Ann. Zool. Fennici 23:157–166. 1986

Bird community dynamics in a boreal forest reserve: the importance of large-scale regional trends

Pekka Helle

Helle, P. 1986: Bird community dynamics in a boreal forest reserve: the importance of large-scale regional trends. — Ann. Zool. Fennici 23:157–166.

I compare the bird community dynamics of the virgin conifer forests of the Oulanka National Park (northern Finland) with those in the surrounding areas characterised by clear cuts, seedling stands and other types of managed forests. The Oulanka Forest had a lower breeding bird density (54 vs. 75 pairs/km^2), a considerably higher species diversity (2.74 vs. 2.29, Shannon index), a higher density of sedentary species, and a lower density of long-distance migrants, than the adjacent forestry area. I compared bird population changes between the early 1970s and the early 1980s in the Oulanka Forest with the changes reported from the whole of northern Finland in recent decades. 16 of the 24 most numerous species at Oulanka had undergone population changes going in the same direction (increase or decrease) as the national trends, while for the remaining eight species changes had occurred in the opposite direction. Between 1980 and 1985 the population levels of the most abundant breeding species in the Oulanka Forest and in the adjacent managed forest areas varied in parallel.

These results suggest that even an area of protected virgin forest as large as 70 km^2 is not a 'closed' unit for bird populations. The populations of such areas are influenced by large-scale changes in source populations on a regional scale (northern Finland), where the impact of forestry on natural habitats is considerable. I discuss these results in relation to nature conservation and the theory of ecological succession.

Pekka Helle, Department of Biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100 Jyväskylä, Finland.

1. Introduction

There has been considerable debate on conservation policy and the role of nature reserves in recent years. Several principles as to the location, size, number and shape of nature reserves have been devised on the basis of the equilibrium hypothesis of island biogeography (MacArthur & Wilson 1967) and advanced as recommendations intended to preserve the highest possible number of species in a given area (e.g. May 1976, Diamond & May 1976). Several studies based on field data (Simberloff & Abele 1976, Järvinen 1982, Blouin & Connor 1985, among others) have questioned the universality of these recommendations. In particular, the fauna of a nature reserve may experience changes due to changes in population levels in the surrounding region, such as those caused by large-scale habitat devastation and other alterations outside the protected area (Järvinen 1978, Haila et al. 1979, Helle & Mönkkönen 1985a, Väisänen et al. 1986). The smaller and more isolated the area, the more probable it is that its fauna and flora will not maintain their original features in the long run. This question is closely related to the relationship between local vs. regional changes in populations (Väisänen et al. 1986). The question of the extent to which bird populations in nature reserves are self-supporting is very important for nature conservation, but very few studies have dealt with it.

In the present paper I compare recent changes in bird population levels in a virgin forest reserve in northern Finland, firstly with population changes in adjacent areas of managed forest, and secondly with population changes in northern Finland as a whole.

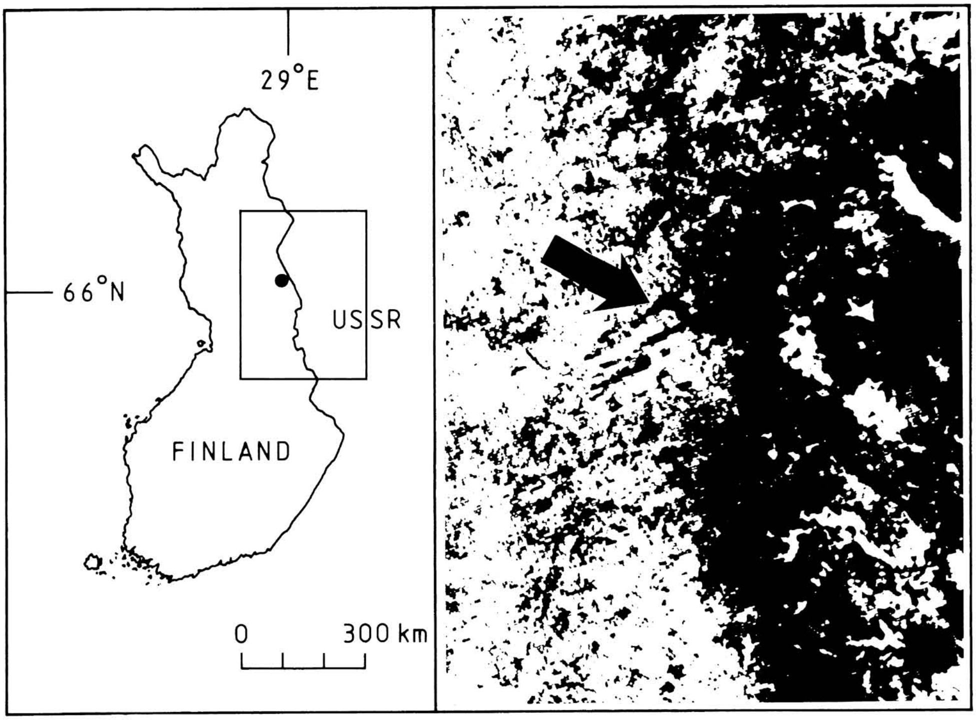

Fig. 1. Location of the study area in northeastern Finland. In the satellite picture, the area of which is shown in the map, black indicates mature (and dense) forest and white different types of open ground as well as young (or sparse) forest (Mikko Punkari/Ursan kuva-arkisto). The arrow indicates the site of the Oulanka National Park in the satellite picture

