

## The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study

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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.

A description is given of the species composition and density fluctuations of the breeding bird community of 9 km<sup>2</sup> of an apparently constant subalpine birch forest habitat, based on the results of territory mapping and line transecting every season over 20 years. The number of species appearing in the forest has shown a slightly increasing trend (average yearly addition: a third of a species) with *Hippolais icterina* as the most conspicuous new-comer. The dominant *Phylloscopus trochilus* has shown a steadily decreasing trend over the last eighteen years. The average community density is 400 territories/km<sup>2</sup> with 260 and 550 as the extreme values (coefficient of variation 19%). The finding that species with similar migration and wintering strategies tend to fluctuate in a similar way indicates that factors operating outside the breeding season have been important in generating the fluctuation patterns of the breeding populations. Only two species, *Carduelis flammea* and *Fringilla montifringilla*, have responded clearly to recorded breeding area factors, namely superabundant birch seed crop and mass outbreak of the geometrid moth *Epirrita autumnata*, respectively. It is argued, on the basis of several observations and results, that the investigated bird community is not saturated.

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### 1. Introduction

An ornithological research program based on field work was started in the Ammarnäs area, Swedish Lapland, in 1963. One of the basic aims of the project (the so-called LUVRE-project, cf Enemar 1969) was to annually perform census work according to a standardized routine not only in the subalpine birch forests, which will be treated here, but also on alpine heaths (Svensson 1979, Svensson et al. 1984).

Bird populations are not stable. It was soon found that more than one season's census work is necessary to describe even the species composition and density of a selected area or habitat (Siivonen 1948). It is easily understood that still more years are needed to grasp the characteristic fluctuation patterns of the species populations and the community. Consequently, the need for long-term census investigations in community research has repeatedly been stressed (cf., e.g., Wiens 1977).

Long-term field studies should not be expected to solve community or population ecology problems simply because of the availability of data from a protracted succession of years. They are, however, useful for the recognition of relevant key problems in this research, and they may point to erroneous conclusions and other mistakes which have been made on the basis of too short-term censuses, let alone single-season excursions (cf. Wiens 1983).

It is generally true that any new season in the subalpine birch forest is a new situation, again and again. No season is like any other one. We have so far looked in vain for a "closing-the-ring-season" which would be the signal to initiate the summarizing reviews and comprehensive analyses and eventually to close the field work.

The main purpose of this first report is to describe the course of the major events in the bird community and the habitat, and to pre-

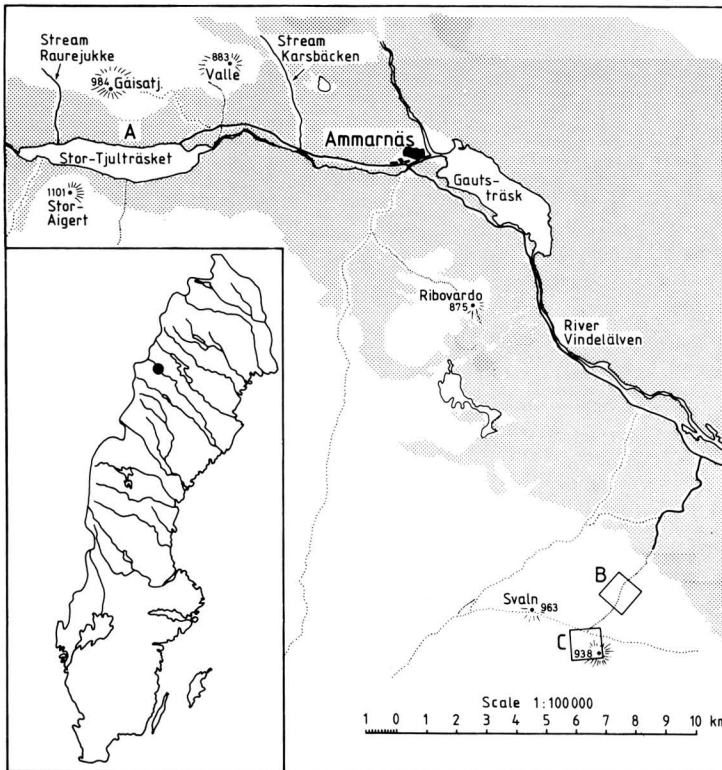


Fig. 1. Map of the Ammannäs area, Swedish Lapland. Its location in Sweden is indicated by the solid circle on the inserted map. A = the investigated subalpine birch wood extending from the stream of Raurejukke to the stream of Karsbäcken. B and C = the study plots on the alpine heath investigated by Svensson et al. (1984). Mountain peaks are denoted by asterisks and figures giving height a.s.l. Wooded areas are stippled. Tracks are denoted by dotted lines.

sent the fluctuation patterns of the species populations together with a survey of the data obtained during the mapping censuses and the line transects.

## 2. The study area

The investigated subalpine birch forest is located on the south-facing slopes of the mountains of Gaisatjåkke (Gaisatj, Kaissats) and Valle (Fig. 1). It extends from the stream of Raurejukke in the west to the stream of Karsbäcken 8 km eastwards. It is bordered in the south by Lake Stor-Tjulträsket and the road from this lake to the village of Ammannäs. The size of the area is 9 km<sup>2</sup> and its approximate position is 65° 58'–65° 59' N, 15° 58'–16° 8' E, 540 to 720 m a.s.l.

The forest is predominantly of the rich type ("meadow birch forest"). It turns locally into the dry heath type, especially in its upper parts. A few very small bogs are found in the eastern part of the area. There are also a few minor clearings mainly near the settlements in the south-east. They are now mostly covered by different successions of growing birch. No tree-felling of any significance has occurred during the years of investigation. In the central part of the forest there are a few hectares of swamp previously used for hay-making. The forest seems to be largely primeval with trees of different ages including

areas with tall birches of apparently considerable age. The conditions are obviously such that a successful establishment of new generations of birches is secured, as no signs of spontaneous forest thinning with following transformation into subalpine dwarf-shrub heath are found (cf. Kullman 1981). This means that regarding its qualities as a habitat for its passerine bird community, the investigated forest has remained constant throughout the study period. A detailed description of the habitat is not necessary in this context as the present account will focus only on the fluctuations of the species populations.

Air-pollution-induced breeding disturbances have been discovered in several insectivorous passerines in the area, manifested in abnormally small clutches and defective egg shells (Nyholm & Myhrberg 1977, Nyholm 1981). As these disturbances occur exclusively in a narrow zone (width about 100 m) along the shore of Lake Stor-Tjulträsket they are considered to have had an insignificant effect on the bird community of the study area.

## 3. Field work and methods

### 3.1. The mapping census

The density of the bird community was estimated by territory mapping in study plots. The field work and the evaluation of the spe-

Table 1. Study plots and census-takers 1963–1982 (AE = Anders Enemar, BS = Bengt Sjöstrand, EN = Erik Nyholm, HM = Harry Myhrberg, LN = Lars Nilsson).

Study plot	Size km <sup>2</sup>	1963	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
A4	0.129	AE	AE	AE	AE	AE	AE	AE	AE	AE	AE	AE	AE	AE	LN	LN	LN	LN	LN	LN	LN
A5	0.111	HM	IL	IL	IL	IL	IL	IL	IL	EN/HM	IL	IL	IL	IL	IL	IL	IL	LN	LN	LN	LN
A6	0.122	BS	BS	BS	BS	BS	BS	BS	BS	BS	BS	-	-	-	-	-	-	-	-	-	-
A7	0.080	-	AE	AE	AE	AE	AE	AE	AE	AE	IL	-	-	-	-	-	-	-	-	-	-
A8	0.080	-	-	-	AE	AE	AE	AE	AE	AE	AE	AE	AE	AE	LN	LN	LN	LN	LN	LN	LN
A9	0.100	-	-	-	-	-	-	-	-	-	AE	AE	AE	AE	LN	LN	LN	LN	LN	LN	LN

cies maps were carried out strictly according to the international recommendations (Anon. 1970). The only exceptions were the thrush species and most non-passerine species which were censused by nest counts. The field work usually started about 10 June and lasted for about three weeks. The number and size of the study plots and the name of the census-takers are given in Table 1. Study plots A5 and A6 were provided with nest-boxes in 1965 and they are, therefore, not used when calculating the density values of the hole-nesting *Ficedula hypoleuca* and *Ph. phoenicurus*.

