Structure and dynamics of an alpine bird community, a 20-year study

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The breeding birds of two square kilometres of alpine heaths and mires (800–940 m. a.s.l.) were censused during twenty years, 1964–1983, at c. 66° N, 16° E, south Swedish Lapland. The territory mapping technique with 5–10 visits was applied. The average number of species was 14, and 27 species bred at least once during the 20 years. The community was dominated by passerines and waders, which were represented by an equal number of species. Few other species occurred. The average density was 70 pairs/km². The three most abundant species (75 % of all pairs) were passerines. Average species turnover between adjacent years was 16 %. Over the census period the number of species increased slightly with no change in total density and so the community became more diverse. The variability of the whole community was (coefficient of variation) 19 %, of the passerines 21 % and of the waders 22 %. The variability of species populations could be described by a Poisson distribution, so they behaved as if they constituted random samples from stable source populations. The dominance sequence of the species was closely described by a geometric series, especially if dominance was based on biomass.

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1. Introduction

Habitats that are tree-less because of cold climate are found in two main kinds of land: in lowland tundra with permafrost and in mountaneous or alpine areas at different elevations depending on latitude. These latter habitats generally do not have permafrost, not even in the vicinity of glaciers. Tundras with permafrost are usually poorly drained while most alpine habitats are well drained. An exception is the bogs and mires that develop on level land and on some slowly climbing slopes.

Some bird communities of tundras and alpine habitats have been studied in the Old as well as in the New World. In this paper we will report results obtained in a study of alpine habitats in Swedish Lapland. The information is important from especially one point of view: the study is probably one of the longest ever undertaken in alpine habitats since it covers 20 years.

The alpine habitats are usually mosaics of different kinds of heaths, meadows, marshes, mires and bogs. These habitats are at least physiognomically similar to tree-less habitats in subalpine and boreal zones, such as mires and raised bogs.

Some of the most interesting problems are connected with the structure of the bird fauna and with its long term fluctuations (stability). These questions will therefore be treated in some detail.

2. Methods

2.1. Study plots

The census work was carried out in two study plots, each covering 1 km² (quadrats of 1×1 km), about 15 km SSE of Ammarnäs (approximate location of the plots: 65° 50′ N, 16° 20′ E). The two plots were located at different elevations. One, the lower plot, called K1, lies about 1 km from the forest line and about 50 m above it. The other, the upper plot, called K2, lies 3 km from the forest line and at a higher elevation

The lower plot, K1 (800–840 m. a.s.l.) is covered by a mosaic of dry scrub heath (with *Betula nana*, *Salix* spp., *Empetrum hermaphroditum*, *Arctostaphylos alpina*, *Vaccinium myrtillus*, and *Juniper communis* as typical components) and mires (with a dominance of *Carex* sp. and low sparse *Salix*). In two parts of the plot, mires are

more extensive and continuous than elsewhere and in another part the dry heath is rather uniform. There are two small brooks that traverse parts of the plot and along them there are a few small fields of about 1 m high *Salix* scrub (together less than 1 ha). There are no lakes and only one small pond within the plot. Parts of the plot are somewhat hilly but the hills are lower than 10 m. Dry heath dominates on the hill-tops and mires in between.

The upper plot, K2, is located about 1 km from K1 on a low mountain ridge (880–940 m a.s.l.). Most parts of K2 are drier than K1, and the vegetation is poorer. *Vaccinium myrtillus* occurs over most of the plot. In more than half the plot there is little or no scrub. In the lower parts there is some mire vegetation with *Carex* fields and low *Salix* and *Betula nana* scrub whereas in the dryer parts of the lower levels there are some scattered *Juniperus* stands creeping along the ground. The upper parts are heavily exposed to winds and are also affected by the lack of a thick, protecting snow cover in the winter. There are also some parts (2–3 ha) with snow fields that do not melt away until late in the breeding season, making them unavailable to birds. The topography is flat, not hilly, but gently undulating.

