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Population fluctuations in two northern land bird communities: effects of habitat, migration strategy and nest-site

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Year-to-year variation in the density of breeding land birds was studied in an alpine heath and mountain birch forest area in northern Finnish Lapland during eight years (1979–1986) using the line transect method. In the alpine heath *Anthus pratensis* was the most numerous species each year. In the birch forest the dominant species was one of the following three species: *Phylloscopus trochilus*, *Carduelis flammea* or *Fringilla montifringilla*. Of the six most common alpine species only three showed a trend toward increasing density during the study period, but of the 14 most common forest species, 13 showed a trend toward increase. In the alpine heath the numbers of *A. pratensis* and *Plectrophenax nivalis* varied more than could be explained by chance. In the birch forest the same was true for *C. flammea* and *F. montifringilla*. Especially in the alpine heath the populations of the most common species fluctuated in parallel annually. Species of similar migration strategy (e.g. the long-distance migrants) did not, however, show similar fluctuation patterns, though ground-nesting species did fluctuate in parallel, the synchronizing factor possibly being mustelid predation.

1. Introduction

In northern Fennoscandia the fluctuations in bird populations over several years in one restricted area have been studied in few sites (e.g. Helle 1986, Virkkala 1989, 1991). Studies have also compared the populations of large areas at different times (e.g. O. Järvinen & Väisänen 1977a). Good examples of long-term studies are the 20-year censuses in Ammarnäs, Swedish Lapland (Enemar et al. 1984, Svensson et al. 1984). The habitats in Ammarnäs are quite similar to habitats in our study area in Finnish Lapland, and the data in Ammarnäs serve as a valuable base for comparison.

Using the line transect method (see O. Järvinen & Väisänen 1976) we censused bird communities in the birch forest and alpine heath in the Malla Nature Reserve in north-western Finland during eight years. These censuses make the bird community of Malla one of the best known of all the nature protection areas in Finland. In this paper we examine community structure and population fluctuations of forest and alpine birds and try to answer three specific questions: 1) Is it possible to group species according to common

fluctuation patterns as Enemar et al. (1984) did? 2) Are population fluctuations similar in birch forest and alpine heath? 3) Are there differences in fluctuation patterns between ground-nesting and tree-nesting species?

2. Study area, material and methods

The Malla Nature Reserve is the oldest Finnish nature protection area. It was established in 1916. The main reason for its establishment was the protection of its unique flora, but also its fauna, including birds, is valuable. The Malla Reserve is situated in NW Finnish Lapland (about 69°05'N, 20°40'E; about 40 km from the Arctic Ocean), in the mountain range which lies mainly in Norway and Sweden. Limestone makes the soil and vegetation of Malla rich.

The Malla Reserve lies between 475 and 960 m above sea level. Because of its altitude and northern location, the region is one of the coldest in Finland, mean temperature in July being +10.6°C and in January −14.1°C. The region belongs to the orohemiarctic vegetation zone of Fennoscandia (Ahti et al. 1968). The vegetation of the lower parts of Malla is mountain birch forest, which alternates with open alpine heath at an altitude of 600 m (A. Järvinen & Pietiäinen 1982). In the birch forest zone are also open peatlands, and parts of the heath zone are boulder fields. We measured the area of the main habitats with a planimeter using maps and aerial photographs (Table 1).

The birds of the Malla Reserve were censused during eight years (1979–86) using the line transect method (O. Järvinen & Väisänen 1976). Transect lengths were 26.4 km (6 transects), 28.1 km (6), 24.0 km (5), 34.9 km (7), 25.0 km (5), 25.0 km (5), 25.0 km (5) and 25.0 km (5) in 1979–86, respectively. The total length of the 44 transects was 210.4 km. Censuses were made only in good weather to minimize the effect of weather on the results.

The densities of birds were estimated from survey belt data (O. Järvinen & Väisänen 1977b, 1983). Because of the different habitat distribution of Malla transects compared to the transect data from which O. Järvinen & Väisänen (1983) calculated their coefficients, we used mainly correction coefficients (K, see Table 2) calculated from the Malla data. If these data were few we combined them with the data of O. Järvinen & Väisänen (1983) and/or with the unpublished data collected in the line transect censuses of other Finnish nature protection areas (A. Rajasärkkä, M. Vickholm & E. Virolainen, unpubl.). In a few cases only the data of O. Järvinen &Väisänen (1983) were used.

In both birch forest and alpine heath, the significance of the density fluctuations of each species was tested with the chi-square test. If the number of observations was too small for yearly testing, we combined the data into two-year periods. Other statistical methods are explained in Zar (1984).

