central and northern Finland. Climatic changes seem a less attractive explanation, because we should then expect *Fringilla coelebs*, for example, to show an increase (which it does not), and *F. montifringilla*, a northern species, to show a decrease (which it does not).

B. Comparison with Merikallio's studies in 1917

MERIKALLIO's (1921) study, based on a long excursion made to northern Kuusamo and adjacent areas in June-August 1917, enables us to discuss briefly the changes which have occurred in the avifauna of Kuusamo during the last 60 years. Of course, detailed comparisons are not possible, because MERIKALLIO did not make accurate censuses, but many of the trends are obvious and deserve emphasis. In what follows, data for 1917 are from MERIKALLIO (1921) and data for the 1970s from our own line transect studies (JÄRVINEN & VÄISÄNEN 1977a, 1977b, 1977c, 1978a, JÄRVINEN *et al.* 1977). However, references to our unpublished line transect data are indicated, in order to prevent confusion. Further, we point out that another study by MERIKALLIO, written in 1917, should also be consulted. Below we have included a few non-forest species, which are best dealt with in the present connection.

Data on raptors, though scanty, suggest a decrease in *Falco columbarius* and *F. tinnunculus*, and possibly in *Pandion haliaetus*. Three waders have apparently increased since 1917: *Vanellus vanellus*, *Pluvialis apricaria* and *Philomachus pugnax*. An increase is also probable in *Numenius arquata*. Owing to paucity of data, other changes in non-passerines are difficult to establish, but *Jynx torquilla* and *Dendrocopos major* were not observed in 1917 (present densities 0.2—0.3 pairs/km^2, unpubl.).

In Kuusamo *Perisoreus infaustus* decreased from the 1940s to the 1970s (Table 5). The density was probably not much higher in 1917 than in the 1940s, for the species was "rare" or "very rare" (which should be interpreted as less than 2 pairs/km^2) in 1917. MERIKALLIO (1946: 108) reported a decrease in a more southern area in E Finland from 1919 to 1943, but the data are meagre, and LEHTONEN (1946) also regarded a decrease as probable.

The tits have apparently experienced great changes. *Parus major* was observed once in 1917 (now 0.4 pairs/km^2, unpubl.). *P. cristatus* was not observed in 1917, but it extended its range northwards in the 1930s (LEHTONEN 1946, MERIKALLIO 1951), and since then has decreased considerably in the north: no specimen was recorded in the line transect censuses made in Kuusamo in the 1970s (Table 3)! *P. cinctus* was one of the commonest species in Kuusamo in 1917: third in the spruce forest (next to *Phylloscopus trochilus* and *Carduelis flammea*) and second in the pine forest (next to *Fringilla montifringilla*). As stated above, the species has now almost disappeared. The decline started in the 1920s or 1930s (MERIKALLIO 1958), and a sharp decrease occurred, according to the line transect data, in the 1940s or early 1950s. No conclusions can be drawn as regards *P. montanus*.

Cinclus cinclus may have decreased during the study period: it was apparently common in 1917, but not observed in line transects in the 1970s (unpubl.). However, the species inhabits rivers and is difficult to census reliably.

As only a few observations were made on *Erithacus rubecula* in 1917, the present density, 1.0 pairs/km^2 (unpubl.), suggests a clear increase. *Turdus merula* has invaded the area since 1917, according to the transect data (unpubl.). *T. pilaris* also seems to have increased (unpubl. transect density 1.6 pairs/km^2). *T. iliacus* has increased sharply in Finland since the 1940s (e.g. Table 3), but in 1917 the species was "relatively abundant" (corresponding to 3—9 pairs/km^2)! LEHTONEN (1946) reports a clear decrease in numbers from the 1920s to the early 1940s in Kainuu, which suggests that, in the 1940s, the populations of *T. iliacus* were low, at least in Kainuu and Kuusamo. The northernmost populations of the species, breeding in Lapland, have increased relatively little in recent decades, while a great increase has occurred in southern Finland (unpubl.). This observation suggests that *T. iliacus* has shown few population changes in northernmost Finland, where the population has always been dense, but has shown somewhat erratic changes in Kainuu-Kuusamo, which lies near the border of dense distribution (i.e. we suggest that the southern border of the dense distribution moved northwards in the 1920s or 1930s), while in southern Finland the trend has been towards a clearly increasing population (this is supported by our unpublished data for 1936—77; cf. also LUMIALA & SUOMALAINEN 1941). The data concerning *T. philomelos* are inconclusive. The decrease of *T. viscivorus* after 1917 was clear by the 1970s (see above) and probably by the 1940s.

Sylvia curruca (present density 0.4 pairs/km^2, unpubl.) was not reported in 1917, nor was *Regulus regulus* (2.0 pairs/km^2, unpubl.). *Bombycilla garrulus* was often observed in 1917, had very high densities in 1941 and very low densities in 1942—45 (at least in Kainuu, LEHTONEN 1946), while the present density is only 0.1 pairs/km^2 (unpubl.). This suggests a decrease, but the species shows wild fluctuations. In MERIKALLIO's time, *Sturnus vulgaris* had been breeding in the village of Kuusamo for about 10 years, but the present density is 0.2 pairs/km^2 (unpubl.), suggesting an increase.

