Ann. Zool. Fennici 30:43-54
Helsinki 31 March 1993

ISSN 0003-455X

Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest. A 12-year study

Olav Hogstad

Hogstad, O., University of Trondheim, The Museum, N-7004 Trondheim, Norway

Received 4 August 1992, accepted 18 January 1993

The breeding passerine bird community in a Norwegian spruce-dominated forest (c. 63°N) was studied in an area of one km^2 during the years 1960 and 1962–72. The number of territorial species varied annually between 22 and 33 (mean = 27, coefficient of variation $CV = 13\%$), and their combined density, the community density, from 142 to 195 territories/km^2 (mean = 170, $CV = 10\%$). About half of the territories each year were defended by the same five species. Twenty-one species were recorded every year, and their annual combined densities accounted for 88–99% of the overall community density. The other 13 species recorded in the community were absent in one or more years. These were all low-density species, with a maximum of three territories/km^2 recorded in any single year. The mean relative species turnover rate between two adjacent years was 0.15, $CV = 42\%$. The variation (CV) in population density of the different species was significantly negatively correlated ($r = -0.86$) with their average population density during the 12 years. Although some species showed some similarity in their fluctuation patterns, none showed a wholly similar pattern, indicating that the different species were influenced by different combinations of factors.

1. Introduction

Most bird populations and communities vary markedly from year to year. As a consequence there is no such thing as a "normal" or an "average" year (e.g. Wiens 1989). A short-term study based on one or a few years will therefore miss, among several factors, the duration and amplitude of variations in ecological systems. Long-term studies are therefore essential to track the factors that influence both the structure and dynamics of bird communities.

In this study, I report on a passerine community of a spruce-dominated forest habitat in the northern coniferous forest region. The study provides information about the variations in community density, species richness and density fluctuations of the different species. Since the

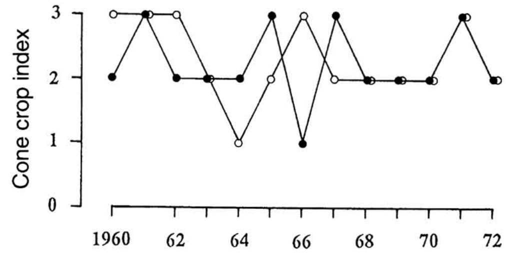

Fig. 1. The cone production of Norway spruce (filled circles) and Scots pine (2-years old cones; open circles) in Central Norway over the period 1960–1972. The crop index: 1 = very small, 2 = small, 3 = good.

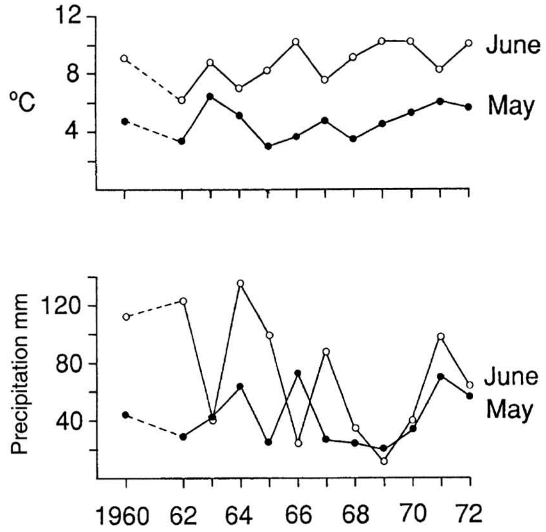

Fig. 2. Mean minimum temperature (above) and the amount of precipitation for May and June (below) in the Estenstad area during the years 1960, 1962–72.

study covers a 12-year period (1960, 1962–72), it is among the longest of bird community studies made in the boreal forest region.

2. Study area

The study was conducted in the Estenstad forest (63°25′N, 10°30′E), a part of a lowland coniferous forest area near Trondheim, Central Norway. The study area was about 1 km^2, most of it sloping north-westward from 385 to 195 m in altitude. The study area is bordered by a steep valley to the south, and elsewhere by *Sphagnum*-bogs and clear-felled areas. The study area itself consisted of about 90% woodland, 7% clear-felled areas with or without small trees present, and 3% bog. The forest was predominantly Norway spruce (*Picea abies*). Most of these trees were older than 60 years and 15–20 m in height. The remaining part consisted of scattered stands of Scots pine (*Pinus silvestris*), juniper (*Juniperus communis*), and of deciduous trees, mostly grey alder (*Alnus incana*) and birch (*Betula odorata*). The field layer was dominated by *Vaccinum myrtillus*, but *Trientalis europea*, *Anemone nemorosa*, *Pyrola* sp., *Deschampsia flexuosa* and ferns such as *Dryopteris linnaeana* and *D. phegopteris*, were also common.

Only small habitat changes occurred within the study area during the period 1960–1970. Although small successional changes did occur, even in the old forest stands in the Estenstad area, the most distinct annual change observed was the growth of deciduous saplings on the previously clearfelled areas. During the winter 1970–71, however, one area of about 100 × 100 m within the study plot was clear-felled, as were two smaller areas during the following winter. Two of these areas were bordered by bogs, the third adjoined an area previously clear-felled.

The cone crops of spruce and pine varied considerably during the study period (Fig. 1). However, the abundance of cones of spruce and of pine did not fluctuate synchronously (Spearman rank correlation coefficient $r_s = -0.23$, $n = 12$, ns).

Weather records for May and June recorded at a meteorological station situated about 10 km away from the study area showed that some variation in the weather pattern did occur during the study period (Fig. 2). The mean minimum temperature showed a slight increase during the study period (Pearson correlation analysis, for May: $r_{10} = 0.29$, slope of regression line 0.08; for June: $r_{10} = 0.50$, slope 0.10). These increases were significant for May after 1964 ($r_{10} = 0.88$, slope 0.40, $P < 0.01$) and for June from 1962 onwards ($r_{10} = 0.63$, slope 0.26, $P < 0.05$). The amount of precipitation was relatively low during the summers of 1963 and 1968–1970.