Using cluster analysis, Enemar et al. (1984) put forward the hypothesis that in mountain birch forest birds with similar migratory strategies tend to have similar fluctuation patterns. They divided the most common forest species into three categories: A) *Turdus philomelos*, *Phylloscopus trochilus*, *Sylvia borin*, *Ficedula hypoleuca*, *Phoenicurus phoenicurus* and *Anthus trivialis*; B) *Turdus pilaris*, *Turdus iliacus*, *Fringilla montifringilla* and *Carduelis flammea* and C) *Prunella modularis*, *Emberiza schoeniclus* and *Luscinia svecica*. With the exception of *T. philomelos*, group A consists of long-distance migrants. All species except *T. iliacus* of group B are short-distance irruptive species. Except *L. svecica*, birds in group C are short-distance non-irruptive species.

We tested the validity of this classification in our forest material using a robust statistical technique, Kendall's coefficient of concordance (W),

Table 1. Main habitats, Malla Nature Reserve.

	Area (ha)	%
Birch forest	1277.6	44.6
Open peatland	276.0	9.6
Alpine heath	943.4	33.0
Boulder field	365.0	12.8
Total land area	2862.0	100.0
Water	68.0	
Total area	2930.0	

Table 2. Correction coefficients (K) of each species. MB and SB are numbers of main belt (MB) and survey belt (SB) observations for calculating K coefficients. Stars indicate statistical significance of difference between our and O. Järvinen & Väisänen's (1983) coefficients.

	MB	SB	K	
Buteo lagopus	3	71	0.854	
Falco columbarius	5	26	4.051	
Lagopus lagopus	35	109	7.042	**
Lagopus mutus	20	68	6.393	
Haematopus ostralegus	1	23	0.879	
Charadrius morinellus	13	29	10.289	
Pluvialis apricaria	9	82	2.259	
Philomachus pugnax	53	209	5.587	
Gallinago gallinago	48	457	2.138	
Scolopax rusticola	36	54	16.906	
Tringa totanus	6	71	1.727	
Tringa nebularia	17	242	1.431	
Tringa glareola	168	961	3.655	
Actitis hypoleucos	14	71	4.160	
Stercorarius longicaudus	8	82	2.001	
Cuculus canorus	33	781	0.855	
Surnia ulula	5	16	6.837	
Asio flammeus	9	50	3.778	
Picoides tridactylus	36	109	7.265	
Delichon urbica	99	480	4.368	
Anthus pratensis	141	729	4.076	*
Motacilla flava	409	1076	8.507	
Motacilla alba	54	179	6.574	
Cinclus cinclus	1	4	5.359	
Prunella modularis	8	51	3.271	
Luscinia svecica	73	482	3.153	***
Phoenicurus phoenicurus	8	52	3.205	
Saxicola rubetra	61	283	4.572	
Oenanthe oenanthe	47	213	4.688	*
Turdus torquatus	5	52	1.972	
Turdus pilaris	16	72	4.723	
Turdus philomelus	63	703	1.834	
Turdus iliacus	32	339	1.935	***
Acrocephalus schoenobaenus	22	111	4.183	
Phylloscopus trochilus	109	852	2.646	
Ficedula hypoleuca	73	352	4.388	
Parus montanus	142	409	7.681	
Parus cinctus	33	62	12.643	
Pica pica	15	96	3.258	
Corvus corone	23	420	1.176	
Corvus corax	5	221	0.455	
Fringilla montifringilla	99	721	2.848	
Carduelis spinus	80	719	2.291	
Carduelis flammea	111	589	3.966	**
Pyrrhula pyrrhula	23	158	3.026	
Calcarius lapponicus	178	591	6.548	
Plectrophenax nivalis	16	73	4.654	
Emberiza pusilla	4	21	4.011	
Emberiza schoeniclus	23	112	4.343	*

partly because our data covered eight study years compared to 20 years in Enemar et al. (1984). Because the density of *F. hypoleuca* and *P. phoenicurus* was very low in the line transect data (natural nest-holes are few in the local mountain birch forests), we used the numbers of breeding pairs of these species in a nearby (5 km distant) nest-box area (see A. Järvinen 1983). Moreover, since *T. philomelos* is rare and *S. borin* and *A. trivialis* are totally absent, in our material group A consists of only three species.

To determine whether nest-site affects fluctuation pattern we further classified our forest and heath species into tree-nesting species (*T. pilaris*, *Corvus corone cornix*, *F. montifringilla* and *C. flammea*) and ground-nesting species (forest: *Lagopus lagopus*, *Anthus pratensis*, *L. svecica*, *P. trochilus* and *E. schoeniclus*; heath: *Lagopus mutus*, *Pluvialis apricaria*, *A. pratensis*, *L. svecica*, *Oenanthe oenanthe* and *Plectrophenax nivalis*).