Carduelis spinus has undoubtedly increased (one observation in 1917, cf. Table 3). At the same time, *C. flammea* has probably decreased, as in 1917 it was one of the four most abundant species (at present ninth, unpubl.). However, the species fluctuates greatly from year to year and the figure for 1917 may be unrepresentative. *Carpodacus erythrinus*, which has increased dramatically in Finland in recent decades, was observed at Paanajärvi in 1917; its present density is not much higher, 0.1 pairs/km^2 (unpubl.). Finally, *Emberiza rustica* was rare in 1917 (one observation), which contrasts sharply with the present density, 2.5 pairs/km^2 (unpubl.). Line transect data do not suggest major long-term trends in Kuusamo from the 1940s to the 1970s (unpubl.), whereas MERIKALLIO 1946:108) reports a clear decrease in E Finland between 1919 and 1943. These observations seem to be compatible only if it is supposed that long-term changes are not important in this species, but that annual fluctuations may be very great (see also VON HAARTMAN *et al.* 1963—1972).

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References

FRETWELL, S. D. 1972: Populations in a seasonal environment. — 217 pp. Princeton N. J.

HAARTMAN, L. VON, HILDÉN, O., LINKOLA, P., SUOMALAINEN, P. & TENOVUO, R. 1963—1972: Pohjolan linnut värikuvin I—II. — 1092+192 pp., Helsinki.

JÄRVINEN, O., KUUSELA, K. & VÄISÄNEN, R. A. 1977: Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana. (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. 1976a: Between-year component of diversity in the communities of breeding land birds. — Oikos 27: 34—39.

—»— 1976b: Species diversity of Finnish birds, II: Biotopes at the transition between taiga and tundra. — Acta Zool. Fennica 145:1—35.

—»— 1976c: Finnish line transect censuses. — Ornis Fennica 53:115—118.

—»— 1977a: Recent quantitative changes in the populations of Finnish land birds. — Polish Ecological Studies 3(4):177—188.

—»— 1977b: Long-term changes of the North European land bird fauna. — Oikos 29:225—228.

—»— 1977c: Kololintujen kannanmuutokset viime vuosikymmeninä. — In: H. HAUTALA, Kololinnut ja muut pökkelöpesijät, 183—184. Helsinki.

—»— 1977d: Constants and formulae for analysing line transect data. — 10 pp. Helsinki. (Mimeo.)

—»— 1978a: Miksi aikaisemmin tehtyjä pesimälinnuston laskentoja kannattaa toistaa? (Trends in the numbers of breeding forest birds in S Finland in the period 1936—77.) — Lintumies 13:1—6.

—»— 1978b: Habitat distribution and conservation of land bird populations in northern Norway. — Holarct. Ecol. (in press).

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

KUJALA, V. 1936: Tutkimuksia Keski- ja Pohjois-Suomen välisestä kasvillisuusrajasta. (Über die Vegetationsgrenze von Mittel- und Nordfinnland.) — Comm. Inst. Forest. Fenniae 22 (4): 1—95.

KUUSELA, K. 1972: Suomen metsävarat ja metsien omistus 1964—70 sekä niiden kehittyminen 1920—70. (Forest resources and ownership in Finland 1964—70 and their development 1920—70.) — Comm. Inst. Forest. Fenniae 76 (5):1—126.

—»— 1977: Forestry resources. — In: Atlas of Finland, folio 234:2—12. Helsinki.

LEHTONEN, L. 1946: Ornitologisia tutkimuksia paksusammal-mustikka (HMT-MT) ja variksenmarja-mustikka-puolukka (EMT-VT) tyyppien metsissä Kainuussa ja Vienan-Karjalassa. — Manuscript.

LUMIALA, O. V. & SUOMALAINEN, H. 1941: Piirteitä Pohjois-Sallan linnustosta. (Züge aus der Vogelfauna von Nord-Salla, Lappland.) — Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo 8 (8):16—31.

MELA, M. 1975: Oulangan kansallispuiston ja sen lähiympäristön linnusto vuosina 1967—1973. — Manuscript, Department of Zoology, University of Oulu, Oulu.

MERIKALLIO, E. 1917: Lintujen runsauden arvioimisesta määrätyllä alueella. — Luonnon Ystävä 21:187—193.

—»— 1921: Oulangan seudun ja Kaakkois-Kuolajärven linnusto. — Acta Soc. Fauna Flora Fennica 48(2):1—168.

—»— 1946: Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I. Allgemeiner Teil. — Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo 12 (1):1—140.

—»— 1951: Der Einfluss der letzten Wärmeperiode (1930-49) auf die Vogelfauna Nordfinnlands. — Proc. Xth Int. Ornithol. Congr. (Uppsala 1950): 484—493.

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

NILSSON, S. G. & ALERSTAM, T. 1976: Resource division among birds in North Finnish coniferous forest in autumn. — Ornis Fennica 53:15—27.

SOVERI, J. 1940: Die Vogelfauna von Lammi, ihre regionale Verbreitung und Abhängigkeit von den ökologischen Faktoren. — Acta Zool. Fennica 27:1—176.

SÖYRINKI, N., SALMELA, R. & SUVANTO, J. 1977: Oulangan kansallispuiston metsä- ja suokasvillisuus. (The forest and mire vegetation of the Oulanka National Park, Northern Finland.) — Acta Forest. Fennica 154:1—150.

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