A certain shift of study plots has occurred during the 20-year period due to other research programmes within the project. This has probably not affected the estimation of the community fluctuation pattern because the separate study plots usually fluctuate in parallel as shown by Enemar & Sjöstrand (1970) for the first six seasons. Moreover, more than half of the area of the mapping census has been the same throughout the two decades. The separate study plots have been investigated by the same observer for many years in sequence (Table 1). A special test has shown that the census data obtained by different experienced observers in the same plot are comparable (Enemar et al. 1978). It is probable, therefore, that the few instances of observer exchange have not significantly disturbed the homogeneity of our sequence of density estimations. The census work is facilitated by the fact that the subalpine forests are relatively easy to survey and the breeding periods of most species are well synchronized.

### 3.2. The line transects

The census-takers of the study plots have also been responsible for the standardized line

transect work which is performed as follows: The observer goes along tracks distributed all over the 9 km<sup>2</sup> of the forest under investigation and records all audible and visible observations of birds, mostly singing males. The tracks were not marked out and therefore their position in the forest may have shifted locally between seasons. This has probably not biased the field data significantly because the observer had to make no less than 80 kilometers, on the average, of line transecting to collect the required amount of data. The size of the area covered by the transects was not considered as the data are only used to calculate the percentage share of each species in the total amount of observations. To estimate these values for the most sparse of the regularly breeding species with sufficient accuracy requires at least 1500 observations (Enemar & Sjöstrand 1967) which in the birch forest takes an average of 30 hours of field work. This minimum number was not achieved in the first two seasons. Thus those records are excluded from certain calculations in the following.

Table 2. Total number of observations and census-takers of the line transects 1963–1982 (AE = Anders Enemar, BS = Bengt Sjöstrand, LN = Lars Nilsson, LÄF = Lars Åke Flodin).

Year	Observ.	Censust.	Year	Observ.	Censust.
1963	809	AE	1973	3233	AE,BS
64	1077	AE	74	3729	AE,BS
65	4129	AE,BS	75	1561	AE
66	3052	AE,BS	76	3025	AE,LN
67	3036	AE,BS	77	2506	AE,LN,LÄF
68	3037	AE,BS	78	3030	AE,LN
69	3057	AE,BS	79	3054	AE,LN
70	3061	AE,BS	80	2416	AE,LN
71	3115	AE,BS	81	2735	AE,LN
72	3110	AE,BS	82	3252	AE,LN

The extent of the line transect work can be read from Table 2. This census technique is more sensitive to observer shifts than the mapping census (Enemar & Sjöstrand 1967). Therefore, one of the observers has done the line transecting throughout the two decades without a break.

### 3.3. Calculation of the bird density index

So-called derived density indices of the species are used to demonstrate the annual fluctuations. They are obtained by combining the data from the study plots and the line transects according to the method, slightly modified, presented previously (Enemar & Sjöstrand 1970). Derived density indices are used because the investigated study plot populations of most species are too small to provide reliable information on the density changes between seasons. The study plot data are therefore only used as a density reference ( $D_R$ ), which is the density of all small passerine species taken together except the thrush species. The latter are excluded because of their more or less marked colonial breeding which biases the density information obtained in the study plots. The derived density index ( $DD$ ) of a species is calculated as follows:

$$DD = nD_R/R$$

where  $n$  is number of observations of a species in the line transect material and  $R$  is the total number of observations of those species which are included in  $D_R$ .  $DD$ -values have been calculated for each observer and averaged by an arithmetic mean.

The derivation of the  $DD$ -values partly compensates for errors in study plot densities due to small sample sizes and the aggregation in colonies. On the other hand, differences in the conspicuousness of the species influence the line transect data more than the results of the mapping census (cf. the diagrams of Fig. 3, and App. I and II). Therefore the derived density figures are index values which are useful mainly for the study of population fluctuations.

### 3.4. The insect census work

The occurrence of insects on the birch has been estimated in special study plots since

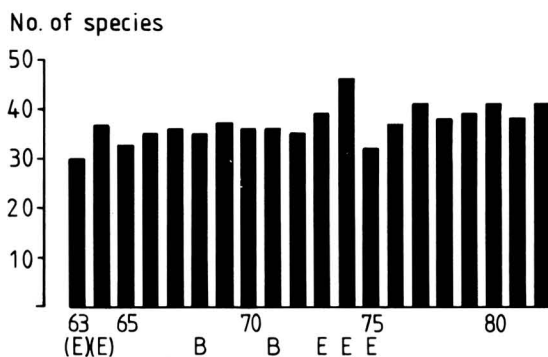


Fig. 2. Yearly number of species recorded during the line transects 1963-1982. B = superabundant birch seed crop, E = mass outbreak of *Epirrita autumnata* caterpillars, (E) = moderate outbreak.

1967. The techniques and the results of the first 13 seasons are described by Andersson & Jonasson (1980). In the present paper only the occurrence of caterpillars of the geometrid moth *Epirrita autumnata* in June will be considered.

### 3.5. Birch seed crop

A quantitative survey of the birch seed production by estimating the flowering frequency of the birch was not started until 1979. The census technique consists of recording the catkin frequency in a standardized way on marked birches in the same plots where the insects are censused.

### 3.6. Rodent cycles

Rodent cycles (mainly vole species) have been recorded periodically with the aid of extensive trapping programs (cf. Hansson 1969, Erik Nyholm pers. comm.). Accuracy varies but the peak years and the bottom years have been identified satisfactorily.

## 4. The census results

### 4.1. Birds

The bird species densities obtained in the study plots are given in Appendix II. The number of records of each species made during the line transects is found in Appendix I. The



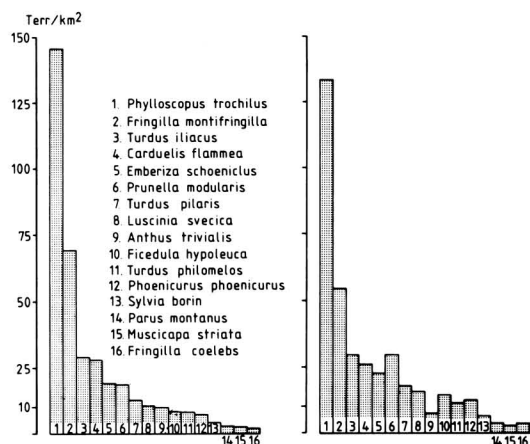


Fig. 3. Species frequency diagrams, based on the mean values of the derived density indices 1965-1982 (left diagram) and the study plot densities 1963-1982 (right diagram).

annual number of species observed during the line transects is presented in Fig. 2. The densities of the sixteen regularly breeding small passerines (mean values of the 20 seasons) are given in the species frequency diagrams of Fig. 3. The fluctuation patterns as shown by the derived density indices of the same species and of the total community are shown in the diagrams of Figs. 4 and 5.

#### 4.2. *Epirrita autumnata* caterpillars

The fluctuation dynamics of the *Epirrita* caterpillars are presented in Fig. 6. A mass occurrence during the first two seasons of the bird census work was of moderate extent. No significant defoliation of the birches was observed and no heavy aggregations of caterpillars were seen. From 1973 to 1975 a second more extensive outbreak occurred which resulted in a significant defoliation. According to Andersson & Jonasson (1980) this outbreak occurred all over the investigated forest although there were local variations in intensity. The density of caterpillars fluctuated in parallel between seasons and peaked in 1974 in the three plots where the caterpillars were counted. In a censused forest of the heath type about 20 kms to the southeast the peak included two seasons (1974 and 1975) with a caterpillar density about twice that of the birch forest of this investigation.

#### 4.3. Birch seed crop

The fluctuations in birch catkin occurrence since 1979 appear in the diagram of Fig. 7. Before 1979 two seasons, 1968 and 1971, displayed such an extremely rich birch flowering followed by a superabundant supply of seeds the following season that this was obvious without quantitative measurements.

### 5. The bird density fluctuations

#### 5.1. The total community

The sixteen most abundant annually breeding species are presented in the species frequency diagram of Fig. 3. *Phylloscopus trachilus* is by far the most abundant species making up about 40% of the community. Its rank has been challenged only once, in the *Epirrita* year of 1975, by *Fringilla montifringilla* whose average share of the community is about 18%. Its position as the second most common species has been undisputed with the exception of 1968 and 1971, when the density of *Carduelis flammea* rose to the same level. As for the rest, neighbouring species in the long tail of the diagram often exchange positions between seasons.

The fluctuation pattern of the community is demonstrated in Fig. 4. The density change is considerable around a mean value of 400 territories/km<sup>2</sup>, with 260 and 550 as the extreme values. The coefficient of variation is 19% which indicates a community stability characteristic of northern bird communities (cf. Järvinen 1979). The four peak densities have been recorded in seasons with superabundant birch seed supply or with a mass occurrence of *Epirrita* caterpillars.