2. Study area and methods

The study area – the Oulanka National Park and the immediately adjacent areas of forest – is located in northeastern Finland close to the Arctic Circle and the border between Finland and the USSR (66°N, 29°E, Fig. 1). It belongs to the the mid-boreal phytogeographical zone of Ahti et al. (1968) and to the north-boreal area in the ornithogeographical zonation of Järvinen & Väisänen (1980). Only brief details of the study area are presented here as more detailed descriptions can be found elsewhere (Söyrinki et al. 1977, Helle 1985a).

The forests of the Oulanka National Park (established in 1956) are old and dominated mainly by pine and spruce. The most common forest types in the Park are *Calluna–Cladina* (dry heath forest), *Empetrum–Myrtillus* (moderately dry heath forest) and *Hylocomium–Myrtillus* (fresh heath forest; see Söyrinki et al. 1977). The shrub layer in these forests is sparse, as it is in most northern coniferous forests. Deciduous areas are small and largely concentrated along the River Oulankajoki, which flows through the National Park. A few small areas of treeless and wooded bogs are also present. Traces of forest felling can be seen in some areas of the Park but this activity ceased at the beginning of this century. Traces of past forest fires abound, particularly in drier forest sites, reflecting the importance of fires for the vegetation in earlier times. The forest area of the Park (about 70 km^2 in area) is referred to below as 'the Oulanka Forest'.

The soil characteristics and productivity of the forestry area south of the National Park, where most of the bird studies outside the Park are conducted, are similar to those in the Oulanka Forest. This area (Ruoppiharju, about 500 ha in area) was clear-cut in the late 1950s and early 1960s. Nowadays the area is dominated by 3–6 m high seedling stands of pine (mainly artificially regenerated). However, some parts of this clear-cut have not been properly reafforested. In addition to the planted pines, some spruce and deciduous saplings can be found in this forest regeneration area. Since the felling of Ruoppiharju, nearly all the other forests bordering the National Park have been cut. Forestry has been so intense here that the National Park is more or less an island of natural stands in the middle of large felled areas. However, the park is connected by a narrow isthmus to large areas of natural forest behind the Finnish–Soviet border (see Fig. 1 and Helle 1985b).

Although the study areas (Ruoppiharju in particular) are not very large, they represent typical biotopes of northern Finland. Forest cutting (mainly clear-cutting) has been very intensive during the last few decades in northern Finland. Nowadays almost 40 % of forest land is covered by young forest and clear cuts (Kuusela 1978, Mikola 1980; for changes in forest structure from the point of view of bird populations see Järvinen et al. 1977, Helle

1985b, Väisänen et al. 1986). Areas of homogeneous natural stands of the size of the Oulanka National Park are not common in northern Finland. In fact, unmanaged forest tracts of this size are rare outside nature reserves.

Line transect censuses were used to count the breeding birds. Mela (1975), whose results are also used in this study, employed a main belt breadth of 60 m in transects. The survey belt variant of the line transect method was used in the censuses performed in 1980—85 in the Oulanka Forest and adjacent felling area (Ruoppiharju). In the survey belt technique all the observations along the transects can be used to calculate the densities of bird species (Järvinen & Väisänen 1983). Between 1980 and 1985 about 10 km of transect line were censused annually both in the Oulanka Forest and in the Ruoppiharju area. More detailed results from this study will be published elsewhere. Only about 60 % of the birds in a given area are detected using the line transect method (Järvinen et al. 1978). This is not important here, as the analyses are based on comparisons and accurate estimates of bird population densities are not needed.

The Shannon index, corrected for sample size, was used to calculate the species diversity of each community. The evenness of the species-abundance distribution was calculated by dividing this diversity index value by the natural logarithm of the number of species. The rarefaction method was used to estimate the species richness of the communities (James & Rathbun 1981). To assess the compositional difference between two communities I employed the diversity-based index of DIV_{diff} (see Järvinen & Väisänen 1976), which is affected both by the identities of the species in the samples and by their frequencies: an index value of zero shows that the samples compared are identical whilst a value of 100 shows that the samples are totally distinct, with not even the most abundant species in common. The classification of bird species as sedentary (including partial migrants), short-distance migrants (wintering in Europe), and long-distance migrants (wintering mainly in Africa) follows that of Väisänen (1983) and Helle & Mönkkönen (1985a).