Both plots belong to the low alpine region (du Rietz 1950) although the vegetation of the upper, exposed parts of K2 show strong resemblance to middle alpine vegetation types. The habitats of the two plots represent extensive areas of alpine vegetation in the Ammarnäs region. They cover hundreds of square kilometres and are the most common ones in the low mountains east of the higher Ammarfjället and Tärnafjällen.

A map of the Ammarnäs area with plots K1 and K2 marked is given in Enemar (1984).

2.2. Census methods

We have applied the territory mapping technique throughout for the majority of the species. We followed the recommendations given by the International Bird Census Committee (see Svensson & Williamson 1969, Svensson 1975). For most of the species we met no particular difficulties and the density figures obtained can be considered accurate. Some species constituted exceptions, however.

For the most common species, *Anthus pratensis*, we had some difficulties in distinguishing neighbouring territories, particularly during the first few years, when the density was very high and our experience limited. In some other species we could not use the territory mapping technique. In *Philomachus pugnax* we combined a search for nests with observations of alarmed Reeves immediately after hatching, but we were never quite sure that we had found all the breedings. On the contrary, over the years we have probably missed a few. In *Gallinago media* we based our abundance estimates on the number of males flushed from a display ground during daytime but, since we did not count them at night during their peak display period our estimates are probably too low. Occasional visits at night in the early season indicated higher numbers. The figures ought to be comparable between years, however. Also in *Gallinago gallinago* we had some difficulties because of their very extensive display flights. The single *Anas crecca* of 1974 was an accidental nest find and there may have been a few more breedings of this species but not, however, of any other duck. We are certain that we have not missed any species breeding in the plots.

In order to ensure that the same principles were applied for all the years, a complete re-evaluation of all species maps was carried out in 1983. The re-evaluation produced estimates very similar to the original ones except for the first two years: In *Anthus pratensis* the original estimates were 69 and 49 pairs in K1 and 28 and 15 pairs in K2. The corresponding new estimates were 60 and 54 pairs, and 30 and 20 pairs, respectively. In the other species and years the revised figures were not at all or only slightly shifted.

Table 1. Specification of census data in plots K1 and K2.

Year	No. of visits	1st visit (June)	Census period (days)	Mean date	Hrs/ visit mean	Census takers[1]
K1						
1964	10	15	16	22	9.0	A,E,Ha,M,S
1965	10	16	15	22	11.5	A,S
1966	9	17	21	28	9.0	A,S
1967	10	12	27	23	10.0	A,S
1968	10	15	17	22	8.2	A,S
1969	8	13	21	22	6.1	A,S
1970	8	16	15	23	6.3	C,S
1971	8	18	15	25	4.9	C,S
1972	8	15	16	23	5.0	C,S
1973	8	17	18	25	5.3	C,S
1974	8	17	14	23	6.1	C,S
1975	8	18	16	25	5.6	H,S
1976	8	14	14	21	6.0	C,S
1977	8	17	15	25	6.0	C,L,S
1978	8	11	19	19	6.6	C,L
1979	8	12	13	18	6.9	C,L
1980	8	9	13	16	6.8	C,L
1981	8	6	19	16	7.2	S,L
1982	8	16	10	21	7.6	C,L
1983	8	10	15	16	6.2	J,L
K2						
1964	5	–	–	–	–	A,E,Ha,M,S
1965	5	23	13	29	–	M,N
1966	5	17	23	22	–	M,N
1967	5	–	–	–	–	M,N
1968	5	–	–	–	–	M,N
1969	5	18	20	28	8.2	A,M,N,S
1970	5	20	12	26	4.8	C,S
1971	5	24	9	29	5.3	C,S
1972	5	21	11	26	3.0	C,S
1973	5	22	17	28	4.0	C,S
1974	5	18	15	25	5.0	C
1975	4	18	15	24	5.0	H,S
1976	5	17	12	20	6.1	C,E,S
1977	5	18	15	26	4.5	C,L,S
1978	5	12	8	16	4.8	C,L,S
1979	5	16	10	21	5.4	C,L
1980	4	14	5	16	4.8	C,L
1981	4	16	10	19	6.2	S,L
1982	5	21	10	25	6.3	C,L,S
1983	5	16	10	21	4.6	J,L,S

[1] Census takers: A = Bengt Alm, C = Ulf T. Carlsson, E = Anders Enemar, H = Lars Hellsborn, Ha = Sven Åke Hanson, J = Ingemar Jönsson, L = Göran Liljedahl, M = Harry Myhrberg, N = Erik Nyholm, S = Sören Svensson

2.3. Census periods

In a multi-visit mapping census the selection of dates and hours for the visits is not as critical as when performing single visit line transects or point counts although care in these respects may help to increase the accuracy for low efficiency species (Svensson 1979). In spite of this, we give here fairly detailed information about our visiting schedules (Table 1).