A conspicuous event is the decline in density which occurred during the six seasons after 1973, and which finally resulted in a reduction of the bird density by nearly 50%. The mean density index of the seven seasons (1976-1982) following the *Epirrita* period is only 327, a 23% reduction from the mean value of 417 for the seven years (1966-1972) preceding the *Epirrita* period ( $t = 3.05$ ,  $P < 0.01$ ).

#### 5.2. The species populations

The following comments on the fluctuation curves (Fig. 5) will emphasize density changes

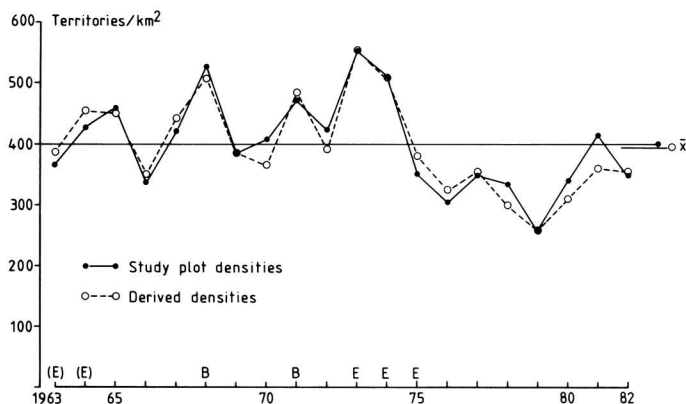


Fig. 4. The density fluctuation of the total bird community over two decades. The level of the mean densities ( $\bar{x}$ ) of the period is indicated by the horizontal lines. B = superabundant birch seed crop, E = mass outbreak of *Epirrita autumnata*.

related to the *Epirrita* years and birch seed years and significant trends.

*Phylloscopus trochilus* was responsible for much of the recent density decrease in the community. It shows a 25% decline when the seven-year periods before and after the *Epirrita* years are compared. It increased only moderately the first year of *Epirrita* outbreak and then started its steep and continuous decline when *Epirrita* was still superabundant.

*Sylvia borin*, *Anthus trivialis* and *Phoenicurus phoenicurus*, all tropical migrants, showed no significant increase during the first *Epirrita* year and they all declined during the following ones. *Ph. phoenicurus* and *A. trivialis* have maintained their population numbers throughout the investigated period, whereas *S. borin* (like *Ph. trochilus*) has been more sparse after the *Epirrita* years than before.

*Ficedula hypoleuca* was censused only outside nest-box plots, but the proximity to nest-box plots could nevertheless have affected the number of singing males of this partly polyterritorial bird in areas devoid of boxes. Therefore, the figures should be treated with caution regarding density levels. The species seems to have participated in the recent community reduction, showing a 50% decrease when the seven years before and after the *Epirrita* period are compared.

*Turdus iliacus*, *T. pilaris* and *T. philomelos* have all contributed significantly to the density decrease of the bird community. The first-mentioned two species often fluctuated similarly in regard to the direction of the density change between years. Their declining trend, which started after their common peak in the birch seed year of 1968, has appeared to the

field workers as one of the most remarkable events of the two decades. The birch seed year of 1971 showed no marked rise in thrush densities.

*Luscinia svecica*, *Prunella modularis* and *Emberiza schoeniclus* show no significant density trends over the whole period. *P. modularis* and *E. schoeniclus* fluctuated in an almost identical way throughout the two decades. *L. svecica* often followed the fluctuations of the other two species (positions of peak and bottom years). All species showed a marked increase in the first *Epirrita* year although the attained densities were not superior to other peak values during the two decades.

The density indices of *Fringilla montifringilla* show no consistent trend. They are distributed on two levels corresponding to about 50 and 75 terr./km<sup>2</sup> with the *Epirrita* years of 1973 and 1974 as outstanding exceptions when the densities suddenly doubled. Interestingly, the density had returned to the upper normal level already in 1975 when *Epirrita* was still abundant. The density rose from the lower to the upper level in both birch seed years.

The fluctuations of *Carduelis flammea* give the impression of an irruptive species. The density indices increased remarkably in the two years of superabundant birch seed crop. The season of 1978 is equally interesting with a density figure near nil. The species shows, apart from these three exceptional years, a significant increasing trend in population numbers (Enemar & Nyström 1981).

The fluctuation curves of *Fringilla coelebs*, *Muscicapa striata* and *Parus montanus* do not say more than that the species belong to those

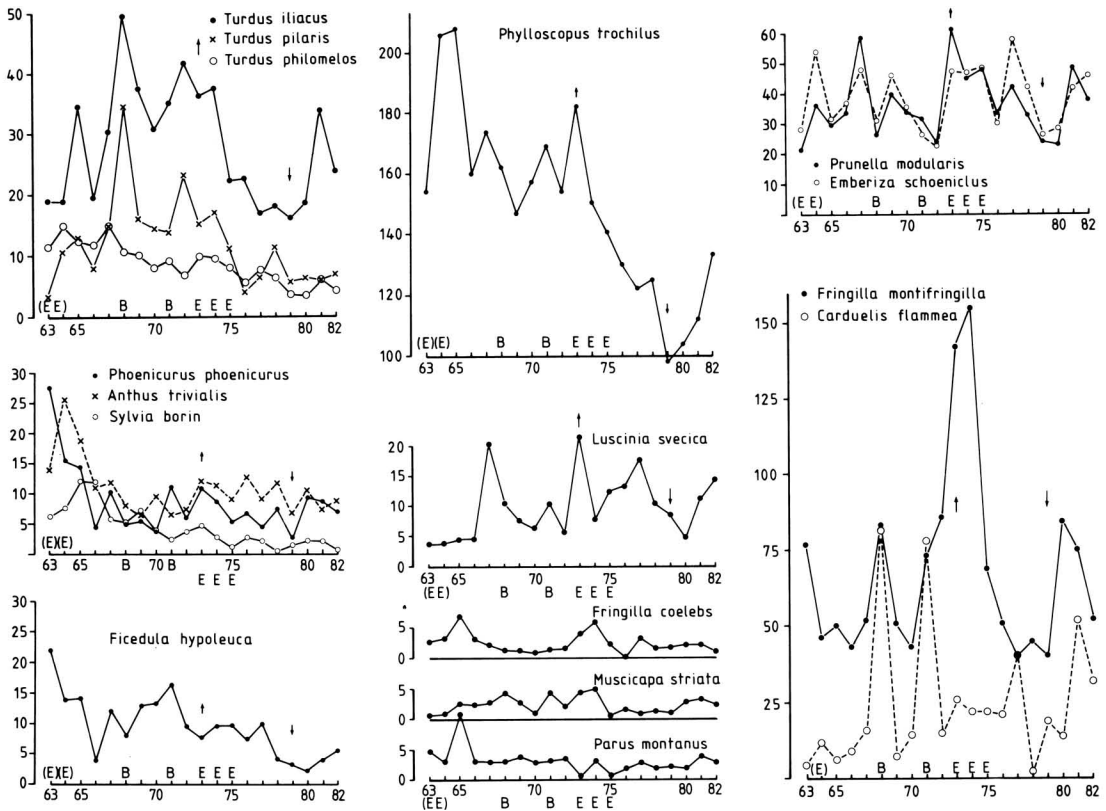


Fig. 5. Fluctuation curves of the 16 regularly breeding small passerine species. Ordinata: numerical values of the derived density index (approx. corresponding to territories/km<sup>2</sup>). Abscissa: years, with occurrence of superabundant birch seed crop, B, and of mass outbreaks, E, or moderate outbreak, (E), of *Epirrita autumnata* caterpillars indicated. Arrows denote peak and bottom years, respectively, of the community density.

annually present in the investigated birch forest. The population numbers are too low to justify an estimate of the fluctuations from these census methods.

## 6. Interpretations and discussion

There are hardly any possibilities to scrutinize the general findings of the present study through comparisons with similar investigations. Many long-term annual census programs are apparently in progress on different scales in several countries although summaries of the results are still lacking. A few study plot investigations of impressive duration (more than 15 years) are available: Kendigh (1982), 50 years of mapping census of an isolated deciduous forest of 24 ha; Beven (1976), 27 years of mapping of 16 ha of oak

wood; and Yapp (1969), 18 years of transects ("contacts per hour") in a 87 ha plot of oak wood. Special cases are the 40-year census program covering the treeless island of Skokholm (96 ha) presented by Lack (1969), and the 34-year census of the warbler populations in 80 ha of oakland and grass orchards (Price 1961). In most cases the mode and accuracy of the census work in these studies are incompletely described. With the exception of the island investigation, any changes uncovered in community composition and density are invariably ascribed to more or less pronounced habitat alterations.