3. Bird community of the Oulanka Forest in relation to adjacent areas

About 4000—6000 pairs of about 50—60 species breed each year in the Oulanka Forest. First I compare the bird community of the National Park with the bird community in the adjacent forestry areas. The characteristics of the bird communities of the Ruoppiharju area and of the Oulanka Forest are given in Table 1. Breeding bird density is higher, and species diversity considerably lower, in managed seedling stands than in the natural forest. The marked difference in species diversity is due to the difference in the evenness of the species-abundance distribution. The other factor affecting the diversity index value is the species richness of a community; in this respect the two communities compared here are equal (Table 1). The Oulanka Forest supports a higher density of sedentary species than do the managed stands. For long-distance migrants, the reverse is true.

Table 1. Comparison of bird community characteristics of the Ruoppiharju area (mainly seedling stands) and the Oulanka Forest (climax conifer forests). The figures are averages of censuses taken in 1980—85 (see *Appendix*). The expected number of species was computed by the rarefaction method to a random sample of 93 pairs, equal to the smallest sample in the censuses. *t*-statistics was used in evaluating the significance of the differences between sample means.

	Ruoppi-harju	Ou-lanka	*P*
Bird density (pairs/km^2	75	54	<0.05
Species diversity	2.29	2.74	<0.001
Evenness	0.71	0.83	<0.001
Expected no. of spp. (93)	19.8	20.9	<0.1
Density of			
sedentary species	4.6	8.9	<0.01
short-distance migrants	24.9	25.9	<0.1
long-distance migrants	45.4	18.9	<0.001

The densities of the ten most abundant species in the Oulanka Forest, in its surroundings, and in the north-boreal ornithogeographical zone of Järvinen & Väisänen (1980) are presented in Table 2. The Oulanka Forest is dominated by coniferous forest species but in the other two areas several species characteristic of open habitats are among the most abundant, which is not an unexpected result. The DIV_{diff} index values between these three areas (using the most numerous species) are as follows:

	Oulanka	Ruoppiharju
Ruoppiharju	51.6	
North-boreal zone	30.3	13.3

Interestingly, the difference between the Ruoppiharju area (mainly seedling stands) and the north-boreal zone is rather small. This suggests that the habitat distribution of the north-boreal zone as a whole is fairly similar to that of Ruoppiharju. On average, clear cuts are more frequent and open bogs less abundant in Ruoppiharju than in the north-boreal zone, but this difference has little effect because clear cuts are frequently occupied by species of open bogs (Helle 1985a). In this comparison, the Oulanka Forest differs markedly both from its surroundings and from the north-boreal ornithogeographical zone as a whole, but these differences are due to habitat differences between Oulanka and the other two areas.

One of the specific goals in establishing nature reserves in old forest areas like the

Table 2. Pair densities (pairs/km^2) of the ten most abundant land bird species in the Oulanka National Park (censuses 1980−85), in the surroundings of the Park, especially Ruoppiharju (see Sect. 2; censuses 1980−85) and in the north-boreal ornithogeographical zone of Järvinen & Väisänen (1980), which the previous areas belong to (their table 3, censuses 1973−77).

Oulanka		Ruoppiharju		North-boreal zone	
Fringilla montifringilla	11.7	*Phylloscopus trochilus*	20.0	*Phylloscopus trochilus*	17.6
F. coelebs	6.3	*Motacilla flava*	12.4	*Fringilla montifringilla*	15.1
Phylloscopus trochilus	3.9	*Turdus iliacus*	11.8	*Turdus iliacus*	9.5
Erithacus rubecula	3.4	*Anthus pratensis*	4.9	*Motacilla flava*	7.2
Muscicapa striata	3.3	*Fringilla montifringilla*	4.0	*Muscicapa striata*	4.2
Anthus trivialis	3.0	*Saxicola rubetra*	2.8	*Carduelis flammea*	3.7
Phoenicurus phoenicurus	2.6	*Anthus trivialis*	2.7	*Anthus trivialis*	3.4
Emberiza rustica	2.1	*Oenanthe oenanthe*	1.8	*Tringa glareola*	2.9
Bonasa bonasia	1.5	*Carduelis flammea*	1.4	*Emberiza rustica*	1.8
Turdus philomelos	1.5	*Emberiza schoeniclus*	1.4	*Anthus pratensis*	1.6

Oulanka Forest is to protect the less abundant habitat specialists of the original forest types. The Oulanka Forest, in particular, is important for the bird species of northern coniferous forest (taiga). These habitat specialists are scarce or rare, however, and it is therefore difficult to obtain statistically reliable census results. The breeding bird censuses taken in the Oulanka Forest and its surroundings in 1980−85 demonstrate this problem (see *Appendix*). Some 18 species, mainly of open habitats, were observed only in the surroundings of the Park whilst 12 species were observed only in the Oulanka Forest. Among the latter species were such true taiga species as *Phylloscopus borealis* and *Parus cinctus*; they were, however, very rare (*Appendix*). Typical taiga species *Bombycilla garrulus* and *Perisoreus infaustus* were found both in the Oulanka Forest and in Ruoppiharju, and *Pinicola enucleator* only in the forestry area (Ruoppiharju). The total numbers of these taiga specialists (above) amount to six in Ruoppiharju (0.6% of all observations) and 11 in the Park (1.1%); the difference is naturally not significant. If those species of the Siberian faunal type which are not taiga specialists (*Turdus pilaris, T. iliacus, Fringilla montifringilla, Emberiza rustica*, Voous 1960) are taken into account the figures are 22.9% for the forestry areas and 27.9% for the Oulanka Forest. The difference is significant ($P<0.05$; see Appendix). Many of the taiga forest bird species are scarce non-passerines (e.g. Helle 1985b), which are particularly difficult to census using a single visit as was done here. Therefore, comparisons of the numbers of taiga specialists should be interpreted with caution.