3. Results

Appendices 1 and 2 show the densities of birds in the birch forest and alpine heath in 1979–1986. In general, the years fall into two groups: birch forest high-density years were (1979), 1981 and 1985–86, and low-density years 1980 and 1982–84. In alpine heath the corresponding groups were 1981–83 and 1986, and 1979–80 and 1984–85. Of the 14 most common forest species, 13 showed positive (increasing) density trends during the study period (binomial test, 2-tailed $P = 0.002$), whereas of the six most common alpine species, only three showed positive trends ($P = 0.63$).

In the alpine heath each year the most numerous species was *A. pratensis*. In contrast, in the birch forest the annually dominant species was either *P. trochilus* (1982–83, 1985), *C. flammea* (1980–81, 1986) or *F. montifringilla* (1979, 1984). Annually, both in the forest and heath the number of pairs/km^2 for most species fluctuated significantly (Table 3).

Birch forest showed more variability in the number of breeding pairs than expected according to the Poisson (random) distribution in *C. flammea* ($t = 14.564$, $df = 7$, $P < 0.001$) and *F.*

montifringilla (t = 3.621, df = 7, P = 0.009; Fig. 1). In the alpine heath (Fig. 2) the same was true for *A. pratensis* (t = 3.413, df = 7, P = 0.011) and *P. nivalis* (t = 3.249, df = 7, P = 0.014).

Among the six most common alpine species, there was close association in the annual number of breeding pairs (Kendall's coefficient of concordance, W = 0.598, P < 0.001; see also Table 4). In the seven most common forest species this association was less strong but also significant (W = 0.364, P = 0.013; see also Table 4). Between the total density of birds in birch forest and alpine heath there was no correlation (r_s = 0.357, n = 8, P = 0.34).

Long-distance migrants (category A in methods; 3 species; W = 0.27, P = 0.59), short-distance irruptive species (category B; 4 species; W = 0.26, P = 0.30) or short-distance non-irruptive species (category C; 3 species; W = 0.22, P = 0.70) did not fluctuate in synchrony. Birds nesting in trees (*T. pilaris*, *C. corone*, *F. montifringilla* and *C. flammea*) did not fluctuate in parallel (W = 0.09, P = 0.92), although birds nesting on the

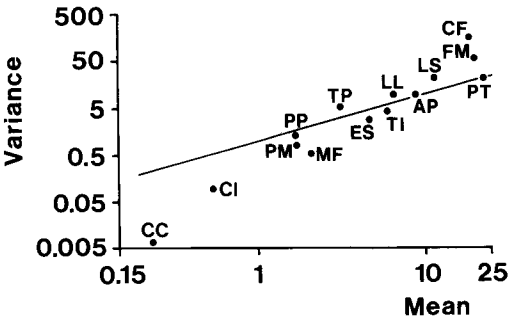

Fig. 1. Poisson test of randomness in variability of annual density of forest birds in Malla Nature Reserve 1979–86. Straight line showing expected relationship between mean population density (pairs/km²) and its variance in hypothetical, randomly fluctuating populations. Both scales logarithmic. Key to species: CC = *C. canorus*, CI = *C. corone*, PP = *P. phoenicurus*, PM = *P. modularis*, MF = *M. flava*, TP = *T. pilaris*, ES = *E. schoeniclus*, TI = *T. iliacus*, LL = *L. lagopus*, AP = *A. pratensis*, LS = *L. svecica*, CF = *C. flammea*, FM = *F. montifringilla* and PT = *P. trochilus*. Points for *C. flammea* and *F. montifringilla* deviate significantly from the line, i.e. their densities vary annually more than expected according to a random process.

Table 3. Significance of annual density fluctuations of birds in Malla Nature Reserve 1979–86. n = number of observations. Number of years for χ^2-tests usually eight. However, if n is too small for χ^2-test, data for two successive years combined and species name denoted by asterisk.

Species	Birch forest n	χ^2	P	Alpine heath n	χ^2	P
Buteo lagopus *	–	–	–	29	10.76	0.013
Lagopus lagopus	91	15.81	0.027	–	–	–
Lagopus mutus	–	–	–	43	6.23	0.513
Pluvialis apricaria	–	–	–	75	11.94	0.103
Gallinago gallinago *	19	2.51	0.474	–	–	–
Tringa totanus	–	–	–	27	1.84	0.605
Actitis hypoleucos *	25	1.69	0.640	–	–	–
Cuculus canorus *	29	1.46	0.692	–	–	–
Anthus pratensis	209	23.14	0.002	520	65.02	<0.001
Motacilla flava *	24	0.78	0.854	–	–	–
Prunella modularis	51	23.10	0.002	–	–	–
Luscinia svecica	350	54.59	<0.001	134	36.96	<0.001
Phoenicurus phoenicurus	52	20.63	0.004	–	–	–
Oenanthe oenanthe	–	–	–	205	20.83	0.004
Turdus torquatus	–	–	–	29	10.97	0.140
Turdus pilaris	72	20.33	0.005	–	–	–
Turdus iliacus	294	36.56	<0.001	–	–	–
Phylloscopus trochilus	820	33.93	<0.001	–	–	–
Corvus corone	60	20.30	0.005	–	–	–
Corvus corax	–	–	–	40	5.68	0.578
Fringilla montifringilla	696	102.17	<0.001	–	–	–
Carduelis flammea	463	180.08	<0.001	126	56.18	<0.001
Plectrophenax nivalis *	–	–	–	73	36.44	<0.001
Emberiza schoeniclus	109	13.95	0.052	–	–	–