The bird fauna of the Fennoscandian sub-alpine birch forest has been repeatedly investigated with widely differing accuracy and at different scales in time and space. See Ytreberg (1972) for references which can now be supplemented with Southern & Venables

(1939), Moksnes (1973), Røv (1975) and Järvinen & Väisänen (1978). Based on the available relatively short-term studies, Hogstad (1975a) has outlined the general features of the bird community of the habitat in question. His conclusions should be considered preliminary until more long-term census results are available. While awaiting the latter, a comparative interpretation of the community structure and behaviour will be omitted here.

### 6.1. The quality of the field data

When the present investigation was designed, three principal requirements were identified which should be fulfilled to justify the use of the census results for the demonstration and interpretation of the species content and the fluctuation patterns of the bird community and its populations in the birch forest: (1) the size of the investigated community, (2) the duration in years, and (3) the uniformity and continuity of the census work. How does this study match these claims?

(1) The investigated bird community consists of roughly 4000 breeding pairs. This means, in our opinion, that the available population size of the regularly breeding passerine species (cf. Fig. 3) is large enough to minimize the risk that a considerable change in estimated number is due to chance only, when a combination of territory mapping (>40 ha) and line transects (about 3000 records) is applied. To be on the safe side, the three most sparse of the regularly breeding species have been excluded from the comparative analyses in the following.

(2) The desirable number of investigated seasons is determined by the length of environmental cycles of importance for the birds. The most protracted of the known cycles in the subalpine forest is that of *Epirrita autumnata*, which displays mass outbreaks at intervals of about ten years (Tenow 1972). This study comprises two such cycles which should be considered a minimum, especially as the first outbreak was a rather moderate one.

(3) As might be understood from the description of the field work and methods (p. 322), the uniformity and continuity of the census work has been maintained without interruption throughout the 20-year period. The only exception is the incomplete line transects of the first two years, which therefore have been omitted from certain analyses.

Thus it seems reasonable to consider the quality of the field data to be good enough to provide reliable information on the species content as well as the dynamics of the bird community as far as general trends and major fluctuations are concerned. This view gains some support from the statements by Wiens (1981) in his meritorious study regarding scale problems in avian censusing. Our study may have reached the required "scale in space", probably also the "scale in time", as it refers to a bird community of a fairly homogeneous forest area censused 20 years in succession. The study thus mainly concerns the  $\alpha$ -diversity level of Wiens.

### 6.2. The number of species

The annual number of species in the line transect material has fluctuated between 30 and 46, with 37 as a mean value, if only the actual and potential breeding species are considered. The coefficient of variation is 9.5 % which is rather low for a northern habitat (cf. Järvinen 1979). As seen from the diagram of Fig. 2 the species number had its peak in 1974, the year when the outbreak of *Epirrita* caterpillars culminated. It is puzzling that the subsequent season, when *Epirrita* was still very abundant (Fig. 6), was the second poorest of the whole period. The diagram also gives the impression that the number of species has increased over the two decades. This is confirmed by regressing the species number on time, which gives an average increase of a third of a species per year ( $b=0.367$ ,  $P<0.05$ ). Interestingly, this increase is not associated with a corresponding increase in the bird density of the community. As shown in the following, the total density has dropped significantly during the last decade.

No annually breeding species has disappeared during the investigated period. The question is whether the general increase in number of species has included an addition of regularly breeding species. Table 3 presents the intermittent appearance in the study area of twelve passerines which breed in more southerly regions of the country or in the prealpine conifer belt nearby. All species but one (*Sylvia curruca*) have been established to have bred at least once in the area. Of these *Hippolais icterina* was first observed in 1969 and has been recorded the last five seasons (incl. 1983) in sequence. It has often been

Table 3. Appearance of irregularly occurring passerine species in the study area 1963–1982.

	1963	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
<i>Troglodytes troglodytes</i>					x							x			x					
<i>Erithacus rubecula</i>			x	x								x	x							
<i>Saxicola rubetra</i>	x	x	x	x							x	x	x	x	x		x	x	x	x
<i>Turdus merula</i>		x	x	x	x	x			x	x	x				x			x		x
<i>Hippolais icterina</i>							x	x			x			x			x	x	x	x
<i>Sylvia curruca</i>		x	x					x												
<i>Sylvia atricapilla</i>							x				x	x						x		x
<i>Phylloscopus sibilatrix</i>	x	x										x							x	
<i>Certhia familiaris</i>		x	x																x	
<i>Pyrrhula pyrrhula</i>		x	x	x			x	x	x		x	x	x	x	x	x	x	x	x	x
<i>Emberiza citrinella</i>				x				x			x	x			x					
<i>Emberiza hortulana</i>		x										x								
Totals	2	8	5	5	2	1	2	5	2	1	6	8	3	3	5	2	3	6	3	5
<i>Epirrita</i> , mass outbreak	(x x)										x	x	x							

represented by several individuals and should now perhaps be included among the annually appearing and breeding species. The status of *Sylvia atricapilla* is still uncertain although the bird has been observed during the last four seasons (incl. 1983). As to the presence of the remaining ten species of Table 3, no trend can be discerned other than that the two peak years are associated with *Epirrita* outbreaks. No new non-passerine species has appeared and settled in the area.

The number of species and many species populations have apparently increased during this century in North European bird communities (Järvinen & Väisänen 1977, Järvinen 1978, 1980, Ulfstrand 1980, Järvinen & Ulfstrand 1980). However, to say that the development of the species richness in the study area is a reflection of that general and large-scale trend is probably going too far. It is definitely going too far to surmise that a causal relationship exists between the rise in species number and decline in density of the community, because the community does not seem to be a saturated one (p. 333).

### 6.3. The influence of the *Epirrita autumnata* outbreaks

The second of the two outbreaks during the 20-year period was an overwhelming one, lasting three seasons (Fig. 6). It was generally observed that the birds used the green cater-

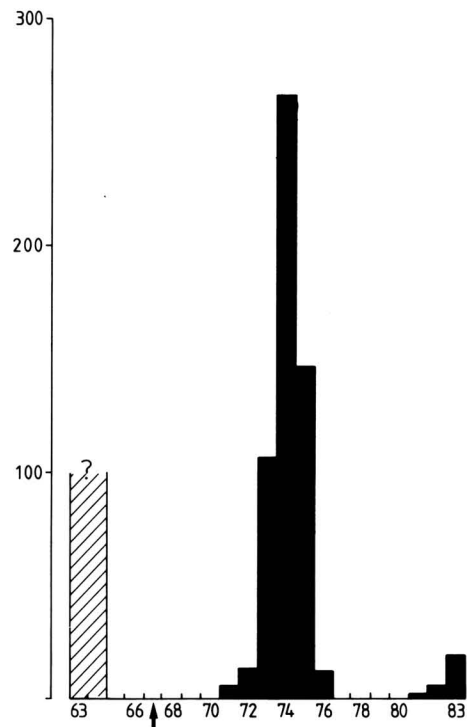


Fig. 6. The occurrence of *Epirrita autumnata* caterpillars. Ordinate: Number of caterpillars per 1000 leaf clusters (short shoots) as averaged from three study plots in the birch forest. The hatched column indicates the first and moderate outbreak although the caterpillar frequency was unknown as the insect census work did not start until in 1967 (arrow). (From Andersson & Jonasson 1980, and G. Andersson and T. von Proschwitz pers. comm.)

pillars for feeding their nestlings. This was confirmed for such species as *T. iliacus* (Arheimer 1978) and *C. flammea* (Enemar & Nyström 1981). However, the bird species showed only a moderate or no density increase when the mass outbreak started, with the exception of *F. montifringilla*. This species gathered and bred in outstanding numbers the first two of the *Epirrita* years. Its decline in the third year could have been due to a movement into the heath birch areas where *Epirrita* culminated that year (Andersson & Jonasson 1980).