4. Recent changes in bird populations in the Oulanka Forest

I deal here with bird population changes during the past 15 years in the forests of the Oulanka National Park. Longer term avifaunal changes in the Kuusamo Uplands are described by Järvinen & Väisänen (1978), Siivonen (1978), and Helle & Mönkkönen (1985a). Recent changes in these bird populations are described here only briefly since detailed analyses can be found elsewhere (Helle & Mönkkönen 1985a). Breeding bird density and species diversity both decreased slightly from the early 1970s (1970−73) to the early 1980s (1980−84) (68 vs. 56 pairs/km^2 and 2.85 vs. 2.78, respectively) but the differences are not significant. The densities of sedentary species and of long-distance migrants decreased but the density of short-distance migrants increased significantly during the study period. Of the individual bird species, *Bonasa bonasia, Phoenicurus phoenicurus, Turdus iliacus, Phylloscopus collybita* and *Ph. trochilus* decreased significantly, whereas *Erithacus rubecula* and *Emberiza rustica* increased in numbers (Table 3).

The factors contributing to changes in bird populations may be diverse. Changes in habitat quality or distribution cannot explain bird population changes in the Oulanka Forest, since it has remained totally unchanged not only during the study period but also over a much longer period (see also Söyrinki et al. 1977 and Section 2 above). Weather conditions in the breeding or wintering grounds may affect populations, but no single such factor can explain the changes in all species as those species which decreased

Table 3. Densities (pairs/km²) of the 24 most abundant land bird species of the Oulanka National Park in the beginning of the 1970s and 1980s. The former data are based on the study of Mela (1975), the latter on the study of Helle & Mönkkönen (1985a). Statistically significant changes are shown by an asterisk ($P<0.05$; t-test).

	1970–73	1980–84	
Bonasa bonasia	2.8	1.6	*
Cuculus canorus	1.1	0.4	
Anthus trivialis	4.2	3.0	
Erithacus rubecula	0.9	3.6	*
Phoenicurus phoenicurus	5.3	2.8	*
Turdus philomelos	2.2	1.6	
T. iliacus	2.9	1.0	*
T. viscivorus	0.3	0.2	
Phylloscopus collybita	2.6	0.7	*
Ph. trochilus	9.1	3.7	*
Regulus regulus	1.5	0.7	
Muscicapa striata	3.5	3.9	
Ficedula hypoleuca	1.4	1.5	
Parus montanus	1.0	0.8	
P. cinctus	0.6	0.4	
P. major	0.4	0.5	
Perisoreus infaustus	1.2	0.8	
Fringilla coelebs	4.5	6.2	
F. montifringilla	10.5	12.1	
Carduelis spinus	2.9	1.7	
C. flammea	2.6	1.3	
Loxia curvirostra/ pytyopsittacus	2.5	0.7	
Pyrrhula pyrrhula	1.4	0.4	
Emberiza rustica	0.5	1.9	*

significantly over the study period have different migratory habits and they also vary in their habitat requirements (or preferences). Population changes within the study periods might merely reflect stochastic variation but I think this is unlikely since both study periods are based on several years' data.

One possible explanation for the population change is that the Oulanka Forest populations are not 'closed' but are part of a wider population affected by regional changes. Studies of recent changes in bird populations are not 'closed' but are part of a 1983, Väisänen et al. 1986) show that *Bonasa bonasia, Phoenicurus phoenicurus* and *Phylloscopus collybita* have decreased whereas *Erithacus rubecula* and *Emberiza rustica* have increased. Helle & Mönkkönen (1985a) found that most of the abundant species have undergone similar changes in the Oulanka Forest and in northern Finland as a whole. If the comparison is extended to the 24 most numerous species in the Oulanka data the result is less convincing: 16 species have undergone population changes in the same direction (decrease or increase), eight the opposite. The figures deviate from that expected by chance at $P\approx0.076$, i.e. nearly significantly. The following points may affect the validity of this test: 1) The study periods in the Oulanka Forest and northern Finland in general are not identical; 2) the test is qualitative, only taking into account the direction of change, and the small samples in the Oulanka data are therefore very sensitive to random variation; 3) since the test is restricted to the most numerous species, the result cannot be generalised to cover the whole of the avifauna without reservation.