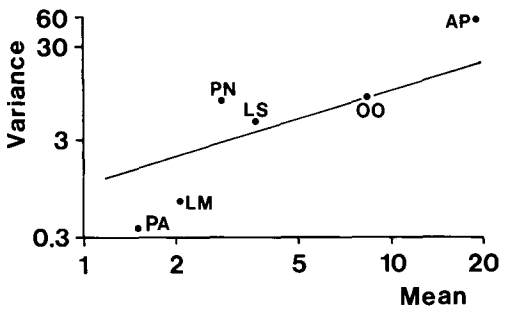

Fig. 2. Poisson test of randomness in variability of annual density (pairs/km²) of alpine birds in Malla Nature Reserve in 1979–86. For legend, see Fig. 1. Key to species: PA = *P. apricaria*, LM = *L. mutus*, PN = *P. nivalis*, LS = *L. svecica*, OO = *O. oenanthe* and AP = *A. pratensis*. Points for *A. pratensis* and *P. nivalis* deviate significantly from the line, i.e. their densities vary annually more than expected according to a random process.

ground did (in forest: *L. lagopus*, *A. pratensis*, *L. svecica*, *P. trochilus* and *E. schoeniclus*; on heath: *L. mutus*, *P. apricaria*, *A. pratensis*, *L. svecica*, *O. oenanthe* and *P. nivalis*; W = 0.262, P = 0.005).

4. Discussion

In the alpine heath the amplitude of annual variation in the total density of birds was more pronounced than in birch forest (coefficient of variation, CV 40% vs. 22%). However, when density fluctuations of the most common species are treated separately in each habitat, and the species-specific CV-values are averaged, the mean of these means is almost the same in the two habitats: 52% (6 species) for alpine heath and 47% (14 species) for birch forest. Thus, especially in the less harsh birch forest, bird species do not fluctuate synchronously, which dampens total density variation in the habitat (compensatory density fluctuations between species; cf. Table 4). In the two habitats total community dynamics was not synchronous. Habitat-linked differences are not uncommon even between nearby areas (e.g. Wiens 1989: 169), and in Malla this was possibly partly due to differing composition of the breeding communities (Appendices 1 and 2).

In general, species with high densities tend to be more variable than those with low densities

Table 4. Spearman's rank correlation coefficients in density among most common forest and heath species in Malla Nature Reserve, 1979–86.

Birch forest

	Llag	Lsve	Tili	Plus	Fmon	Cfla
Lagopus lagopus	–					
Luscinia svecica	0.429	–				
Turdus iliacus	0.262	0.119	–			
Phylloscopus trochilus	0.476	0.524	0.762	–		
Fringilla montifringilla	–0.476	–0.524	0.500	0.191	–	
Carduelis flammea	0.619	–0.143	0.214	0.238	0.143	–
Emberiza schoeniclus	0.405	0.381	0.500	0.381	0.119	0.286
Mean r_S	0.258					

Alpine heath

	Lmut	Papr	Apra	Lsve	Ooen
Lagopus mutus	–				
Pluvialis apricaria	0.181	–			
Anthus pratensis	0.743	0.443	–		
Luscinia svecica	0.755	0.012	0.595	–	
Oenanthe oenanthe	0.695	0.407	0.429	0.691	–
Plectrophenax nivalis	0.850	0.036	0.738	0.786	0.405
Mean r_S	0.518				

(e.g. Taylor & Woiwod 1982), and this pattern seems to hold in several bird communities (Svensson et al. 1984, Holmes et al. 1986, present study Figs. 1 and 2). In birch forest *C. flammea* and *F. montifringilla* fluctuated more than expected due to chance (Fig. 1) probably due to non-random variation in environmental conditions (e.g. seed crops of mountain birch). During the study period (except for 1983) Kilpisjärvi Biological Station (K. Laine, pers. comm.) monitored the size of the birch-seed crop in the area (no. of seeds/m^2). *C. flammea* density correlated with birch-seed crop, but possibly due to the small number of years (n = 7) the correlation coefficient was not significant (r_s = 0.643, P = 0.12; see also Enemar et al. 1984). During the latter half of our study period the fluctuations of both bird species in the whole of Finland (Väisänen et al. 1989) are similar to those of Malla.