The response of the bird community density to caterpillar outbreaks differs between census investigations probably because of varying proportions of responding species or varying interference by other environmental factors (e.g. Morris et al. 1958, Holmes & Sturges 1975, Morse 1978). Other study plot investigations in the subalpine birch forest indicate that *Epirrita* outbreaks are followed by an increase in community density (Silvola 1967, Ytreberg 1972) and that *F. montifringilla* seems to be the main responding species (Silvola 1967, Hogstad 1969) whereas the abundant and foliage-gleaning *Ph. trochilus* is unaffected (Ytreberg 1972). It is necessary to examine more *Epirrita* outbreaks to understand the "hesitating" reactions of the bird fauna to this apparently superabundant food supply. The next mass occurrence in our study area will be around 1985.

#### 6.4. The influence of the birch seed crop

The seed production of the birch shows annual fluctuations as does the quality of the nuts (e.g. Sarvas 1952). According to the experiences in the investigated forest superabundant seed production is a rare and irregular event, which has occurred only twice in 20 years. The thrush species, *T. iliacus* and *T. pilaris*, showed a marked peak in the first birch seed season (1968) but not in the second one (1971). This indicates that they are not necessarily influenced by the birch seed supply, and nor would this be expected given their known diet. *F. montifringilla* increased in density in both seasons but only to the upper normal density level of the species. The significance of this reaction remains uncertain. *C. flammea* is the only species showing outstanding population peaks in both years of the superabundant seed crop. Enemar & Nyström (1981) have

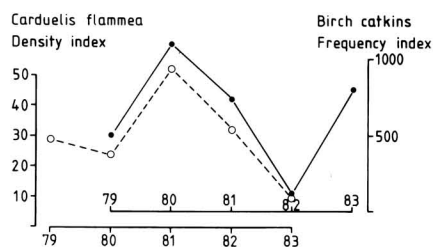


Fig. 7. The relation between the density of *Carduelis flammea* (circles) and the supply of birch seeds, expressed as the catkin frequency (dots) of the preceding year. (The birch flowering data from G. Andersson and T. von Proschwitz, pers. comm.)

shown that this species benefits from a rich birch seed supply which influences several aspects of the breeding activities. They also suggested that this has promoted the development of occasional nomadic behaviour, i.e. more or less extensive movements in the breeding region in search of a rich birch seed crop. Such movements have apparently caused not only the density peaks in 1968 and 1971 but also the bottom value in 1978. However, the results of the birch catkin census indicate that the species may also adjust its population density very closely to minor changes in the seed crop (Fig. 7), although the number of investigated seasons are few and therefore the correlation may be considered "too good to be true".

#### 6.5. The influence of the rodent cycles

Other investigations have indicated a correlation between fluctuations in the number of passerine birds and small mammals in subalpine and alpine areas (Moksnes 1973, Lien et al. 1974) although only single rodent cycles were studied. The vole cycles have been conspicuous in our study area and the number of breeding *Buteo lagopus* has fluctuated accordingly (Fig. 9). However, no significant correlation with the fluctuations of the passerine bird community, its species groups or single species populations has yet been found.

#### 6.6. Comparing the species fluctuations

As seen from the density fluctuation diagrams (Fig. 5) certain species tend to fluctuate



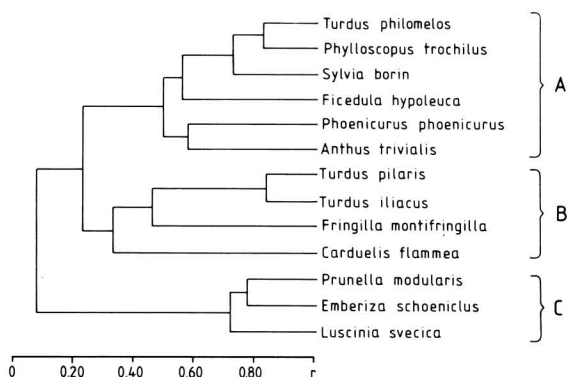


Fig. 8. Dendrogram showing the grouping of the species according to the degree of similarity, expressed as the correlation coefficients ( $r$ ), of their density fluctuations 1965–1982. The derivation of the dendrogram (see below) unveils three “fluctuation groups”: A, B, and C.

in a similar way. The species relationships in this respect have been the subject of a cluster-analysis following the technique used by Cody (1974) to demonstrate how the niche overlap is distributed among the species of a community. As a measure of the degree of coincidence between the fluctuation patterns, the ordinary coefficients of correlation ( $r$ ) have been calculated. To compensate for the bias which appears especially when pooling species with widely differing population densities, the density indices have first been transformed to proportional values ( $P$ ) according to the formula  $P = (x - x_{\min}) / (x_{\max} - x_{\min})$  where  $x$  is the derived density index of a species (cf. p. 324) and  $x_{\max}$  and  $x_{\min}$  are the peak and bottom densities, respectively, of the investigated seasons. The new indices thus fluctuate from zero to unity for all species. The analysis has been restricted to the 18-year period 1965–1982 and to the thirteen most abundant of the passerine species (mean study plot density  $> 5$  terr./km<sup>2</sup>). The resulting grouping of the species according to their “fluctuation relationships” are shown in the dendrogram of Fig. 8.

The dendrogram displays three distinctly separated clusters. Interestingly, with the exception of *T. philomelos*, cluster A includes all the long-distance migrants destined for tropical Africa. *T. philomelos* would be expected to occur in cluster B or C which consist of short-distance migrants with winter quarters mainly in western parts of Central Europe. *L. svecica*, a long-distance migrant bound for south Asia (SOF 1978), is the only exception in

the latter two clusters.

All species except one (*T. iliacus*) of cluster B are known to intermittently show more or less obvious irruptive migratory behaviour, whereas those of cluster C do not. Roughly speaking, according to the dendrogram clusters A, B and C represent three modes of population fluctuation patterns and these are related to three different migratory strategies, namely long-distance African, short-distance irruptive, and short-distance non-irruptive, respectively.

The explanation for this situation is that events affecting the survival rates in common wintering areas and along common migration routes are of great importance in determining the size of populations in the study area. This is not very surprising considering the fact that all species, with the occasional exception of *C. flammea*, are away from the breeding area for two-thirds of the year, or more. The importance of remote wintering grounds for the short-term or long-term dynamics of northern bird communities has been stressed previously (e.g. Lack 1968, Järvinen 1978, 1980, Järvinen & Ulfstrand 1980). This is not to say that annual environmental changes in the breeding area are of no interest. In fact, it is possible to roughly outline common features of the breeding area ecology of the species within each cluster. This is to be expected since the breeding and non-breeding ecologies have not evolved independently. Thus cluster A is made up of exclusive insect-eaters (except *T. philomelos*). The species of the “tight” cluster C are all typical “bottom-dwellers” in the habitat. The breeding area ecology of the loose cluster B is rather heterogenous as regards the breeding behaviour as well as the feeding habits, although non-insect food is important (seeds or lumbricids).

It is evident that certain breeding area factors affect the bird numbers in the area. The relation between the superabundant birch seed crop and the *C. flammea* density is a good example. But we have consistently found that other important breeding area factors such as adverse weather conditions (periods of cold spells, heavy rain or snow) strike most species irrespective of the cluster to which they belong resulting in abandoned clutches, chick starvation etc. (Enemar et al. 1965, Pulliainen 1978, Hildén et al. 1981). We think therefore that factors operating during the migration and in the wintering areas are more important than breeding area factors in generating the

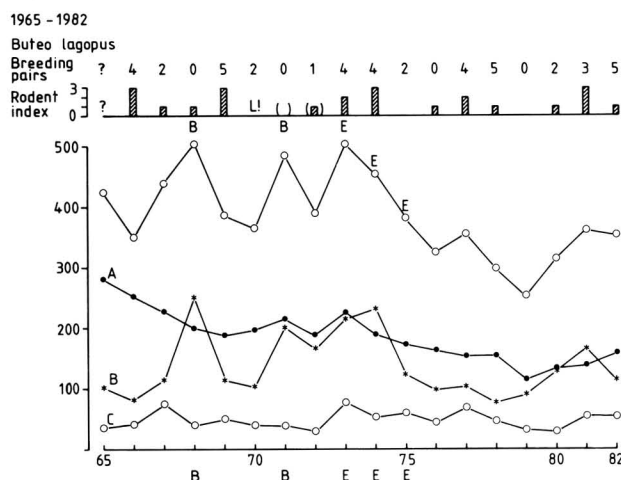


Fig. 9. The fluctuation curves of the species groups A, B, and C (see Fig. 8) and of the total community. The cycles of the small rodents are indicated as are the number of breeding pairs of *Buteo lagopus*. L! = invasion of *Lemmus lemmus* in large numbers during the breeding season, B = superabundant birch seed crop, E = mass outbreak of *E. autumnata* caterpillars.

three principal patterns of population fluctuations among the species of this bird community.