3. Methods

The density of the bird community was estimated by the territory mapping method, mainly in accordance with the international recommendations (Anon. 1970). The positions of individual singing males were plotted on a gridded census map, and great care was taken in mapping simultaneously singing neighbours. In addition, other territorial behaviour, such as courtship feeding, nest building behaviour, and copulation, was used to delimit the individual territories. Considerable time was spent in searching for nests. Mapping of colourringed individuals was also used to determine the number of territories involved.

Each year, 13–20 census visits were made, of which about two thirds took place during the mornings. Each visit lasted for about 5 to 5 1/2 h, and was started alternatively from the eastern and the western parts of the area. The census work was carried our from the last week of May to the end of June.

Data were analysed using Mann-Whitney *U*-tests, Spearman rank correlation (r_s) and Pearson correlation analyses (r_n where the subscript denotes *df*). All tests were two-tailed. Bird species diversity was calculated as

$$H' = \sum_{i=1}^{n} p_i \log p_i,$$

where p_i is the proportion of the density of *i*th species in the total community consisting of *n* species.

4. Results

4.1. Community patterns

Structure

Thirty-four passerine species were recorded as territorial within the study area (Table 1). Their combined density, the community density, varied from 142 to 195 territories/km², with a mean of 170.

The species diversity (*H*′) varied from 1.14 in 1964 to 1.28 in 1971 with a mean of 1.22 ± 0.04 *SD* (Table 2). About a half of all territories in the community were held by the following five species, *Turdus philomelos*, *Erithacus rubecula*, *Fringilla coelebs*, *Phylloscopus collybita* and *Prunella modularis*, for each of which the mean relative density (100 × density of a species / community density) varied from 6.2 to 11.8% (Fig. 3). Three species (*T. philomelos, E. rubecula, F. coelebs*) each comprised more than 10% of the community, three other species (*Ph. collybita, P. modularis, Turdus iliacus*) each accounted for 5–10%, while each of the remaining 28 species accounted for less than 5%. Of these 28 species,

Table 1. Mean density (territories/km^2) with coefficient of variation (*CV* = 100 *SD*/mean) and mean relative density (density as a per cent of the total bird density) for each of the 34 passerines constituting the community. Mean change in density is denoted by the slope of the regression line for species density vs. the years 1960–1972.

Density:	mean	*CV*	relative	change
Anthus trivialis	6.5	28.9	3.8	0.15
Motacilla alba	0.5	104.4	0.3	0.12
Troglodytes troglodytes	3.1	26.3	1.9	0.07
Prunella modularis	10.5	11.8	6.2	0.05
Erithacus rubecula	19.4	14.0	11.4	0.24
Phoenicurus phoenicurus	2.8	27.4	1.6	0.01
Saxicola rubetra	0.5	104.4	0.3	0.04
Turdus merula	7.8	26.0	4.7	–0.38
Turdus pilaris	4.7	98.5	2.6	0.20
Turdus philomelos	20.1	20.7	11.8	0.90
Turdus iliacus	9.4	16.0	5.5	0.21
Sylvia curruca	0.4	122.6	0.2	0.04
Sylvia borin	0.3	180.8	0.1	0.04
Sylvia atricapilla	0.7	132.5	0.4	0.18
Phylloscopus collybita	15.4	15.5	9.1	0.17
Phylloscopus trochilus	5.8	40.6	3.5	–0.29
Regulus regulus	7.7	38.8	4.5	–0.03
Muscicapa striata	0.3	248.8	0.1	0.06
Ficedula hypoleuca	1.3	37.0	0.8	0.07
Aegithalos caudatus	0.2	233.5	0.1	0.03
Parus cristatus	2.1	13.9	1.2	0.0
Parus ater	2.8	36.4	1.7	–0.10
Parus montanus	5.8	16.1	3.5	–0.02
Parus major	1.3	48.9	0.8	0.11
Certhia familiaris	1.3	97.6	0.7	0.17
Garrulus glandarius	1.3	49.8	0.7	0.04
Pica pica	0.3	149.1	0.2	0.07
Corvus corone cornix	3.1	73.9	1.8	0.51
Fringilla coelebs	18.3	11.2	10.8	0.26
Fringilla montifringilla	5.5	66.9	3.2	0.22
Pyrrhula pyrrhula	3.7	17.7	2.2	–0.03
Carduelis chloris	0.4	123.5	0.2	0.05
Carduelis spinus	5.8	29.1	3.5	–0.09
Emberiza citrinella	1.0	74.0	0.6	0.11
Total	170.1	9.9		3.20

13 were "irregular", i.e. absent in one or more years. Twenty-one species were "regular", i.e. recorded every year, and their combined densities contributed 88–99% (mean = 93% ± 3.8 *SD*) to the annual community density.

The species richness

The number of territorial species, the species richness, varied from 22 in 1964 to 33 in 1971 (Fig. 4), with a mean of 27 species per year during the 12 years study ($CV = 13.2\%$). Despite a decrease in the number of species between 1960 and 1964, a significant increase in the number of territorial species was recorded during the entire study period (Pearson correlation coefficient $r_{10} = 0.81$, slope 0.77, $P < 0.01$). The marked increase from 1966 to 1967 was mainly due to the first recorded occurrences of *Motacilla alba*, *Sylvia borin*, *Sylvia atricapilla*, and *Sylvia*

Table 2. Annual numbers of territories/km^2 of the different passerine species, together with totals (community density), number of species and diversity (Shannon Wiener index, H').