Väisänen et al. (1986) divided the most abundant bird species of northern Finnish forests into three groups on the basis of their recent population development: increasing, stable and decreasing species. The densities of the species belonging to these groups in the Oulanka Forest in the early 1970s and 1980s were as follows:

Trend observed in northern Finland (Väisänen et al. 1986)	The Oulanka Forest (pairs/km²) 1970–73	1980–84	Change (%)
Decrease	18.3	10.3	−44
Stable	14.8	13.8	− 7
Increase	34.1	29.2	−14

The figures for the species in the groups 'decrease' and 'stable' agree well with those obtained by Väisänen et al. (1986) for the whole of northern Finland. There is a considerable difference in the increasing species. These have increased their numbers by about 30% in northern Finland during recent decades, but in the Oulanka Forest they have decreased by 14%. The deviation from the general pattern is mainly due to five species (*Turdus philomelos, T. iliacus, Phylloscopus trochilus, Regulus regulus* and *Carduelis spinus*), which have increased in northern Finland (many of them remarkably), but decreased in the Oulanka Forest. *Turdus iliacus* and *Phylloscopus trochilus* prefer young phases of forest succession whereas the other three species breed in old (mainly spruce) forest. This result is difficult to explain. It is possible that the population trends of these species changed after the late 1970s, i.e. after the reference period for the whole of northern Finland (1977; Väisänen et al. 1986), but later studies suggest that this is not the case (Väisänen 1984). The question must remain unanswered, as it is impossible to exclude all the sources of error in this comparison (the periods to be compared are not equal, inter-observer differences exist in census-taking, etc.).

5. Annual fluctuations in bird communities in the Oulanka Forest and adjacent forestry area

Next I examine whether the year-to-year changes in bird populations in the Oulanka Forest take place in parallel with those in the surrounding areas. Census results from six years' study are presented in the *Appendix*. The correlations between the two areas in total bird density, species diversity and the densities of the different migratory groups of species are not significant, but all are positive (Table 4). The correlation between densities is positive in 10 of the 12 species for which there are adequate data (at least five pairs observed in the smaller of the two data sets). This distribution is non-random ($P \approx 0.019$). I conclude that the population (and community) changes in these two areas are taking place in parallel, caused probably by similar changes in weather conditions. This conclusion is based only on the most abundant bird species (those which breed in both of these habitats), and therefore it cannot be generalised to cover the whole of the avifauna. However, the species used in the comparison make up about 70 % of the bird communities.

It is well known that *Carduelis spinus, C. flammea* and *Loxia* species all show large between year fluctuations in density; all of them showed a fairly high correlation in their densities in the six study years between the Oulanka Forest and the forestry area (Table 4). If these species are excluded from the comparison of the total bird density, the correlation coefficient is +0.635, which is only slightly poorer than when these irruptive species were included (Table 4). Thus, the parallel fluctuations observed between the National Park and adjacent forestry area are not merely due to fluctuations in the populations of these species.

The census results from the Oulanka Forest and the adjacent area can also be used to study bird community succession. The general principle of succession states that there should be a directional change in community structure in the course of succession (here: from clear cuts to climax forest). Thus the dissimilarity between the year 1980 and subsequent years (1980 vs. 1981, 1980 vs. 1982 and so on) should increase in Ruoppiharju (young phases of forest succession) whereas in the climax forest of Oulanka it should be more or less stable. The DIV_{diff} index values between the first study year (as a reference) and subsequent years for Ruoppiharju and Oulanka are as follows:

	1980	1981	1982	1983	1984	1985
Ruoppiharju	(0)	11.8	9.1	15.5	16.0	19.7
Oulanka	(0)	11.6	11.6	8.3	12.5	9.4

These results support the idea that the change in community composition in young forest is more rapid and directional than in climax forest. Secondly, the difference in community composition between the seedling stand and the climax forest should decrease in the course of succession (time). The value of DIV_{diff} index between Ruoppiharju and Oulanka varied in 1980−85 as follows:

1980	1981	1982	1983	1984	1985
32.6	33.2	26.4	28.9	30.6	23.0

As expected there is a negative correlation between the date and the index values ($r=-0.731$), but it is not significant. The study period — six years — is a very short period indeed with respect to the whole time span of secondary forest succession in these areas (100−150 years). The succession in the Ruoppiharju area may be modelled further. When the area was clear felled (1960) the

Table 4. Correlation coefficients (r) in selected community parameters and densities of the most abundant bird species in the six study years (1980−85) between the Oulanka Forest and adjacent forestry area (Ruoppiharju). The critical value for $P<0.05$ is 0.811 and that for $P<0.01$ 0.917 (see also text and Appendix).

	r
Total bird density	+0.700
Species diversity	+0.359
Density of sedentary species	+0.077
short-distance migrants	+0.605
long-distance migrants	+0.034
The most abundant bird species:	
Tringa glareola	+0.921
Cuculus canorus	−0.371
Anthus trivialis	−0.397
Phoenicurus phoenicurus	+0.755
Turdus iliacus	+0.233
Phylloscopus trochilus	+0.108
Corvus corone	+0.389
Fringilla coelebs	+0.450
F. montifringilla	+0.497
Carduelis spinus	+0.601
C. flammea	+0.859
Loxia curvirostra/pytyopsittacus	+0.671