The amplitude of the relative density fluctuations differs widely among the species. The coefficient of variation for the 13 most abundant and regularly breeding species varies from less than 20% (*Ph. trochilus*) to more than 80% (*C. flammea*, *S. borin*). This is in agreement with Järvinen's (1979) characterization of the stability of a northern bird community. According to the *V*-test suggested by the same author (Järvinen 1979:61: *V* = the ratio of the sum of the variances of the species densities and the variance of the sum of the species densities) the community instability (cf. p. 325) is due to the scarcity of compensating species fluctuations (*V* = 0.44). In other words, rather clear parallel fluctuations are common. These are also identified and grouped by the cluster-analysis above, resulting in the species groups A, B and C. Interestingly, not even these groups show compensating fluctuations among themselves as *r* > 0 (Fig. 7) and *V* < 1 (= 0.77). The interpretation is, again, that the species populations are similarly affected, by (a), common environmental factors in the non-breeding season within each species group independently of the other groups and (b), breeding area factors common to the whole community.

The results of the analyses give the impression that the studied bird community is not a competitive one. The results of other investigations in similar habitats are at

variance with this assumption as competitive interrelations have been suggested to be important especially between *Ph. trochilus* and *F. montifringilla* (Hogstad 1975a, b, Røv 1975, Angell-Jacobsen 1980).

#### 6.7. General trends in the community dynamics

The reduction of the community density after the *Epirrita* years 1973–75 is a significant event (Fig. 9) which is hard to explain with the data at hand and as no observable habitat change had occurred. This decline is strengthened by the preliminary census results from 1983 which turn the slight density increase during the last few years into another density low. Many species of groups A and B have taken part in the decline with *Ph. trochilus* and the *Turdus* species as the main contributors to the density loss during the last decade. The fact that the birch seed years occurred during the first decade explains only a minor proportion of the density change. Two possible causes, which suggest themselves, are:

(1) Increased mortality during the non-breeding seasons of recent years due to general deterioration of the conditions in the winter quarters or during migration.

(2) Impaired reproductive success as a consequence of e.g. a climate change in the breeding area during the last decade. Both factors may contribute, but the fact that species with widely differing migration and wintering strategies are involved indicates that the common breeding area conditions such as the

frequency and length of harsh weather periods should be given primary consideration. This remains to be done.

As expected, each of the species groups displays its own fluctuation course. Group A, the tropical migrants + *T. philomelos*, making up an average of 47% of the community, shows a steadily declining trend over the eighteen years which is significant ( $b = -6.3$ ,  $P < 0.001$ ). The dominant *Ph. trochilus* is responsible for most of this decrease, which, to our knowledge, has not been reported from other long-term census projects within or outside Sweden.

It is obvious that group B, the irruptive species, is the cause of the marked changes in the community density although these species amount to only 35% of the community. This is mainly a consequence of the fact that two species of the group seem to show clear response to the occasional superabundance of birch seeds or *Epirrita* caterpillars. Group C, finally, displays no dramatic events or trends whatsoever.

#### 6.8. On community saturation

The general view that bird communities are saturated as regards species content and density has been doubted for northern bird faunas by Järvinen (1978, 1980) and Ulfstrand (1980). Wiens (1977, 1983) has reviewed the different opinions on these matters and critically evaluated the possibilities of reaching safe conclusions regarding the existence of a saturated state. Järvinen (1980) argues that this requires community investigations lasting for decades. This is surely a sound instruction, although the recommended scale in time is of no use unless the quality of the habitat under study remains constant (Järvinen 1978). It is of minor interest, in the present context, to establish that a change in community composition has occurred in parallel with a habitat perturbation of some kind, as is often the case. A good example of reliable information is the one obtained in a constant peatland area in Finland (Järvinen 1978). The subalpine birch forest of the present investigation may be another one. The following observations and results speak in favour of the view that the community of the birch forest is not saturated.

(1) The comparative analysis of species fluctuations indicates that compensating fluctuations are not characteristic features of the

community (p. 332). It is presumed that the intensified competition following saturation should have generated a significant number of such fluctuations.

(2) The comparative analysis also indicates that factors operating in the wintering areas affect the breeding area densities (p. 331). This connection is expected to be manifested more clearly in an unsaturated than in a saturated community.

(3) The interpretation of the *Epirrita* outbreak as a superabundant food supply does not result in unequivocal statements. One can only observe that most species populations declined in seasons when *Epirrita* was still superabundant which is hardly compatible with the view that the community remained saturated (provided that the caterpillar quality remained constant throughout the three *Epirrita* seasons and that the supply of other necessary food components persisted unaffected).

(4) The community has so far displayed a slow and significant increasing trend in number of species inhabiting the study area (p. 328) although no observable habitat change has occurred.

(5) A substantial increase in the density of *F. hypoleuca* brought about with the aid of nest-boxes did not affect the density of the other species, at least not over a six-year period (Enemar & Sjöstrand 1972).

Generally speaking, the mere fact that practically all birds disappear from the study area every late summer or autumn and that many species breed there at or near their distributional fringe makes a saturated state of the breeding community less probable. What mechanism guarantees that the required minimum number of birds returns and settles every spring, often from far distant winter quarters, to saturate the habitat? There is none as far as we know. It seems reasonable, therefore, that it is the advocates of the community saturation hypothesis who bear the burden of proof.

Moreover, findings from the bird assemblage in the investigated subalpine birch forest recall the questions put forward by Wiens (1980): Are bird communities real? Do they really exist at all, in any functional biological sense? In fact, the analyses and interpretations of the 20-year census results presented here have not yet provided good reasons to answer these questions in the affirmative.

*Acknowledgements.* The field work was supported by grants B2180-8, -10, -13, -14, -17, -19, -21, -117, -121

from the Swedish natural science research council (to A. Enemar). Grants have been received also from the Royal Swedish Academy of Sciences, Carl Trygger's Foundation, the foundation "Seth M. Kempes Minne" and the University of Göteborg. Our thanks are due to Yrjö Haila and Olli Järvinen for useful comments and suggestions on the

manuscript, and to Mona Möllerstedt (typing out the manuscript), to Aino Falck-Wahlström (drawing the diagrams), to Catherine Louise Lamb (linguistic revision) and to fellow field workers of the LUVRE project, especially Ingvar Lennerstedt for mapping study plot A5 for us.

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Received 30.IX.1983

Printed 16.XI.1984

Appendix 1. Number of observations made during the annual line transects in the rich subalpine birch forest on the south-facing slopes of the mountains of Gaisfjället and Valle, Swedish Lapland. The figures are given for the two census-takers separately (left number = Anders Enemar 1963–1982, right number = Bengt Sjöstrand 1965–1974 or Lars Nilsson 1976–1982).