Species	1960	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
Anthus trivialis	7	6	9	2	6	6	5	7	6	7	8	9
Motacilla alba	–	–	–	–	–	–	1	1	1	1	1	1
Troglodytes troglodytes	2	4	3	2	4	3	2	4	4	3	4	3
Prunella modularis	12	10	9	10	9	12	10	11	9	12	10	12
Erithacus rubecula	19	16	16	20	22	24	19	15	19	20	22	21
Phoenicurus phoenicurus	2	2	3	2	4	4	3	3	3	3	2	2
Saxicola rubetra	1	–	–	–	–	1	1	1	–	–	1	1
Turdus merula	11	9	11	8	9	8	7	4	6	6	7	8
Turdus pilaris	3	–	–	–	15	7	10	8	3	3	2	5
Turdus philomelos	15	16	16	19	16	18	22	22	28	24	20	25
Turdus iliacus	10	8	9	7	9	8	9	10	12	10	9	12
Sylvia curruca	2	–	–	–	–	–	1	–	1	–	1	1
Sylvia borin	–	–	–	–	–	–	1	1	–	–	1	–
Sylvia atricapilla	–	–	–	–	–	–	1	1	2	–	2	2
Phylloscopus collybita	13	11	14	19	16	18	19	14	15	15	16	15
Phylloscopus trochilus	9	6	7	10	5	5	1	7	4	4	6	6
Regulus regulus	12	10	7	3	6	4	8	7	12	5	8	10
Muscicapa striata	–	–	–	–	–	–	–	–	2	–	1	–
Ficedula hypoleuca	1	1	1	1	2	1	1	2	1	1	2	2
Aegithalos caudatus	–	–	–	–	–	–	–	1	1	–	–	–
Parus cristatus	2	2	2	2	2	2	3	2	2	2	2	2
Parus ater	5	4	3	1	3	2	3	2	2	3	3	3
Parus montanus	8	6	4	5	6	5	6	6	6	6	6	6
Parus major	1	1	1	1	1	1	1	1	1	3	2	2
Certhia familiaris	–	–	3	–	1	–	1	1	3	1	3	2
Garrulus glandarius	1	2	1	–	1	1	1	2	2	1	2	1
Pica pica	–	–	–	1	–	–	–	–	–	1	1	1
Corvus corone cornix	1	1	1	2	3	2	2	2	3	7	6	7
Fringilla coelebs	18	14	18	16	20	20	20	16	20	20	18	20
Fringilla montifringilla	1	2	3	7	8	12	9	2	10	2	4	6
Pyrrhula pyrrhula	3	4	4	4	4	5	3	3	4	3	4	3
Carduelis chloris	–	1	–	–	1	–	–	–	–	1	1	1
Carduelis spinus	8	6	6	6	7	2	7	4	5	6	8	5
Emberiza citrinella	1	–	–	–	1	2	1	1	2	1	2	1
Total	167	142	151	148	181	173	178	161	189	171	185	195
Species	26	23	23	22	26	25	30	30	30	28	33	31
Diversity, H'	1.24	1.23	1.24	1.14	1.22	1.17	1.18	1.26	1.24	1.19	1.28	1.25

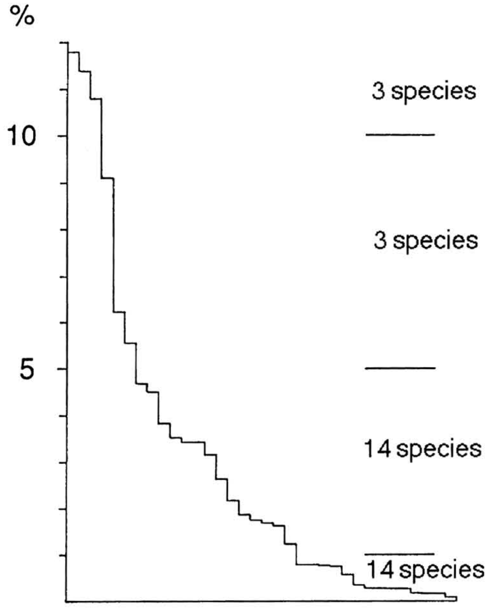

Fig. 3. Distribution of mean relative density values (100 × density of one species /combined density of all species) of the 34 passerine species present within the study area.

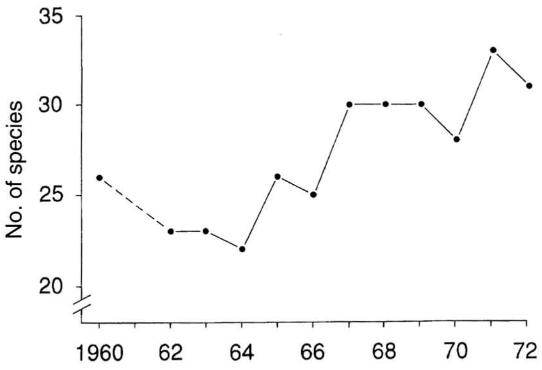

Fig. 4. Annual numbers of territorial species found in the study area.

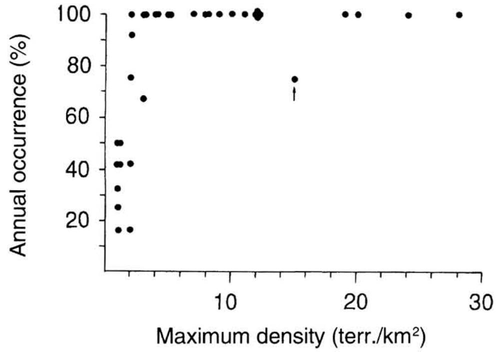

Fig. 5. The relationship between the maximum densities of 34 species found in the study area and their annual occurrence (%) during the 12 year study period. Arrow denotes values for the colonial *Turdus pilaris*.

curruca. The last-mentioned species was also present in 1960.

All the irregular species were present at low-densities with a maximum of three (mostly one or two) territories within the study area in any single year (except the colonial *Turdus pilaris* with 0 to 15 territories annually; Fig. 5). The regular species had higher maximum densities than the irregular ones. However, three of the regular species also showed a maximum of two or three territories/km². These were hole-nesters, with limited access to nesting sites (*Ficedula hypoleuca*, *Parus cristatus* and *Parus maior*). The species that were recorded in fewer than six years were mainly birds belonging to the "forest-edge", i.e. they established their territories along the margins of open areas such as bogs or clear-felled areas (*Motacilla alba*, *Saxicola rubetra*, *Carduelis chloris, Pica pica*). Three species, however, were "rich-forest" species (*Sylvia* species). Other irregular species included *Aegithalos caudatus* and *Muscicapa striata* (recorded only in two years).