The reasons for the fluctuations in *F. montifringilla* at Malla Nature Reserve are not known. In mountain birch forest in Swedish Lapland (Ammarnäs, 66°N) the density of *F. montifringilla* clearly increased during an *Epirrita autumnata* caterpillar outbreak (Enemar et. al. 1984). In NW Finnish Lapland *Epirrita* outbreaks are unknown. According to mist-netting data collected at Kilpisjärvi, *F. montifringilla* produced very few young in some years (e.g. 1981; Hildén et al. 1982), but the reasons for this poor success are unknown. The population size of *F. montifringilla* may depend on birch-seed crop-size (Mikkonen 1983). However, at Malla there was no correlation between the density of *F. montifringilla* and birch-seed crop-size (r_s = 0.036, P = 0.94).

Possibly due to territorial competition some species tended to fluctuate less than expected (points below the straight line in Fig. 1, notably *Cuculus canorus* and *C. corone*), but these deviations from the 'random' line were not significant. *C. canorus* and *C. corone* are relatively large species, and for this reason alone, their populations may fluctuate less than those of small species (cf. also *P. apricaria* and *L. mutus* in Fig. 2).

In alpine heath *A. pratensis* and *P. nivalis* showed pronounced annual density variations (Fig. 2) possibly connected with annual snow conditions and the weather in general. These same species seemed to fluctuate greatly also in an alpine area in Swedish Lapland (Svensson et al. 1984). The population fluctuations of *A. pratensis* in northern Finland during 1984–86 (Väisänen et al. 1989) are similar to those of Malla.

In Ammarnäs, about 350 km south of the present study area, the two most numerous forest species were also *P. trochilus* and *F. montifringilla*, but in Ammarnäs the former clearly outnumbered the latter (*P. trochilus* comprising about 40% of the bird community), and during 20 years it was in 19 the most common species (Enemar et al. 1984; cf. our Appendix 1). Another clear difference between Malla and Ammarnäs is the high density of *L. svecica* in Malla.

Our results did not support the suggestion of Enemar et al. (1984) that along the common migratory route and in the common wintering area mortality has similar effects on birds with the same migratory habits and is of great importance in determining the size of breeding bird populations in different strategy groups. Since our study area lies about 350 km north of Ammarnäs, the reason that in Finnish Lapland birds with common migratory habits do not fluctuate in parallel may be its harsher breeding conditions. Thus, different species — breeding at different times in different microhabitats and using different nest sites — may have different numbers of nesting losses annually, an effect which may disturb the synchrony of population fluctuations.

In our material there seems to be a clear difference in the pattern of population fluctuation with respect to nest site. The explanation for the parallel fluctuations of ground-nesting species is probably simultaneous nesting losses due to predation. Ground-nesting species usually suffer more from predation than do species nesting higher in the vegetation (Wiens 1989: 97, A. Järvinen 1990).

The further north one goes in Fennoscandia, the steeper and more synchronous the population fluctuations of small rodents become (Hansson & Henttonen 1985). When small rodents are scarce in NW Finnish Lapland, birds breeding in accessible sites and/or in open habitats suffer from heavy mustelid predation (A. Järvinen 1990). In Malla five common alpine bird species

correlated with small rodent density, whereas between seven common forest birds and small rodents there was no corresponding correlation. In Malla the main factor synchronizing the population fluctuations of small rodents and some alpine bird species seems to be mustelid predation.

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Selostus: **Maalintujen kannanvaihtelut Mallan luonnonpuistossa: biotoopin, muuttostrategian ja pesäpaikan vaikutus**

Enontekiön Lapissa sijaitsevan Mallan luonnonpuiston linnuston tiheyksiä arvioitiin linjalaskentamenetelmällä kahdeksan vuoden ajan (1979–1986). Maalinnuston kannanvaihteluita seurattiin kahdella eri biotoopilla: tunturikoivikossa ja paljakalla. Paljakan runsain laji oli kaikkina tutkimusvuosina niittykirvinen. Koivikossa runsain laji oli vuodesta riippuen joko pajulintu, urpiainen tai järripeippo. Tutkimusajanjakson aikana paljakan kuudesta runsaimmasta lajista kolme runsastui. Vastaavasti koivikon 14 yleisimmästä lajista peräti 13 runsastui. Paljakalla niittykirvisen ja pulmusen määrät vaihtelivat enemmän kuin voidaan olettaa pelkästä sattumasta johtuvaksi. Vastaavanlaisia koivikon lajeja olivat urpiainen ja järripeippo. Varsinkin paljakalla yleisimpien lajien vuosittaiset runsauden vaihtelut olivat keskenään hyvin samansuuntaisia. Samanlaisen muuttostrategian lajit (esim. pitkänmatkan muuttajat) eivät vaihdelleet samalla tavalla. Maassa pesivät lajit sitä vastoin vaihtelivat hyvin samankaltaisesti. Näiden lajien kannanvaihteluita synkronoivat mitä ilmeisimmin pikkupedot kärppä ja lumikko.