Year	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
<i>Anthus trivialis</i>	29/-	61/-	126/46	56/48	34/48	18/31	26/30	28/54	16/26	24/32	33/39	51/31	37/-	52/65	37/28	58/61	40/38	28/51	28/21	45/34
<i>A. pratensis</i>	-	13/-	2/-	-	4/-	3/-	2/-	3/1	-	-	1/-	3/1	3/-	1/-	1/-	1/3	6/5	1/2	3/-	6/-
<i>Motacilla flava</i>	1/-	-	-	-	-	1/-	1/1	-	1/1	1/-	3/1	7/3	5/-	8/-	7/-	9/3	7/6	3/5	6/1	10/3
<i>M. alba</i>	-	-	-	-	-	-	-	-	-	-	-	-	1/-	1/-	4/-	6/3	1/-	-	1/-	1/1
<i>Bombicilla garrulus</i>	-	-	-	-	-	-	1/-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cinclus cinclus</i>	-	-	-	-	-	-	-	1/-	1/1	2/-	-	-	1/-	2/-	-	-	-	-	-	-
<i>Troglodytes troglodytes</i>	-	-	-	-	1/-	-	-	-	-	-	-	3/2	-	-	2/-	-	-	-	-	-
<i>Prunella modularis</i>	22/-	43/-	93/37	79/72	85/118	30/48	79/84	83/59	50/51	54/38	77/104	101/69	98/-	84/73	97/55	90/72	78/60	33/52	79/89	101/72
<i>Erithacus rubecula</i>	-	6/-	-	1/-	-	-	-	-	-	-	-	4/2	1/-	-	-	-	-	-	-	-
<i>Luscinia svecica</i>	8/-	9/-	25/12	21/20	87/53	35/28	35/27	32/23	36/30	25/19	62/66	41/17	50/-	58/71	76/49	55/52	44/55	10/31	37/40	62/71
<i>Phoenicurus phoenicurus</i>	58/-	37/-	117/28	24/15	42/29	18/12	21/23	22/10	39/33	31/14	36/27	37/26	21/-	33/31	22/11	42/33	12/19	25/45	26/35	21/43
<i>Saxicola rubetra</i>	5/-	6/-	4/1	1/1	-	-	-	-	-	-	2/-	1/1	6/-	2/-	5/-	-	7/4	-	2/-	5/1
<i>Oenanthe oenanthe</i>	-	-	-	-	-	1/-	1/-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Turdus torquatus</i>	-	-	-	-	2/1	-	-	1/-	-	1/2	3/2	-	-	-	2/-	-	-	-	3/-	1/1
<i>T. merula</i>	-	2/-	2/-	2/-	3/-	1/-	-	-	2/-	2/-	-	-	-	-	1/-	-	-	1/-	-	1/-
<i>T. pilaris</i>	6/-	25/-	115/21	62/13	61/41	95/111	89/41	78/46	48/42	100/83	53/37	81/47	46/-	20/20	27/20	61/53	26/38	17/31	16/25	21/42
<i>T. philomelos</i>	24/-	36/-	93/27	64/42	54/50	35/28	59/21	38/29	34/25	34/20	39/20	45/25	33/-	30/22	24/26	39/26	27/18	10/19	21/19	22/17
<i>T. iliacus</i>	40/-	45/-	212/91	94/84	106/106	148/146	163/152	127/135	113/113	179/148	137/79	151/124	91/-	94/116	76/45	72/111	101/91	42/112	92/147	99/119
<i>Acrocephalus schoenobaenus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hippolais icterina</i>	-	-	-	-	-	-	-	1/-	-	-	2/-	-	-	-	-	-	1/-	5/2	3/4	-
<i>Sylvia curruca</i>	-	1/-	1/-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. borin</i>	13/-	18/-	73/33	60/47	20/19	17/14	20/40	14/21	3/12	14/14	22/6	13/8	5/-	18/7	8/6	4/-	13/7	9/3	9/5	5/3
<i>S. atricapilla</i>	-	-	-	-	-	-	-	-	-	-	3/-	3/1	-	-	-	-	-	2/-	-	1/-
<i>Phylloscopus borealis</i>	-	-	-	-	-	-	-	-	-	-	1/-	-	-	-	-	-	-	-	-	-
<i>Ph. sibilatrix</i>	1/-	3/-	-	-	-	-	-	-	-	-	-	1/-	-	-	-	-	-	1/1	-	-
<i>Ph. trochilus</i>	321/-	488/-	1357/520	642/801	579/632	465/500	533/679	636/704	533/561	592/616	542/543	588/513	573/-	629/586	502/356	645/622	629/533	284/518	347/433	658/572
<i>Muscicapa striata</i>	1/-	2/-	16/1	10/2	9/2	13/1	11/4	8/4	14/8	9/3	13/2	20/1	3/-	7/7	4/2	9/3	5/9	6/17	10/12	14/6
<i>Ficedula hypoleuca</i>	46/-	34/-	115/28	26/10	57/26	27/23	75/30	66/46	62/46	48/28	24/22	63/14	40/-	43/27	49/24	30/13	21/20	6/13	11/18	17/34
<i>Parus montanus</i>	10/-	7/-	74/18	13/10	10/11	9/12	15/8	12/8	10/15	14/8	1/6	13/11	3/-	7/9	9/10	11/6	13/8	3/10	13/13	14/10
<i>P. cinereus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1/-	-
<i>P. major</i>	3/-	1/-	12/4	1/4	5/-	4/2	4/3	5/6	1/-	3/1	4/2	5/4	7/-	1/-	7/3	5/2	6/4	2/2	4/5	5/2
<i>Certhia familiaris</i>	-	1/-	2/-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lanius excubitor</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1/1	-	-	-	-



Year	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
<i>Fringilla coelebs</i>	5/-	8/-	45/21	13/15	7/8	4/3	5/1	4/4	4/6	6/4	12/3	24/13	9/-	-/1	18/5	6/9	12/5	10/2	8/6	6/4
<i>F. montifringilla</i>	160/-	108/-	338/120	198/188	172/193	251/244	213/212	170/202	219/256	298/374	444/405	590/525	284/-	212/266	167/119	219/235	230/254	214/405	233/294	240/239
<i>Carduelis spinus</i>	3/-	2/-	14/-	2/1	2/-	2/-	3/-	2/-	19/2	8/-	-	12/-	-	-	4/-	-/2	3/5	2/5	10/13	1/-
<i>C. flammea</i>	9/-	28/-	38/13	43/39	58/54	249/241	24/31	60/62	258/250	55/64	73/80	95/70	91/-	96/99	149/130	11/7	153/195	49/152	137/232	108/187
<i>C. hornemanni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-/1	-	-	-
<i>Loxia sp.</i>	-	-	-	-	-	4/-	-	1/-	1/-	1/1	-	-	-	2/2	1/-	-	1/-	-/1	-	1/-
<i>Pinicola enucleator</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1/-	-	-	-	-	-
<i>Pyrrhula pyrrhula</i>	-	1/-	8/3	5/-	-	-	3/-	-/1	1/2	-	2/3	1/5	2/-	6/1	5/2	7/3	4/6	1/6	9/10	5/2
<i>Emberiza citrinella</i>	-	-	-/1	-	-	-	-/1	-	-	-	2/-	2/1	-	-	3/-	-	-	-	-	-
<i>E. hortulana</i>	-	1/-	-	-	-	-	-	-	-	-	-	1/-	-	-	-	-	-	-	-	-
<i>E. schoeniclus</i>	29/-	64/-	104/38	87/76	77/91	58/34	98/91	88/60	47/38	54/39	81/61	100/74	99/-	80/62	136/74	100/117	64/92	30/85	68/77	93/120
<i>Bucephala clangula</i>	-	-	-	-	-	-/2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Circus cyaneus</i>	-	-	-	-	-	-	2/-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Buteo lagopus</i>	2/-	3/-	-	7/1	4/2	-	14/15	8/6	-	1/1	6/8	3/6	9/-	-	9/6	13/16	2/2	3/3	6/11	14/16
<i>Falco tinnunculus</i>	1/-	-	1/-	-	-	1/-	-	-	-	1/-	-	-	-	-	-	-	-	-	-	-
<i>F. columbarius</i>	1/-	2/-	4/2	2/2	2/2	1/2	1/-	2/3	-/4	3/1	1/1	3/1	3/-	-/2	3/-	1/-	-/2	-	1/-	2/2
<i>Bonasia bonasia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-/1	-	-	-	-	-	-
<i>Lagopus lagopus</i>	1/-	8/-	18/3	8/3	11/8	8/4	16/10	21/10	8/14	7/6	3/3	4/5	17/-	4/11	7/12	11/15	7/15	4/6	5/5	12/13
<i>Tetrix tetrix</i>	4/-	2/-	16/8	12/5	6/10	7/12	5/2	6/2	3/7	2/-	1/2	2/-	-	1/2	1/4	1/1	-/2	-/1	-	-/1
<i>Tetrao urogallus</i>	1/-	2/-	6/2	3/1	-/1	1/1	4/-	4/1	1/1	-/1	2/2	2/-	1/-	3/2	5/1	1/-	2/-	-/1	2/-	-
<i>Gallinago gallinago</i>	-	-	-	-	-	-	4/-	-	-/1	-/1	1/-	2/-	-	2/-	-/1	-/4	-/1	-/3	1/1	2/3
<i>Scolopax rusticola</i>	-	1/-	-	1/2	5/4	5/5	5/-	2/4	10/2	5/2	-	1/1	-	-	-	-	-/1	1/2	-	4/5
<i>Tringa glareola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-/1	-	-
<i>T. hypoleucos</i>	-	-	-	-	-	-	-/1	-	-	-	-	-	-	-/1	-	-	-/2	-	-	-/2
<i>Columba palumbus</i>	-	-	-	-	-	-	-	-	-	-	-	2/-	-	-	-	-	-	-	-	-
<i>Cuculus canorus</i>	2/-	2/-	4/1	1/2	-	1/3	1/3	1/2	2/4	4/-	5/-	3/1	1/-	4/11	5/5	7/11	6/11	2/7	-/6	1/3
<i>Surnia ulula</i>	2/-	3/-	-	-/1	1/1	-	-	-/1	2/2	-	-	9/2	-	-	3/2	1/-	-	-	-/2	4/6
<i>Jynx torquilla</i>	-	-	3/1	-/1	2/-	-/1	4/1	4/1	-	-	5/3	3/-	6/-	2/1	6/5	5/2	3/9	1/3	4/3	-/2
<i>Dendrocopos minor</i>	-	-	-	1/-	-	-	-	-	2/-	-	1/-	-	-	-/1	-	-	-	-	1/3	1/3
<i>Picoides tridactylus</i>	-	1/-	2/1	1/2	1/1	2/-	1/2	-	1/-	-/1	1/1	4/2	-	1/-	1/1	2/1	-/2	-/1	1/1	1/1
<i>Pica pica</i>	-	-	-	-	-	1/-	-	-	-	-	-	-	-	-	-	1/-	-	-	-	-
<i>Corvus corone cornix</i>	1/-	3/-	8/1	3/-	10/2	7/6	2/3	10/13	7/6	6/2	2/3	13/9	12/-	10/10	10/8	3/11	1/8	2/4	2/3	4/3
<i>C. corax</i>	-	-	-	-	3/1	1/-	-/1	-/2	2/4	2/-	2/-	-/2	3/-	3/-	2/1	1/1	1/-	3/-	-	-
Total	809/-	1077/-	3048/-	1543/-	1522/-	1521/-	1540/-	1538/-	1550/-	1586/-	1700/-	2101/-	1561/-	1515/-	1495/-	1528/-	1525/-	810/-	1200/-	1608/-
			1081	1509	1514	1516	1517	1523	1565	1524	1533	1628		1510	1011	1502	1529	1606	1535	1644