The mean coefficient of variation for the 13 irregular species was $CV = 132.3\% \pm 58.3$ *SD*; while the mean *CV* for the 21 regular species was significantly lower (29.4% ± 17.3, Mann Whitney *U*-test, $U = 2.0$, $W = 363$, $P < 0.001$). The degree of yearly variation in density of a species population seemed to be related to its abundance. Thus, the variation in density of the different species was negatively correlated with their average population densities (Pearson $r_{32} = -0.86$, $P < 0.001$; Fig. 6). Also when considering only the regular species, there was found a negative correlation between the variation in density and average density of the species ($r_{19} = -0.48$, $P < 0.05$), i.e. the higher the mean density of a population, the lower was its variation in density.

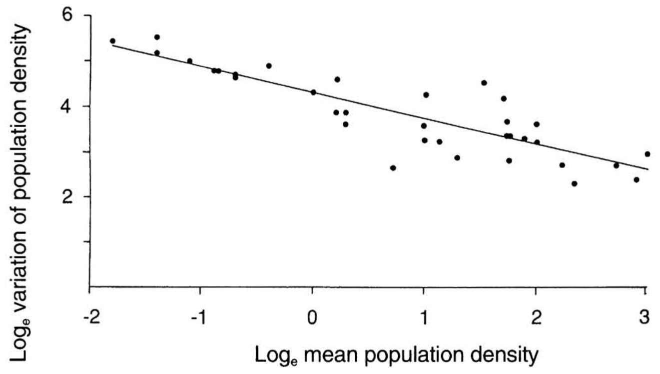

Fig. 6. Variance in population size over the 12-year period as a function of mean population density for the 34 territorial species found in the study area.

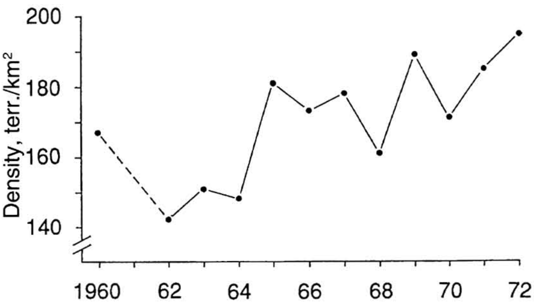

Fig. 7. Variation in the density of the passerine community during the 12-year period.

Relative species turnover rates in the community, $RT = (I+E)/0.5(S_1+S_2)$; where I = immigrations, E = extinctions, S_1 and S_2 the number of species recorded in the years t and t+1 (cf. Wiens 1989), varied from 0.06 to 0.20 for any two consecutive years during the study period (mean = 0.15, CV = 41.8%).

Variation in density

The community density increased significantly during the study period (Pearson $r_{10} = 0.71$, $P < 0.01$; Fig. 7). This overall trend was mainly due to an increase in the numbers of *Turdus philomelos*, but also to increases of *Turdus iliacus*, *Fringilla coelebs*, *Fringilla montifringilla* and *Corvus corone cornix*. Although community density was positively correlated with species richness ($r_{10} = 0.79$, $P < 0.01$), this relationship is accidental, because the combined density of the 21 regular species increased significantly more ($r_{10} = 0.64$, slope of regression line = 2.02) during the study period than that of the irregular species ($r_{10} = 0.63$, slope = 1.18; $t_{20} = 2.74$, $P < 0.02$). It is more likely that the irregular species settled in the area in response to factors that also favoured the increase in density of some of the regular species. No significant correlation was found between the community density in any one year and that in the previous one during the period 1962–72 (log N_t with log N_{t-1}: $r_8 = 0.44$, ns).

No correlation was found between the body mass (ln weight) of the 34 species and their variation in population size (CV) over the 12 years ($r_{32} = 0.01$, ns) or with their mean density over the 12 years ($r_{32} = 0.03$, ns; bird weights from Haftorn 1971).

When the species were classified into the groups residents, partial migrants and migrants, no differences in density variation between the groups were found (residents: mean $CV = 60.6 \pm 55.4$ SD, $n = 5$; partial migrants: mean $CV = 72.6 \pm 66.0$, $n = 10$; migrants: mean = 68.8 ± 66.8, $n = 19$).

4.2. Population fluctuations

Two species increased significantly in density during the study period, viz. *Turdus philomelos* (slope of regression line = 0.90, $P < 0.01$) and *Corvus corone cornix* (slope = 0.51, $P < 0.001$; Table 2, Fig. 8). Species that increased slightly, but non-significantly, in density were *Erithacus rubecula*, *Turdus iliacus*, *Fringilla coelebs* and *F.*