The field work started as soon as the snow had melted away from most parts of the study plots. In some years most of the snow had been absent for one or two weeks before the first visit. The time of snow-melting varied widely from year to year, but the start of the breeding season for the birds was much more constant. In all the years, hatching started during the last week of June or the first week of July.

In 1974 only one half of plot K2 was censused. The density figures for that year have been calculated on the basis of the results from that half of the plot assuming that the average ratio of birds in the two halves was the same in 1974 as in other years.

The census periods were adapted to coincide with the laying and incubation periods of the birds. The breeding synchrony between different species is pronounced and therefore all species can be accurately counted during such a brief period as 2–3 weeks or less. The reason why we made only five visits to plot K2 was of course that this plot was very easily surveyable. We compensated the lower number of visits by staying in the plot during each visit almost as many hours as in K1 in spite of the very low density of birds in the dryer parts of the plot.

2.4. The effects of change of observers

It is known that different observers may evaluate the same species maps in different ways (Svensson 1974). By the re-evaluation of all the maps this source of error could be eliminated. But different observers may also differ in the collection of field observations. Although it has been shown (Enemar et al. 1978) that the experienced observers of our team at Ammarnäs will differ only slightly when carrying out contemporary censuses in the same plot, we will here briefly consider the possibility of errors because of the changes of observers. The observers in different years are given in Table 1.

The data that we have at our disposal do not allow an assessment of the capability of each single participant, but for plot K1 we have some data that can be used. Observer S has been working in one half of that plot in 12 years with two other observers in the other half in 5 and 7 years, respectively (Table 1). For the most common species we have calculated the ratio of the density estimates in the two halves. In 1965–1969 the mean ratio for A/S was 0.92 ($s = 0.185$) in *A. pratensis* and 1.05 ($s = 0.146$) in *C. lapponicus*. In 1970–1974 and 1976–1977 the ratio for C/S was 0.96 ($s = 0.163$) in *A. pratensis* and 1.35 ($s = 0.224$) in *C. lapponicus*. The difference between A/S and C/S was 0.04 in *A. pratensis*, which is not significant, and 0.30 in *C. lapponicus* which is significant. Provided that there has been no change in the relative abundance of *C. lapponicus* in the two halves of the plot this might indicate a difference between A and C compared to S, or a change in the efficiency of S. The difference is small enough, however, to cause no trouble for the analysis in this paper. Other species are easier to census and a small difference in

efficiency between the different observers will hardly be possible to detect. We therefore conclude that observer differences can be ignored.

3. Results

3.1. Taxonomic composition and number of species

Two groups of birds dominate the community, Passeriformes and Charadriidae (Table 2 and 3). They are represented by about the same number of species. In plot K1 the average number of species each year was 11.6 and out of these 5.7 were passerines and 5.4 waders. In K2 the corresponding figures were 8.0, 4.1 and 3.5. As to the number of pairs, the passerines dominated over the waders in both plots. Over all the twenty years 82 % were passerines, 18 % waders and less than 1 % other species.

The number of species varied somewhat from year to year. In K1 the number varied between 9 and 14, and in K2 between 5 and 11, giving coefficients of variation of 14 and 22 %. A total of 22 species bred at least once in K1 and 17 species in K2. In both plots together 27 species bred at least once. Thus, it is a species-poor community that we are dealing with and, as we shall see below, only a few of these species are regular and still fewer are abundant.