DIV_{diff} value between the clear cut and the Oulanka Forest was probably about 80 units. This is an approximation based on recent measures of the dissimilarity between bird communities in clear cut and climax forest (Helle 1985a and unpubl.). In the early 1970s the community dissimilarity between Ruoppiharju was on average 41 units (calculated from the data of Mela (1975) for the Oulanka Forest and from unpublished data collected during field courses on ecological zoology (University of Oulu) for Ruoppiharju). In the 1980s this difference averaged 29 (above). The correlation coefficient for these points (with a logarithmic transformation in the time scale) is close to unity ($r = -0.999$). The regression line predicts that the bird communities of Ruoppiharju and Oulanka will be similar in the year 2020 (the difference will then be about 10 DIV_{diff} units, which may be taken as an average level of 'noise' (stochastic variation) in such samples (see Helle & Mönkkönen 1985b). In 2020 the Ruoppiharju area will be about 60 years old; this is a fairly short time for the whole succession compared to earlier studies (e.g. Helle 1985a). However, the present estimate is based on few observations, and the first point (1960) is an approximation based on later studies.

6. Conclusion

The main conclusion from this study is that the bird community of a large virgin forest area is not a 'closed' unit, but reflects large-scale (regional) changes in species populations as well as the similar short-term fluctuations occurring in nearby forestry areas. It can be discussed from two points of view, that of nature conservation and that of succession studies.

Väisänen et al. (1986) reported that the bird community of a small (approx. 1 km^2) virgin forest in northern Finland changed considerably from 1915 to 1983, although the forest itself has remained totally unchanged during the period. In the 1980s the vegetation of the old forest differed strikingly from surrounding areas, but the bird community resembled that of any managed forest. It is more surprising that the Oulanka Forest, which is fairly large (70 km^2), has not managed to preserve its 'original' charateristics (see also Järvinen & Väisänen 1978, Helle 1985b). This problem is closely linked to the relationship between regional and local changes in bird populations (Wiens 1981, Väisänen et al. 1986): How large an area is needed for species of birds to have self-supporting populations? The answer varies according to the abundance of a species. The rarer species are often species of the forest interior and require a larger area of forest reserve (see e.g. Diamond 1978, Wiens 1981). Very small nature reserves (or habitat islands) include a large proportion of edge in their area and correspondingly small areas of interior, and may readily be invaded by more generalist competitors from the surrounding habitats (Butcher et al. 1981, Ambuel & Temple 1982; for a discussion on boreal forest areas see Haila 1986).

One possible reason why the Oulanka Forest is not a 'closed' area can be seen in Fig. 1. The Oulanka Forest lies just on the western edge of a "peninsula" of more or less virgin forest extending westwards into the area of intensive forestry and is therefore particularly susceptible to invasion from these managed areas (see also Helle & Mönkkönen 1985a). If this explanation is correct the forests further to the East should have preserved their original bird communities better, but unfortunately no data are available from those areas.

It has been customary to study successions (especially long lasting ones) by studying areas of different age simultaneously; the data are then sequenced so as to describe the succession (for studies on bird communities in relation to boreal forest succession using this method see Haapanen 1965, Helle 1985a, Helle & Mönkkönen 1985b). This approach creates a problem, however, as one assumes that the bird community in a given habitat (succession stage) is more or less constant for a long period (see also Aspi & Helle 1984). This study shows that this assumption is unsafe, for changes in bird communities may occur where there have been no changes. Changes in weather are more likely to produce short-term fluctuations than long-term trends. The reference stage which is normally used when studying succession series is the climax stage, as this is supposed to be the most stable (see Horn 1974 for a review). The Oulanka Forest should be in a good phase for studying vegetation succession in northern forests because of its unmanaged reserve status (see Söyrinki et al. 1977). However, it is no longer a reliable reference phase in avian studies, since it has experienced major changes in its avifauna during recent decades. When

Appendix. Densities (pairs/km^2) and total number of pairs (N) of the species observed in the line transect censuses in the Oulanka Forest and adjacent forestry area (Ruoppiharju) in 1980–85 (see also text).