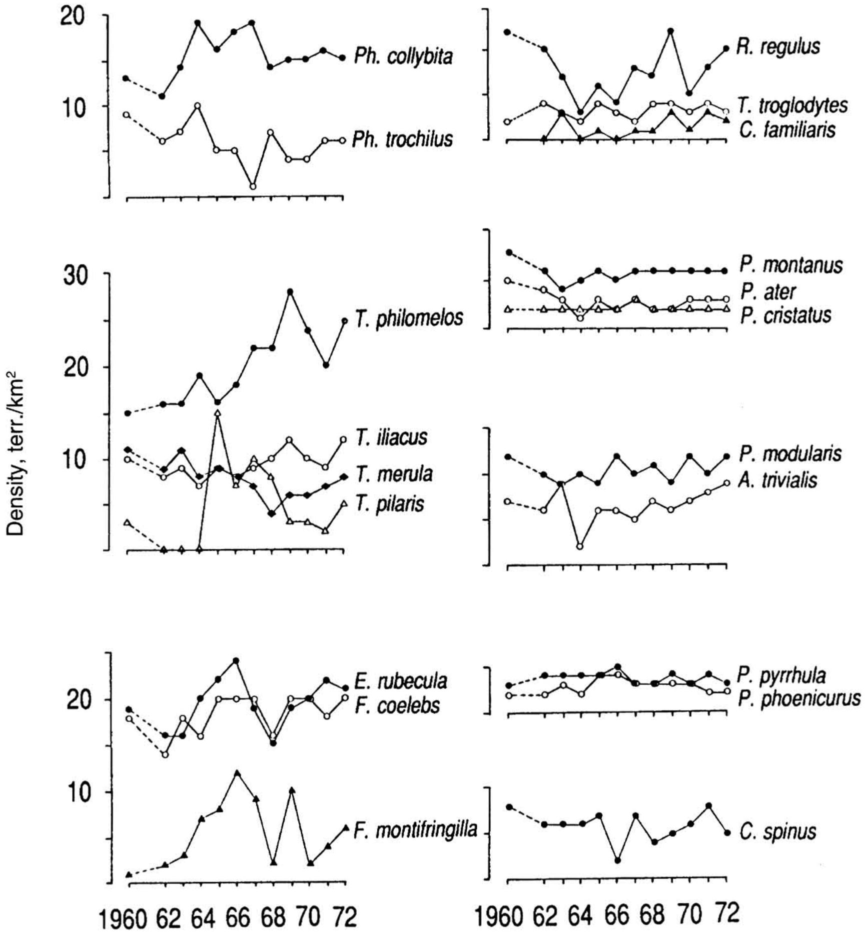

Fig. 8. Variation in the population densities of the most abundant species.

montifringilla (slope 0.21–0.26). The density of *Turdus merula* decreased significantly (slope = –0.38, $P = 0.01$). One species that decreased slightly in density was *Phylloscopus trochilus* (slope –0.29).

The densities of *Parus montanus*, *Parus ater* and *Regulus regulus* fluctuated roughly in parallel during the 12 years (*R. regulus* and *P. montanus*, and *R. regulus* and *P. ater*, both $r_{10} = 0.61$, $P < 0.05$; *P. montanus* and *P. ater*, $r_{10} = 0.63$, $P < 0.05$; Fig. 8). The fluctuation patterns of these species showed no significant relationships with the mean temperature in January or February, or the total amount of snow fall in the same months. The population fluctuations of *Parus ater* showed a positive, but non-significant, correlation with the cone crop index for the Scots pine (Spearman $r_s = 0.37$, $n = 12$, $P = 0.12$).

Other species whose densities fluctuated in a rather similar way were *Phylloscopus collybita* and *Fringilla montifringilla* (Pearson $r_{10} = 0.72$, $P < 0.01$), *Ph. collybita* and *Erithacus rubecula* ($r_{10} = 0.59$, $P < 0.05$), *E. rubecula* and *Fringilla coelebs* ($r_{10} = 0.62$, $P < 0.05$), *E. rubecula* and *F. montifringilla* ($r_{10} = 0.61$, $P < 0.05$) and *F. montifringilla* and *F. coelebs* ($r_{10} = 0.55$, $P < 0.05$). Among the thrushes, *Turdus philomelos* and *T. iliacus* showed a great similarity in their patterns of population fluctuation ($r_{10} = 0.69$, $P < 0.01$).

The population density of *Carduelis spinus* varied from two to eight territories/km², and the variation was closely related to the abundance of spruce seeds (Spearman $r_s = 0.73$, $n = 12$, $P < 0.01$), but not with the abundance of Scots pine seeds ($r_s = 0.20$, $n = 12$, ns).

5. Discussion

Five of the 34 species that constituted the passerine community in Estenstad, formed about half of the community density, while most species were represented by one or a few territories/km^2. This seems to be the general shape of the species-density distributions in central and northern coniferous forests in the Palearctic (cf. Haila & Järvinen 1990). However, the density of the passerine community in Estenstad (mean 170 territories/km^2) seems low when compared with values for bird communities studied in similar forest types in Scandinavia. The mean bird density, studied over two years in a 14 ha area of spruce-dominated forest near Oslo, was 418 territories/km^2 (Hogstad 1967a). In southern Sweden the density of a passerine community was estimated to be 308 territories/km^2 (Engström 1953).

Although bird density values are dependent on the census method used, local variation in density is evident, even within the same type of coniferous forests. On the basis of extensive line transect censuses, Haila et al. (1980a) found that the average breeding density of bird communities in different coniferous forests in southern Finland varied between 124 and 633 pairs/km^2 (see also Nowikow 1962). Considerable variation in bird densities was also found in boreal forests in Canada (Erskine 1977).

The relatively low community density value found for Estenstad is probably due to the relatively uniform habitat, viz. mostly mature spruce trees with a height of 15–20 m. Habitat diversity is important for both community density and species richness (e.g. Cody 1975, Røv 1975, Haila et al. 1985b, Tiainen et al. 1985). Thus, even within the Estenstad area, the estimates of mean passerine densities in different habitats during the years 1960, 1962–66 showed marked differences (Hogstad 1967b). In an area of uniform spruce forest there were 130 territories/km^2, whereas in a 100 m-wide zone of the same forest type bordering either a clear-felled area or a bog, there were 190 and 220 terr./km^2, respectively. The highest density, 430 terr./km^2, was found in a 2.5 ha plantation of mixed forest consisting of spruce, pine and deciduous trees. Thus, habitat heterogeneity, as found in the transition zones between different habitats, and the number of tree species present, clearly influence the population density of birds (Hogstad 1967b).

The non-significant relationship noted between the mean density of passerines in the Estenstad study area and their body mass, contrasts with the inverse relationship between body size and population density found elsewhere (e.g. Damuth 1981, Juanes 1986, Carrascal & Telleria 1991, but see Peters & Wassenberg 1983).