3.2. Continuity of occurrence and species turnover

Only a few species occurred regularly in the study plots (Table 2 and 3). In plot K1 3 passerines and 4 waders were breeding every year. In K2 there were also 3 passerines but only one wader that bred every year. A few more species bred almost every year. The bird community of our sample plots is therefore amply characterized by the following species list: *Anthus pratensis, Calcarius lapponicus, Oenanthe oenanthe, Phylloscopus trochilus, Luscinia svecica, Eremophila alpestris, Gallinago gallinago, Gallinago media, Calidris alpina, Philomachus pugnax, Pluvialis apricarius,* and *Charadrius morinellus.*

The species turnover $T = (I+E)/(S_1+S_2)$ (I is the number of species present in year 2 but absent in year 1, and E is the number of species present in year 1 but absent in year 2; S_1 and S_2 is the number of species in year 1 and 2) varied

Table 2. Number of permanent territories or breeding pairs in the low elevation alpine plot K1 in 1964–1983. Size of plot: 1 square kilometre.

	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Mean	CV %	Yrs
Anthus pratensis	60	54	56	48	38	40	35	24	24	31	34	33	27	32	33	30	43	41	36	36	37.75	26.8	20
Calcarius lapponicus	15	15	29	26	23	19	20	25	24	20	22	24	22	24	23	21	29	32	32	23	23.40	20.0	20
Phylloscopus trochilus	10	4	10	2	0	20	15	5	4	2	10	4	7	7	8	3	2	20	2	6	7.05	81.5	19
Oenanthe oenanthe	3	3	3	2	2	4	2	3	2	1	2	2	2	5	5	3	2	5	4	4	2.80	39.5	20
Luscinia svecica	7	4	2	0	0	0	0	0	1	1	5	7	6	0	2	4	3	8	5	5	3.00	91.8	14
Turdus iliacus	0	0	0	0	0	2	0	0	0	0	3	2	1	2	1	0	0	0	0	0	0.55		6
Carduelis flammea	0	0	0	0	2	2	0	2	0	0	0	1	0	0	0	0	0	2	2	0	0.45		5
Emberiza schoeniclus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	1	2	0	0	0.40		6
Turdus pilaris	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0.15		3
Anthus cervinus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0.10		1
Gallinago gallinago	3	6	6	7	3	5	4	7	5	5	7	5	5	4	5	5	4	6	8	6	5.30	25.3	20
Calidris alpina	3	1	2	5	3	5	2	3	4	3	5	3	4	3	4	4	3	5	4	4	3.50	31.4	20
Philomachus pugnax	2	4	2	5	3	3	2	2	2	2	5	4	4	4	3	2	2	8	5	1	3.25	50.8	20
Pluvialis apricaria	3	2	2	1	2	2	3	4	2	3	2	4	2	3	5	2	2	2	3	5	2.70	40.0	20
Gallinago media	2	0	3	3	3	3	2	2	1	2	2	2	1	3	3	3	1	6	1	1	2.20	58.2	19
Tringa glareola	3	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0.45		7
Calidris temminckii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05		1
Charadrius morinellus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0.10		2
Anas crecca	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0.05		1
Stercorarius longicaudus	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0.30		5
Lagopus lagopus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0.05		1
L. mutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.10		2
Passerines total	95	80	100	78	65	86	72	59	56	55	77	73	67	68	74	62	80	111	81	74	75.65	19.1	
Waders total	16	15	16	21	15	19	13	18	15	15	21	17	18	16	20	16	14	27	22	17	17.55	19.0	
Other species total	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	0	1	1	2	1	0.50	165.4	
Total no. of pairs	111	95	116	99	80	105	85	77	71	70	101	91	85	84	95	78	95	139	105	92	93.70	17.7	
No. of species, pass.	5	5	5	4	4	6	4	5	6	5	7	7	7	6	7	6	6	8	6	5	5.70	19.8	
No. of species, waders	6	6	6	5	6	6	5	5	6	5	5	5	5	5	5	5	7	5	6	5	5.45	11.1	
No. of species, total	11	11	11	9	10	12	9	10	12	10	14	13	12	11	13	11	14	14	14	11	11.60	14.1	

Table 3. Number of permanent territories or breeding pairs in the high elevation alpine plot K2 in 1964–1983. Size of plot: 1 square kilometre.