References

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

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.

Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — Oecologia (Berl.) 67:394–402.

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

Hildén, O., Järvinen, A., Lehtonen, L. & Soikkeli, M. 1982: Breeding success of Finnish birds in the bad summer of 1981. — Ornis Fennica 59:20–31.

Holmes, R. T., Sherry, T. W. & Sturges, F. W. 1986: Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. — Ecol. Monogr. 56:201–220.

Järvinen, A. 1983: Breeding strategies of hole nesting passerines in northern Lapland. — Ann. Zool. Fennici 20:129–149.

— 1990: Changes in the abundance of birds in relation to small rodent density and predation rate in Finnish Lapland. — Bird Study 37: 36–39.

Järvinen, A. & Pietiäinen, H. 1982: The breeding land bird community of the Malla nature reserve, NW Finnish Lapland. — Memoranda Soc. Fauna Flora Fennica 58:21–26.

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

— 1977a: Recent quantitative changes in the populations of Finnish land birds. — Polish Ecol. Stud. 3(4):177–188.

— 1977b: Constants and formulae for analysing line transect data. — Mimeograph, University of Helsinki, Department of Zoology. 10 pp.

— 1983: Correction coefficients for line transect censuses. — Ornis Fennica 60:97–104.

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

Svensson, S., Carlsson, U. T. & Liljedahl, G. 1984: Structure and dynamics of an alpine bird community, a 20-year study. — Ann. Zool. Fennici 21:339–350.

Taylor, L. R. & Woiwod, I. P. 1982: Comparative synoptic dynamics. I. Relationships between inter- and intraspesific spatial and temporal variance / mean population parameter. — J. Animal Ecol. 51:879–906.

Virkkala, R. 1989: Short-term fluctuations of bird communities and populations in virgin and managed forests in Northern Finland. — Ann. Zool. Fennici 26:277–285.

— 1991: Annual variation of northern Finnish forest and fen bird assemblages in relation to spatial scale. — Ornis Fennica 68:193–203.

Väisänen, R. A., Hildén, O. & Pulliainen, E. 1989: Suomen pesivä maalinnusto 1979–88 piste- ja linjalaskentojen valossa. (Summary: Monitoring of Finnish land bird populations in 1979–88.) — Lintumies 24:60–24.

Wiens, J. A. 1989: The ecology of bird communities 2. Processes and variations. — Cambridge Univ. Press, Cambridge. 316 pp.

Zar, J. H. 1984: Biostatistical analysis. — Prentice-Hall, New Jersey. 718 pp.

Appendix 1. Annual densities (D, pairs/km²) of birds in mountain birch forest in Malla Nature Reserve 1979–1986 and mean densities for entire study period. N = number of survey belt observations. Species in parenthesis do not breed in birch forest.

	1979		1980		1981		1982	
	D	N	D	N	D	N	D	N
Buteo lagopus	0.1	1			0.1	1	0.2	3
Falco columbarius	0.5	2			1.0	3	0.2	1
Lagopus lagopus	4.9	11	5.0	11	9.2	16	6.2	15
(Lagopus mutus)					0.5	1	0.4	1
(Haematopus ostralegus)								
Pluvialis apricaria	0.1	1	0.3	2			0.5	4
Gallinago gallinago	0.3	2			0.3	2	0.3	2
Scolopax rusticola			1.1	1				
Tringa totanus	0.4	4	0.1	1			0.4	4
Tringa nebularia	0.2	2						
Tringa glareola					0.3	1	0.2	1
Actitis hypoleucos	1.6	6	0.5	2			1.2	5
Stercorarius longicaudus							0.1	1
Cuculus canorus	0.3	5	0.2	3	0.1	1	0.2	4
Surnia ulula							0.4	1
Asio flammeus	0.2	1					0.2	1
Picoides tridactylus							0.9	2
Delichon urbica								
Anthus pratensis	4.1	16	7.1	27	9.9	30	8.9	37
Motacilla flava	1.1	2	2.2	4	1.4	2	2.5	5
Motacilla alba								
Cinclus cinclus								
Prunella modularis	0.2	1	1.5	7	4.0	15	1.0	5
Luscinia svecica	6.9	35	6.3	31	7.7	30	13.9	75
Phoenicurus phoenicurus	0.2	1	1.4	7	3.4	13	1.3	7
Saxicola rubetra								
Oenanthe oenanthe	0.3	1			0.4	1	0.8	3
Turdus torquatus	0.2	2	0.3	2	0.2	1	0.2	2
Turdus pilaris	0.3	1	3.7	12	3.1	8	1.9	7
Turdus philomelos			0.1	1			0.1	1
Turdus iliacus	6.9	47	3.0	24	9.8	62	4.6	40
Acrocephalus scoenobaenus			0.3	1				
Phylloscopus trochilus	19.1	115	17.2	101	26.7	124	17.3	111
Ficedula hypoleuca					1.8	5	0.5	2
Parus montanus	0.5	1			1.9	3		
Parus cinctus								
Pica pica							0.2	1
Corvus corone	0.4	6	0.2	3	0.4	4	1.1	16
Corvus corax	0.0	1	0.1	4	0.1	4	0.1	3
Fringilla montifringilla	33.5	187	14.7	80	24.1	104	11.2	67
Carduelis spinus								
Carduelis flammea	20.7	83	18.9	74	36.4	113	5.8	25
Pyrrhula pyrrhula	0.2	1						
Calcarius lapponicus					0.5	1		
Emberiza pusilla								
Emberiza schoeniclus	7.6	28	2.5	9	4.2	12	4.3	17
Total	110.8	563	86.7	407	147.5	557	87.1	469
Number of species	27		22		25		32	
Transect length	15.9		15.5		12.3		17.0	