Bird density and species richness in the Estenstad study area varied relatively little over the 12 years, the *CVs* being only slightly higher than the values reported by Enemar (1966) in his 10-year study of a rich deciduous lowland forest strip in southern Sweden and by Solonen (1986) for a luxuriant mixed forest in southern Finland over 10 years (Table 3). The *CV*-values reported from these studies were markedly lower than those calculated for subalpine and alpine bird communities in Fennoscandia (Table 3). Similarly, the recorded variations in density and species richness were high for bird communities in North American subalpine and alpine coniferous forests (Hall 1984, DeSante 1990). These findings indicate strongly that the bird communities in subalpine habitats are more variable than those found in lowland forests. Also the population stability tends to be greatest in areas of high densities (cf. Järvinen 1979, 1981, Noon et al. 1985, Tomiałojć & Wesołowski 1990). The relatively small variations in density and species richness in Estenstad may also be a consequence of the relatively southern situation of the boreal forest (c. 63°N). Fluctuations in bird density are generally greater in northern than in southern areas, probably because of the greater unpredictability of environmental conditions and their harshness in the north (Järvinen 1979). The overall density of bird communities in northern Fennoscandia varies considerably (mean $CV = 22.2\%$) and the variation is clearly greater than for those in southern Scandinavia and in Central Europe (mean $CV = 8.4\%$). The number of species also varies to the greatest extent in the north (mean $CV = 14.2\%$ vs 7%; Järvinen 1979).

Differences in size of the areas studied, even within types of forest, may also lead to dissimilar conclusions being drawn regarding both community composition and the magnitude of the temporal variability in species density (cf. Wiens

& Dyer 1975, Rotenberry & Wiens 1980, Wiens 1986). The larger the study area, the smaller the impact of random events. The relative stability of the situation in Estenstad, compared with that found in other studies, may therefore also to some degree be the result of the greater size of the Estenstad study area.

Since small populations are those most likely to suffer local extinction, and so must recolonize the area repeatedly, it seems reasonable to suggest, as was in fact noted in the present study, that it is the density of the less abundant species that varies most. The same pattern was found in a subalpine bird community in Sierra Nevada (DeSante 1990), where the more numerous species showed less variation from year to year (*CV* = 22.5%) than did the rare species (*CV* = 77.8%). The species turnover in the Sierran subalpine study was entirely due to the disappearances and reappearances of the rare species, and there was an indication that the prevailing weather conditions affected the breeding ranges of these particular species. A similar species turnover, due to rare species, was found by Williamson (1981, 1983) and James & Wamer (1982). Also Järvinen & Väisänen (1977a, b) analysing the results of line-transects made in Finland between 1945 and 1975, found that the most stable species were often abundant, and that the densities of the two most abundant species, *Phylloscopus trochilus* and *Fringilla coelebs*, varied little during that period. In contrast, Holmes et al. (1986), in a temperate deciduous forest in New Hampshire, found that the species with high densities were more variable in number than those occurring at low densities. According to Taylor & Woiwod (1980, 1982), species occurring at high densities tend to be the most variable ones in several animal and plant groups. The suggested explanation is that of stochastic environmental influences on demographic events (cf. Anderson et al. 1982).

The species with the highest *CV* values for density in the Estenstad area, were either "forest-edge" species, i.e. those that established their territories in the transition zone between the forest and open areas, or "rich forest" species that were only found in forest areas that included deciduous trees (*Sylvia* species, *Aegithalos caudatus*, *Carduelis chloris*). All these species maintained territories in some years in habitats that are usually sub-optimal for them (cf. Haftorn 1971). The occurrence of the *Sylvia* species after 1966 may partly be related to the growth of deciduous vegetation on clear-felled areas, but probably most to the higher ambient temperatures, especially in May. Correspondingly, the expansion and increased density of *Phylloscopus sibilatrix* in Central Norway after the period 1960–1970 up to the 1980's, has been suggested to be mainly a result of a prolongation of the spring migration due to higher May temperatures, which increased steadily from a mean of

Table 3. Variation (*CV* = 100 *SD*/mean) of bird density and species richness in lowland and subalpine bird communities.

Forest type, locality	Years	*CV* density	*CV* species	References
Spruce-dominated, Central Norway	12	9.9	13.2	Present study
Deciduous, Southern Sweden	10	5.4	10.9	Enemar (1966)
Mixed, Southern Finland	20	9.3	3.6	Solonen (1986)
Mixed, Southern Finland	5		5.5	Nordström (1953)
Lowland forests, mean		8.2	8.3	
Subalpine birch, Central Norway	25	20.4	13.0	Hogstad, unpubl.
Subalpine birch, Northern Sweden	20	18.7	10.6	Enemar et al. (1984)
Subalpine birch, Northern Finland	10	20.1	20.7	Järvinen & Väisänen (1976)
Alpine heath, high, Northern Sweden	20	37.1	21.8	Svensson et al. (1984)
Alpine heath, low, Northern Sweden	20	17.1	14.1	Svensson et al. (1984)
Subalpine coniferous, Sierra Nevada	7	26.7	28.3	DeSante (1990)
Subalpine spruce, South Appalachian	22		16.5	Hall (1984)
Subalpine-alpine forests, mean		23.4	17.9	

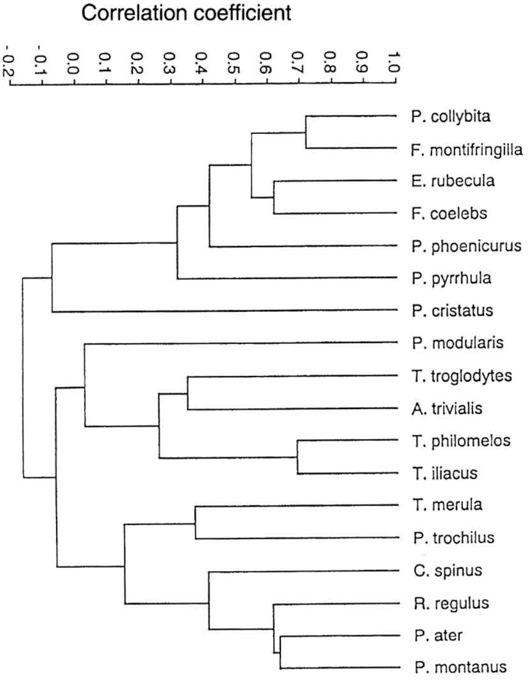

Fig. 9. Cluster dendrogram for the 18 most abundant species in the Estenstad study area, clustered according to the degree of correlation between their yearly population densities during the 12-year period.