	Forest regeneration area (Ruoppiharju)							Climax conifer forest (Oulanka)						
	1980	-81	-82	-83	-84	-85	*N*	1980	-81	-82	-83	-84	-85	*N*
Buteo buteo				0.3			(1)	0.2						(1)
Falco tinnunculus	0.1			0.1			(2)							
F. columbarius			0.3				(1)							
Bonasa bonasia								1.1	2.3	1.1	2.3	1.1	1.1	(8)
Lagopus lagopus	1.2				1.7		(2)							
Tetrao tetrix	1.1	0.7					(5)							
T. urogallus				1.7			(1)					1.6		(1)
Grus grus				0.0			(1)							
Gallinago gallinago	0.6			0.2		0.3	(5)							
Numenius phaeopus	0.3	0.6	0.3	0.6	0.8	0.2	(17)							
Tringa nebularia		0.2	0.3	0.7	0.2	0.9	(12)							
T. ochropus								0.3			1.0	1.0		(7)
T. glareola		0.7	0.4	2.1	2.3	2.8	(20)				0.7	1.0	0.7	(7)
Cuculus canorus	0.4		0.1	0.2	0.4	0.4	(16)	0.2	0.5	0.2	0.5	0.4	0.3	(28)
Asio flammeus		0.4		0.8			(3)							
Apus apus				0.1			(1)		0.1					(1)
Dryocopus martius				0.1			(1)			0.1	0.1		0.1	(3)
Dendrocopos major					0.6	1.3	(3)			0.5		0.5	0.5	(3)
Hirundo rustica				0.2			(1)							
Anthus trivialis	0.6	1.7	3.0	5.0	2.3	3.8	(51)	2.7	4.4	2.7	2.5	2.7	2.7	(65)
A. pratensis	9.8	2.3	8.2	4.5	1.9	0.6	(55)					0.5		(1)
Motacilla flava	11.2	4.8	10.6	18.0	25.6	6.7	(82)	0.8						(1)
M. alba	0.6		2.0	1.3			(6)		0.6					(1)
Bombycilla garrulus				0.6	0.8		(4)					0.6		(2)
Erithacus rubecula								2.4	2.8	1.2	6.3	5.2	2.8	(52)
Phoenicurus phoenicurus			0.3	0.9	1.9	1.2	(12)	2.5	2.5	1.4	2.2	5.2	2.2	(58)
Saxicola rubetra	5.8	2.5	4.1	1.8	0.6	0.6	(35)							
Oenanthe oenanthe	4.1		5.1	0.6			(16)							
Turdus pilaris					0.6		(1)			0.4		0.8		(3)
T. philomelos				0.4	0.2	0.2	(4)	0.8	1.3	0.7	1.2	4.0	1.0	(54)
T. iliacus	4.8	5.2	16.3	20.7	16.5	8.8	(168)	0.4	1.1	1.5	0.4	1.8		(14)
T. viscivorus						0.3	(1)		0.2	0.2	0.5		0.2	(5)
Sylvia curruca						0.5	(1)							
S. communis												0.6		(1)
S. borin		0.7				1.2	(7)		0.2					(1)
Phylloscopus borealis										0.4				(1)
Ph. sibilatrix												0.2		(1)
Ph. collybita					0.3		(1)	1.0	0.6	0.8	0.6	0.4	0.6	(20)
Ph. trochilus	16.9	14.8	18.9	22.9	19.4	29.8	(356)	1.5	5.3	6.2	5.6	0.9	4.1	(80)
Regulus regulus									0.7	1.4	0.7	0.7	1.4	(7)
Muscicapa striata	0.8				1.1		(2)	2.3	3.9	3.1	5.4	4.6	0.8	(26)
Ficedula hypoleuca					0.6		(1)	1.2	2.4	1.6	1.6	0.8	1.6	(23)
Parus montanus									0.7	0.7	1.4	1.4		(6)
P. cinctus											1.0	1.0	2.0	(4)
P. cristatus									2.7					(3)
P. major		0.4			0.6		(2)		0.4	0.9	0.9	0.4	1.7	(10)
Certhia familiaris									1.8			0.9		(3)
Lanius excubitor				0.5			(1)							
Perisoreus infaustus			1.1				(1)			3.0	1.0			(4)
Corvus corone	0.4	0.1	0.1	0.1	0.3	0.3	(10)	0.1			0.1		0.4	(5)
C. corax				0.1			(1)			0.1				(2)
Fringilla coelebs		0.3	1.0	1.3	0.4	0.9	(11)	3.1	3.4	7.7	6.5	10.5	6.8	(123)
F. montifringilla	0.3	2.4	3.3	5.8	5.0	9.2	(71)	5.1	9.5	8.9	18.8	17.9	10.1	(236)
Carduelis spinus	0.2	0.6		1.1	0.3		(10)	0.6	1.9	0.8	2.1	2.9	0.2	(41)
C. flammea	1.5	1.8	0.8	3.3	0.7		(30)	0.5	2.5	0.5	2.5	0.3		(25)
Loxia leucoptera					0.5		(1)							
Loxia sp.			0.3	0.9	1.2	0.2	(15)	0.1	0.6	1.1	0.7	1.3		(27)
Carpodacus erythrinus	0.3	0.8	0.3	0.3	1.4	0.7	(12)			0.3	0.3	0.3		(3)
Pinicola enucleator					1.2		(1)							
Pyrrhula pyrrhula				0.6		0.4	(3)	0.5	0.3	0.5	1.1		0.3	(10)
Emberiza citrinella	0.6						(2)							
E. hortulana		0.4					(1)							
E. rustica				2.1			(2)	3.8	1.0	2.9	1.0	1.0	2.9	(13)
E. schoeniclus	1.8		0.7	1.3	3.3	1.7	(12)			0.6		0.6		(2)
Transect length (km)	11.0	11.0	10.0	10.3	7.9	7.9		11.1	11.1	11.1	11.1	11.1	11.1	

considering these questions the importance of scale must be stressed. Forest succession phases are not temporally or spatially 'closed' units with respect to their avian communities, but are affected by the regional distribution and abundance of the different stages of forest regeneration.