Appendix 1. (continued)

	1983		1984		1985		1986		Total	
	D	N	D	N	D	N	D	N	D	N
Buteo lagopus	0.3	3	0.2	2			0.1	1	0.1	11
Falco columbarius							0.4	1	0.3	7
Lagopus lagopus	3.0	4	4.2	6	7.8	11	12.7	17	7.0	91
(Lagopus mutus)			1.3	2	0.6	1	0.7	1	0.4	6
(Haematopus ostralegus)							0.1	1	0.0	1
Pluvialis apricaria									0.2	7
Gallinago gallinago	0.7	3	0.6	3	0.6	3	0.5	2	0.4	17
Scolopax rusticola							1.8	1	0.3	2
Tringa totanus	0.2	1	0.2	1	0.3	2	0.2	1	0.2	14
Tringa nebularia									0.0	2
Tringa glareola									0.1	2
Actitis hypoleucos	1.3	3	1.7	4	0.4	1	1.8	4	1.0	25
Stercorarius longicaudus									0.0	1
Cuculus canorus	0.2	2	0.3	4	0.2	2	0.3	3	0.2	24
Surnia ulula									0.1	1
Asio flammeus									0.1	2
Picoides tridactylus									0.1	2
Delichon urbica	0.5	1					0.9	2	0.0	3
Anthus pratensis	12.9	30	9.0	20	13.2	32	6.5	15	8.6	207
Motacilla flava	2.7	3	1.7	2	3.4	4	1.8	2	2.1	24
Motacilla alba							0.7	1	0.1	1
Cinclus cinclus							0.6	1	0.1	1
Prunella modularis	2.4	7	2.0	6	1.3	4	1.4	4	1.6	49
Luscinia svecica	13.3	40	10.4	33	14.3	45	20.5	61	11.0	350
Phoenicurus phoenicurus	2.0	6	1.9	6	0.3	1	3.1	9	1.6	50
Saxicola rubetra					0.5	1			0.0	1
Oenanthe oenanthe					0.5	1			0.4	6
Turdus torquatus	0.2	1	0.4	2	1.0	5	0.4	2	0.3	17
Turdus pilaris	5.0	10	0.9	2	7.6	16	3.0	6	2.9	62
Turdus philomelos	0.2	1	0.2	1	0.2	1	0.4	2	0.1	7
Turdus iliacus	6.1	30	4.8	25	7.6	39	5.6	27	5.9	294
Acrocephalus scoenobaenus									0.0	1
Phylloscopus trochilus	21.4	77	23.3	88	30.2	113	25.6	91	21.8	820
Ficedula hypoleuca	0.9	2	0.9	2	1.3	3			0.6	14
Parus montanus					0.8	1	2.5	3	0.6	8
Parus cinctus	1.3	1							0.1	1
Pica pica									0.0	1
Corvus corone	0.2	2	0.6	5	0.6	5	0.8	6	0.6	47
Corvus corax	0.1	2	0.1	2	0.2	5	0.1	2	0.1	23
Fringilla montifringilla	20.4	68	26.2	92	15.5	54	13.3	44	19.9	696
Carduelis spinus					0.9	4			0.1	4
Carduelis flammea	5.4	13	12.7	32	12.0	30	39.2	93	18.5	463
Pyrrhula pyrrhula									0.0	1
Calcarius lapponicus									0.1	1
Emberiza pusilla							0.4	1	0.0	1
Emberiza schoeniclus	3.2	7	3.9	9	6.6	15	5.5	12	4.8	109
Total	103.9	317	107.5	349	127.9	399	150.9	416	112.6	3477
Number of species	24		23		26		30		46	
Transect length	9.5		10.0		9.9		9.4		99.5	

Appendix 2. Annual densities (D, pairs/km²) of birds in alpine heath in Malla Nature Reserve 1979–1986 and mean densities for entire study period. N = number of survey belt observations. Species in parentheses usually breed in mountain birch forest, not on alpine heath.