Appendix II. Densities of birds (number of stationary males/km<sup>2</sup>) as obtained by territory mapping (m) or nest search (n) in study plots in rich subalpine birch forest on the south-facing slopes of the mountains of Gaisatjåkko and Valle, Swedish Lapland, 1963–1982. Census-takers and study plots are accounted for in Table 1. \* = breeding established at least once within the plots.

Year	1963	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
Investigated area, km <sup>2</sup>	0.362	0.442	0.422	0.522	0.522	0.522	0.522	0.522	0.522	0.622	0.420	0.420	0.420	0.420	0.420	0.420	0.420	0.420	0.420	0.420
<i>Anthus trivialis</i> *(m)	8.3	15.8	6.8	5.7	9.6	3.8	3.8	3.8	5.7	4.8	2.4	4.8	14.3	11.9	14.3	9.5	4.8	4.8	4.8	9.5
<i>Anthus pratensis</i> (m)	-	6.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Motacilla flava</i> (m)	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-	-	-	-	2.4	2.4
<i>Cinclus cinclus</i> (m)	-	-	-	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	-
<i>Troglodytes troglodytes</i> (m)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	2.4	-	-	-
<i>Prunella modularis</i> *(m)	22.1	33.9	22.6	21.1	36.4	21.1	40.2	19.2	26.8	16.1	35.7	35.7	31.0	35.7	40.5	38.1	23.8	19.0	42.8	33.3
<i>Erithacus rubecula</i> *(m)	-	-	-	-	-	-	-	-	-	-	-	7.1	-	-	-	-	-	-	-	-
<i>Luscinia svecica</i> *(m)	2.8	6.8	13.6	13.4	38.3	21.1	7.7	3.8	15.3	14.5	47.6	21.4	11.9	26.2	16.7	21.4	4.8	2.4	16.7	19.0
<i>Phoenicurus phoenicurus</i> *(m)	22.1	15.8	23.9	6.9	20.8	6.9	3.5	6.9	3.5	12.9	16.2	6.5	9.7	12.9	9.7	22.6	3.2	9.7	19.4	16.2
<i>Saxicola rubetra</i> *(m)	8.3	4.5	-	1.9	-	1.9	-	-	-	-	-	-	-	2.4	2.4	-	-	-	-	-
<i>Turdus merula</i> *(n)	-	-	-	2.0	-	-	-	-	-	-	-	2.4	-	-	-	-	-	-	-	-
<i>Turdus pilaris</i> *(n)	-	6.8	15.8	1.8	19.2	46.0	23.0	32.6	28.7	30.5	7.1	19.0	4.8	7.1	7.1	47.6	14.3	21.4	19.0	14.3
<i>Turdus philomelos</i> *(n)	2.8	13.6	15.8	23.0	9.6	15.3	19.2	13.4	3.8	9.6	11.9	16.7	7.1	4.8	4.8	14.3	7.1	14.3	14.3	9.5
<i>Turdus iliacus</i> *(n)	16.6	6.8	47.5	17.2	24.9	55.6	44.1	59.4	24.9	49.8	59.2	40.5	11.9	7.1	14.3	19.0	7.1	28.6	45.2	16.7
<i>Hippolais icterina</i> *(m)	-	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	4.8	-	-
<i>Sylvia borin</i> *(m)	13.8	9.0	9.0	17.2	7.7	9.6	9.6	3.8	5.7	1.6	9.2	4.8	4.8	9.5	2.4	-	2.4	4.8	4.8	2.4
<i>Sylvia atricapilla</i> *(m)	-	-	-	-	-	-	-	-	-	-	2.4	2.4	-	-	-	-	-	-	-	-
<i>Phylloscopus sibilatrix</i> *(m)	-	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phylloscopus trochilus</i> *(m)	135.4	192.3	199.1	114.9	141.8	151.3	130.7	178.2	147.5	154.3	154.8	131.0	123.8	107.1	121.4	92.8	90.5	81.0	97.6	131.0
<i>Muscicapa striata</i> *(m)	2.8	-	2.3	1.9	-	-	-	-	3.8	3.2	9.5	4.8	-	2.4	4.8	2.4	4.8	-	11.9	2.4
<i>Ficedula hypoleuca</i> *(m)	16.6	20.4	28.7	13.8	20.8	10.4	17.3	10.4	34.6	15.4	12.9	22.7	12.9	6.5	9.7	6.5	3.2	3.2	6.5	6.5
<i>Parus montanus</i> *(m)	11.0	4.5	9.0	1.9	3.8	3.8	3.8	-	5.7	8.0	-	4.8	2.4	-	2.4	4.8	-	2.4	2.4	2.4
<i>Certhia familiaris</i> *(m)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	2.4	-	-	-
<i>Fringilla coelebs</i> *(m)	2.8	4.5	2.3	9.6	3.8	1.9	1.9	1.9	1.9	-	2.4	11.9	-	-	9.5	4.8	7.1	2.4	4.8	2.4
<i>Fringilla montifringilla</i> *(m)	63.5	38.5	36.2	44.1	32.6	61.3	49.8	30.7	51.7	64.3	123.8	123.8	61.9	38.1	23.8	31.0	35.7	73.8	59.5	52.4
<i>Carduelis spinus</i> (m)	-	-	-	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	2.4	-
<i>Carduelis flammea</i> *(m)	5.5	11.3	2.3	5.7	21.1	90.0	7.7	23.0	86.2	19.2	23.8	26.2	28.6	11.9	31.0	2.4	21.4	50.0	40.5	11.9
<i>Pyrrhula pyrrhula</i> *(m)	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	2.4	-	-	2.4	-	-
<i>Emberiza citrinella</i> *(m)	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-	-	-	-	-
<i>Emberiza schoeniclus</i> *(m)	33.1	31.7	24.9	34.5	28.7	21.1	19.2	13.4	17.2	17.7	26.2	21.4	26.2	19.0	21.4	11.9	19.0	19.0	31.0	21.4
<i>Anas crecca</i> *(n)	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Buteo lagopus</i> *(n)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-
<i>Falco columbarius</i> *(n)	-	-	-	-	-	-	-	1.9	1.9	-	-	2.4	-	-	-	-	2.4	-	-	-
<i>Lagopus lagopus</i> *(n)	-	2.3	-	1.9	1.9	-	-	3.8	1.9	-	-	-	-	2.4	2.4	-	-	-	-	-
<i>Tetrao urogallus</i> *(n)	-	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tringa hypoleucos</i> *(n)	-	-	-	-	1.9	1.9	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-
<i>Jynx torquilla</i> (m)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-
<i>Surnia ulula</i> (n)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.8
<i>Dendrocopos minor</i> *(n)	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	2.4	-	2.4	-	-	-
<i>Corvus corone cornix</i> *(n)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-	-
Total community	367.4	427.6	459.9	338.8	422.7	526.9	384.7	408.1	472.9	422.2	550.6	512.5	360.9	311.5	349.5	346.6	264.5	348.6	425.0	360.8