Acknowledgements. I thank M. Mönkkönen for participating in the censuses and data analyses. My thanks are also due to S. Baillie, Y. Haila, O. Järvinen and R.J. O'Connor, whose comments considerably clarified both the phrasing and ideas of the article. Grants from the Emil Aaltonen Foundation and the Academy of Finland are gratefully acknowledged.

References

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

Ambuel, B. & Temple, S. A. 1983: Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. — Ecology 64: 1057—1068.

Aspi, J. & Helle, P. 1984: Ecological succession: convergence and turnover rate of communities. — Luonnon Tutkija 88:186—193. (In Finnish with English summary)

Blouin, M. S. & Connor, E. F. 1985: Is there a best shape for nature reserves? — Biol. Conserv. 32:277—288.

Butcher, G. S., Niering, W. A., Barry, W. J. & Goodwin, R. G. 1981: Equilibrium biogeography and the size of nature reserves: An avian case study. — Oecologia (Berl.) 49:29—37.

Diamond, J. M. 1978: Critical areas for maintaining viable populations of species. — In: Holdgate, M. W. & Woodman, M. J. (eds.), The breakdown and restoration of ecosystems, Plenum Press, N.Y., pp. 27—40.

Diamond, J. M. & May, R. M. 1976: Island biogeography and the design of natural reserves. — In: May, R. M. (ed.), Theoretical ecology, Principles and applications, Blackwell, Oxford, pp. 163—186.

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

Haila, Y., Järvinen, O. & Väisänen, R. A. 1979: Effect of mainland population changes on the terrestrial bird fauna of a northern island. — Ornis Scand. 10:48—55.

Haila, Y. 1986: North European land birds in forest fragments: Evidence for area effects? — In: Verner, J., Morrison, M. L. & Ralph, C. J. (eds.), Modeling habitat relationships of terrestrial vertebrates. Univ. of Wisconsin Press, Madison (in press).

Helle, P. 1985a: Effects of forest regeneration on the structure of bird communities in northern Finland. — Holarct. Ecol. 8:120—132.

—"— 1985b: Effects of forest fragmentation on bird densities in northern boreal forests. — Ornis Fennica 62:35—41

Helle, P. & Mönkkönen, M. 1985a: On the forest bird fauna of the Oulanka National Park, northern Finland. — Aureola 10:21—29, 31. (In Finnish with English summary)

—"— 1985b: Measuring turnover rates in secondary succession in European forest bird communities. — Ornis Scand. 16:173—180.

Horn, H. S. 1974: The ecology of secondary succession. — Ann. Rev. Ecol. Syst. 5:23—37.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98:785—800.

Järvinen, O. 1978: Are northern bird communities saturated? — Anser, Suppl. 3: 112—116. (In Swedish with English summary)

—"— 1982: Conservation of endangered plant populations: single large or several small reserves? — Oikos 38:301—307.

Järvinen, O. & Väisänen, R. A. 1976: Species diversity of Finnish birds, II: Biotopes at the transition between taiga and tundra. — Acta Zool. Fennica 145:1—35.

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

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

—"— 1983: Correction coefficients for line transect censuses of breeding birds. — Ornis Fennica 60:97—104.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945—1975. — Silva Fennica 11:284—294. (In Finnish with English summary)

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

Kuusela, K. 1978: Forest resources and ownership in Finland 1971—76. — Comm. Inst. Forest. Fenn. 93:1—107. (In Finnish with English summary)

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

May, R. M. 1975: Island biogeography and the design of wild life preserves. — Nature (London) 254: 177—178.

Mela, M. 1975: Oulangan kansallispuiston ja sen lähiympäristön linnusto vuosina 1967—1973. — Unpubl. M.Sc. Thesis, Dept. Zoology, Univ. Oulu.

Mikola, P. 1980: Suomen Sampo. — In: Mikola, P. (ed.), Metsät. Suomen Luonto 2, Kirjayhtymä, Helsinki, pp. 275—307. (In Finnish)

Siivonen, L. 1978: Outstanding features of the mammalian and avian fauna of Kuusamo. — Acta Univ. Ouluensis A 68, Biol. 4:107—119. (In Finnish with English summary)

Simberloff, D. S. & Abele, L. G. 1976: Refuge design and

island biogeographic theory: effects of fragmentation. — Am. Nat. 120:41—50.
Söyrinki, N., Salmela, R. & Suvanto, J. 1977: The forest and mire vegetation of the Oulanka National Park, Northern Finland. — Acta Forest. Fenn. 154:1—50. (In Finnish with English summary)
Väisänen, R. A. 1983: Long-term population changes of the most abundant north Finnish land birds during the past 40 years. — Aureola 8:58—65. (In Finnish with English summary)
—"— 1984: Population changes of land birds in Finland in 1978—84. — Lintumies 19:134—153. (In Finnish with English summary)
Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How do large-scale, human-caused habitat alterations translate to the scale of local bird populations in boreal forests? — Ornis Scand. (in press)
Voous, K. H. 1960: Atlas of European birds. — Nelson, London.
Wiens, J. A. 1981: Scale problems in avian censusing. — Stud. Avian Biol. 6:513—521.

Received 10.X.1985
Printed 22.IV.1986