	1979		1980		1981		1982	
	D	N	D	N	D	N	D	N
Buteo lagopus	0.2	2			0.1	1	0.2	5
(Falco columbarius)								
(Lagopus lagopus)					2.4	4	0.8	2
Lagopus mutus	1.2	2	2.0	4	2.2	4	3.6	10
Charadrius morinellus					0.9	1	2.3	4
Pluvialis apricaria	1.7	8	1.3	7	1.4	7	2.8	22
Philomachus pugnax							0.3	1
Gallinago gallinago					0.4	2		
Tringa totanus			0.1	1	0.1	1	0.5	5
Tringa glareola							0.2	1
Stercorarius longicaudus			0.2	1	0.3	2		
Cuculus canorus	0.1	1	0.1	1			0.0	1
Delichon urbica			0.3	1				
Anthus pratensis	17.1	44	14.6	45	33.8	97	26.9	118
Motacilla alba					0.6	1	0.4	1
(Prunella modularis)								
Luscinia svecica	1.2	4	1.3	5	5.7	21	6.5	37
(Phoenicurus phoenicurus)								
Oenanthe oenanthe	4.5	10	6.3	17	10.0	25	12.8	49
Turdus torquatus			0.2	1	0.2	1	0.6	5
(Turdus pilaris)			0.4	1	0.8	2	1.6	6
(Turdus iliacus)	0.7	4	0.2	1	1.7	10	1.5	14
(Phylloscopus trochilus)	0.8	3			2.0	9	0.4	3
(Corvus corone)	0.2	2					0.3	5
Corvus corax							0.1	4
(Fringilla montifringilla)	0.8	3			1.2	5	0.5	3
Carduelis flammea	5.3	14	1.9	6	9.5	28	4.2	19
Calcarius lapponicus							0.4	1
Plectrophenax nivalis	0.9	2	1.5	4	3.6	9	8.3	32
Emberiza schoeniclus							0.2	1
Total	34.7	99	30.4	95	76.9	230	75.4	349
Number of species	13		14		19		24	
Transect length	10.5		12.6		11.7		17.9	

Appendix 2. (continued)

	1983		1984		1985		1986		Total	
	D	N	D	N	D	N	D	N	D	N
Buteo lagopus	0.3	5	0.2	3	0.1	2			0.1	18
(Falco columbarius)			0.3	1					0.0	1
(Lagopus lagopus)							1.9	4	0.6	10
Lagopus mutus	2.5	6	1.8	4	0.9	2	2.2	5	2.1	37
Charadrius morinellus									0.5	5
Pluvialis apricaria	1.3	9	1.6	10	1.1	7	0.8	5	1.5	75
Philomachus pugnax									0.1	1
Gallinago gallinago									0.0	2
Tringa totanus	0.1	1	0.1	1	0.2	2	0.2	2	0.2	13
Tringa glareola					0.3	1			0.1	2
Stercorarius longicaudus	0.1	1					0.3	2	0.1	6
Cuculus canorus			0.1	1			0.1	1	0.0	5
Delichon urbica			0.3	1			0.3	1	0.1	3
Anthus pratensis	17.6	67	14.3	49	13.0	45	15.4	55	19.1	520
Motacilla alba									0.1	2
(Prunella modularis)	0.4	2							0.1	2
Luscinia svecica	4.5	22	1.8	8	2.7	12	5.4	25	3.8	134
(Phoenicurus phoenicurus)			0.2	1			0.2	1	0.1	2
Oenanthe oenanthe	9.7	32	10.4	31	5.0	15	8.3	26	8.7	205
Turdus torquatus			0.1	1	0.4	3	0.1	1	0.2	12
(Turdus pilaris)			0.3	1					0.4	10
(Turdus iliacus)	0.6	5	0.1	1	0.8	6	0.5	4	0.8	45
(Phylloscopus trochilus)	0.2	1	0.6	3	0.8	4	1.6	9	0.8	32
(Corvus corone)			0.3	3	0.2	2	0.1	1	0.1	13
Corvus corax	0.1	4	0.1	4	0.1	2	0.1	3	0.1	17
(Fringilla montifringilla)	0.4	2	0.8	4	0.4	2	1.2	6	0.6	25
Carduelis flammea	1.0	4	1.1	4	5.3	19	8.7	32	4.5	126
Calcarius lapponicus	0.4	1	0.5	1	1.4	3			0.4	6
Plectrophenax nivalis	2.4	8			0.7	3	5.1	16	3.1	74
Emberiza schoeniclus									0.0	1
Total	41.6	170	35.0	132	33.4	130	52.5	199	48.5	1404
Number of species	16		20		17		19		30	
Transect length	15.5		14.0		14.1		14.6		110.9	