8.9°C (1961–70) to 11.0°C (1981–84; Hogstad & Moksnes 1986).

To determine the degree of synchrony between the population fluctuations of the different species, I used cluster analysis of the data, based on the variation in the correlation coefficients for species density (see Cody 1974). Three groups seem to be delimited in the resultant dendrogram (Fig. 9). One includes *Phylloscopus collybita*, *Fringilla montifringilla*, *F. coelebs* and *Erithacus rubecula*, the second comprises *Turdus philomelos* and *T. iliacus*, and the third consists of *Regulus regulus*, *Parus ater* and *P. montanus*. All the other species seem to vary relatively independently of each other.

The relative similar fluctuation patterns of *R. regulus*, *P. ater* and *P. montanus* are probably due to their small body sizes and high metabolic rates, which result in a relatively high mortality in winter, because of cold weather and insufficient food in some years. Although no significant correlation was found between the density of these species and either the temperature or the amount of snow in mid winter, temperature fluctuations around 0°C may cause problems for such small birds, because ice forms on the branches and twigs where they forage. A marked reduction in the winter populations of these species was also recorded in spruce-dominated forests in southern Norway and Finland (Hogstad 1967b, 1984, Hildén 1982).

Some similarity in the fluctuation patterns of *Phylloscopus collybita*, *Erithacus rubecula*, *Fringilla coelebs* and *F. montifringilla* was noted. Their main wintering areas are in western Europe and the Mediterranean countries. One may speculate as to whether major events in these areas, in winter or during their migration period, affected their numbers (cf. Enemar et al. 1984). *Turdus philomelos* and *T. iliacus*, both of which winter in western and south-western Europe, also showed some similarity in the pattern in their patterns of fluctuation (cf. Väisänen 1984).

Although some of the species in the Estenstad area had somewhat similar fluctuation patterns, most species had not. The independent fluctuations of the species forming the passerine community may therefore indicate that different species are influenced by different combinations of factors. Similar independent species fluctuations have also been reported from long-term community studies elsewhere (Rice et al. 1983, Svensson et al. 1984, Holmes et al. 1986, Tomiałojć & Wesołowski 1990). Factors operating on the local scale may affect some populations (e.g. as, in the present study, the cone crop those of *Carduelis spinus*, and probably the winter weather conditions for *Regulus regulus* and the small *Parus* species), while the general conditions in the wintering areas may be important for other bird populations (e.g. Enemar et al. 1984, Terborgh 1989).

Since no species-specific compensatory density fluctuation was found, it seems that each species responded to environmental variations in a specific way. It has been suggested that most Holarctic passerines have surplus of breeding resources and more restricted resources during the non-breeding season (Alerstam & Högstedt 1982). If so, population fluctuations of many northerly breeding passerine species may reflect winter survival more than interactions within or between species in the breeding areas. On the other hand, removal experiments during the breeding season strongly indicates that at least some bird species are limited by territoriality (e.g. Brown 1969, Rappole et al. 1977, Wesołowski et al. 1987, Hogstad 1989, Mönkkönen 1990). Wether or not breeding bird populations in northern forest regions are kept below the carrying capacity of their environment is still under debate.

Acknowledgements. I thank A. Enemar, R. T. Holmes, M. Mönkkönen, T. Slagsvold, G. Sonerud and B.-E. Sæther for comments on the manuscript and P. Tallantire for improving the English.

References

Alerstam, T. & Högstedt, G. 1982: Bird migration and reproduction in relation to habitats for survival and breeding. — Ornis Scand. 13:25–37.

Anon. 1970: Recommendations for an international standard for a mapping method in bird census work. — In: Svensson, S. (ed.), Bird census work and environmental monitoring. Bull. Ecol. Res. Comm. 9:49–52. NRF, Stockholm.

Anderson, R. M., Gordon, D. M., Crawley, M. J. & Hassel, M. P. 1982: Variability in the abundance of animal and plant species. — Nature 296:245–248.

Brown, J. L. 1969: Territorial behavior and population regulation in birds: a review and re-evaluation. — Wilson Bull. 81:293–329.

Carrascal, L. M. & Telleria, J. L. 1991: Bird size and density: a regional approach. — Amer. Nat. 138:777–784.

Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton University Press, Princeton.

— 1975: Towards a theory of continental species diversities: bird distributions over mediterranean habitat gradients. — In: Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 214–257. Harvard Univ. Press, Cambridge.

Damuth, J. 1981: Population density and body size in mammals. — Nature 290:669–670.

DeSante, D. F. 1990: The role of recruitment in the dynamics of a Sierran subalpine bird community. — Amer. Nat. 136:429–445.

Enemar, A. 1966: A ten-year study on the size and composition of a breeding passerine bird community. — Vår Fågelvärld, Supplement 4:47–94.

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.

Engström, K. 1953: Ett försök att klarlägga fluktuationerna i den svenske fågelfaunan. — Vår Fågelvärld 12:165–171.

Erskine, A. J. 1977: Birds of boreal Canada: communities, densities and adaptations. — Can. Wildlife Serv., Rep. 41:1–71.

Haftorn, S. 1971: Norges fugler. — Universitetsforlaget, Oslo.

Haila, Y. & Järvinen, O. 1990: Northern conifer forests and their bird species assemblages. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 61–85. SPB Academic Publ, Hague.

Haila, Y., Järvinen, O. & Väisänen, R. A. 1980a: Habitat distribution and species associations of land bird populations on the Åland Islands, SW Finland. — Ann. Zool. Fennici 17:87–106.

— 1980b: Effects of changing forest structure on long-term trends in bird populations. — Ornis Scand. 11:12–22.

Hall, G. A. 1984: A long-term bird population study in a Appalachian spruce forest. — Wilson Bull. 96:228–240.

Hildén, O. 1982: Winter ecology and partial migration of the Goldcrest Regulus regulus in Finland. — Ornis Fennica 59:99–122.

Hogstad, O. 1967a: Seasonal fluctuation in bird populations within a forest area near Oslo (Southern Norway) in 1966–67. — Nytt Mag. Zool. 15:81–96.

— 1967b: The edge effect on species and population density of some passerine birds. — Nytt Mag. Zool. 15:40–43.

— 1984: Variation in numbers, territoriality and flock size of a Goldcrest Regulus regulus population in winter. — Ibis 126:296–306.

— 1989: The presence of non-territorial males in Willow Warbler Phylloscopus trochilus populations — a removal study. — Ibis 131:263–267.

Hogstad, O. & Moksnes, A. 1986: Expansion and present status of the Wood Warbler Phylloscopus sibilatrix in Central Norway. — Fauna Norv. Ser. C, Cinclus 9:49–54.

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.

James, F. C. & Wamer, N. O. 1982: Relationships between temperate forest bird communities and vegetation structure. — Ecology 63:159–171.

Järvinen, O. 1979: Geographical gradients of stability in European land bird communities. — Oecologia 38:51–69.

— 1981: Dynamics of North European bird communities. — Proc. Int. Ornithol. Congr. 17:770–776.

Järvinen, O. & Väisänen, R. A. 1976: Between-year components of diversity in communities of breeding land birds. — Oikos 27:34–39.

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

— 1977b: Long-term changes in forest bird populations in northern Finland. — Ann. Zool. Fennici 15:279–289.

Juanes, F. 1986: Population density and body size in birds. — Amer. Nat. 128:921–929.

Mönkkönen, M. 1990: Removal of territory holders causes influx of small-sized intruders in passerine bird communities in northern Finland. — Oikos 57:281–288.

Noon, B. R., Dawson, D. K. & Kelly, J. P. 1985: A search for stability gradients in Noth American breeding bird communities. — Auk 102:64–81.

Nordström, G. 1953: Boniteringsundersökningar över häckfågelfaunan inom tre olika skogsområden under en följd av fem somrar. — Ornis Fennica 30:56–67.

Nowikow, G. A. 1962: Die geographisch bedingten Untershiede in der Siedlungsdichte der Waldvögel im europäischen Teil der UdSSR und in den angrenzenden Ländern. — Der Falke 9:376–382, 403–406.

Peters, R. H. & Wassenberg, K. 1983: The effect of body size on animal abundance. — Oecologia (Berlin) 60:89–96.

Rappole, J. H., Warner, D. W. & Ramos, O. M. 1977: Territoriality and population structure in a small passerine community. — Amer. Midl. Nat. 97:110–119.

Rice, J., Ohmart, R. D. & Anderson, B. W. 1983: Turnovers in species composition of avian communities in contiguous riparian habitat. — Ecology 64:1444–1445.

Rotenberry, J. T. & Wiens, J. A. 1980: Temporal variation in habitat structure and shrubsteppe bird dynamics. — Oecologia 47:1–9.

Røv, N. 1975: Breeding bird community structure and species diversity along an ecological gradient in deciduous forest in western Norway. — Ornis Scand. 6:1–14.

Solonen, T. 1986: Stability of a bird community in southern Finland. — Ornis Scand. 17:106–116.

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

Terborgh, J. 1989: Where have all the Birds gone? — Princeton University Press, Princeton.

Taylor, L. R. & Woiwod, I. P. 1980: Temporal stability as a density-dependent species characteristic. — J. Anim. Ecol. 49:209–224.

— 1982: Comparative synoptic dynamics. I. Relationships and temporal variance/mean population parameters. — J. Anim. Ecol. 51:879–906.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. & Virolainen, E. 1985: Impact of the amount of edges and habitat diversity on the breeding bird community in southern Finnish forests. — In: Taylor, K., Fuller, R. J. & Lack, P. C. (eds.), Bird Ccnsus and atlas studies. Proc. VIII Int. Conf. Bird Census Atlas Work: 231–241. BTO, Tring.

Tomiałojć, L. & Wesołowski, T. 1990: Bird communities of the primaeval temperate forest of Białowieża, Poland. — In: Keast, A. (ed.), Biogeography and ecology of forest bird communities: 141–165. SPB Academic Publ, Hague.

Väisänen, R. A. 1984: Population changes of land birds in Finland in 1978–1984. (In Finnish with English summary) — Lintumies 19:134–153.

Wesołowski, T., Tomiałojć, L. & Stawarczyk, T. 1987: Why low numbers of Parus major in Białowieża Forest? — removal experiments. — Acta Ornithol. 23:303–315.

Wiens, J. A. 1986: Spatial scale and temporal variation in studies of shrubsteppe birds. — In: Diamond, J. & Case, T. J. (eds.), Community ecology: 154–172. Harper & Row, New York.

— 1989: The ecology of bird communities. Vol 2. Processes and variations. — Cambridge University Press, Cambridge.

Wiens, J. A. & Dyer, M. I. 1975: Rangeland avifaunas: Their composition, energetics, and role in the ecosystem. — In: Smith, D. R. (ed.), Symposium on management of forest and range habitats for nongame birds: 176–182. USDA Forest Service General Technical Report WO-l, Washington.

Williamson, M. 1981: Island populations. — Oxford University Press, Oxford.

— 1983: The land-bird community of Skokholm: ordination and turnover. — Oikos 41:378–384.