|	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Mean	CV %	Yrs
Anthus pratensis	30	20	20	18	4	20	19	10	11	14	23	12	7	8	9	5	10	15	14	11	14.00	47.3	20
Calcarius lapponicus	10	2	4	7	2	7	14	11	12	9	28	11	9	10	7	8	8	9	15	10	9.65	56.8	20
Oenanthe oenanthe	13	4	7	5	2	6	5	4	4	9	10	5	8	4	8	8	7	8	6	7	6.50	39.1	20
Eremophila alpestris	1	2	3	4	2	2	2	3	2	2	4	2	3	0	1	0	0	0	0	0	1.65	81.7	14
Plectrophenax nivalis	0	0	0	0	0	0	2	1	0	0	10	0	1	0	0	0	0	1	0	0	0.75		5
Turdus pilaris	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0.10		2
Luscinia svecica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0.10		1
Pluvialis apricaria	4	2	3	4	2	3	3	3	4	3	6	3	3	2	2	1	1	4	3	3	2.95	38.8	20
Charadrius morinellus	2	0	2	3	0	0	2	2	2	3	3	0	2	2	1	1	2	2	1	3	1.65	63.0	16
Calidris alpina	0	1	1	2	0	1	1	0	1	2	0	0	2	1	1	2	1	2	2	2	1.10	71.6	15
Gallinago gallinago	0	0	0	0	0	0	0	0	2	2	2	0	0	1	1	0	0	1	2	1	0.60		8
Calidris temminckii	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0.35		7
Charadrius hiaticula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05		1
Calidris maritima	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05		1
Philomachus pugnax	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0.15		3
Cuculus canorus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0.15		3
Stercorarius longicaudus	0	0	0	1	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0.25		4
Passerines total	54	28	34	34	10	35	42	29	29	35	75	30	28	23	25	21	25	35	35	28	32.75	40.4	
Waders total	7	5	7	9	2	4	6	5	9	10	11	3	9	7	5	4	4	11	10	10	6.90	41.0	
Other species total	0	0	0	1	0	0	2	0	1	1	0	0	1	1	0	0	1	0	0	0	0.40	149.6	
Total no. of pairs	61	33	41	44	12	39	50	34	39	46	86	33	38	31	30	25	30	46	45	38	40.05	37.1	
No. of species, pass.	4	4	4	4	4	4	5	5	4	5	5	4	5	4	4	3	3	5	3	3	4.10	17.5	
No. of species, waders	3	4	4	3	1	2	3	2	4	4	3	1	5	5	4	3	3	6	6	5	3.55	40.3	
No. of species, total	7	8	8	8	5	6	9	7	9	10	8	5	11	10	8	6	7	11	9	8	8.00	21.8	
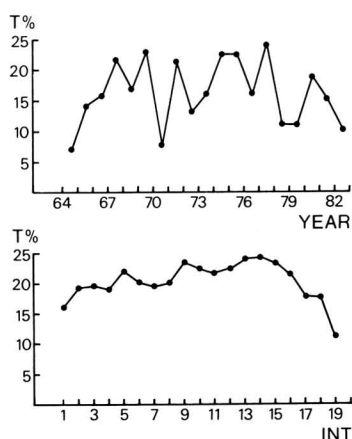
Fig. 1. Species turnover rates (T) in the pooled communities of the sample plots K1 and K2. The upper diagram shows the annual variation in T between adjacent years. The lower diagram shows the average T between two years different number of years apart. INT = years apart.

between years (Fig. 1). Average T between two adjacent years ($n = 19$) was for K1 13.5 % ($CV = 28.8$), and for K2 18.6 % ($CV = 48.7$). The difference between the two plots is far from significant and T for both plots combined was 16.1 % ($CV = 33.9$). In K2 there was a rather high turnover during the last five years but otherwise there was no trend over the years.

The estimate of turnover calculated as above, using the average turnover between adjacent years, may underestimate the average long-term turnover since one would expect adjacent years to be serially correlated. Birds that survive from one year to another tend to return to the same site, even the same territory. We have therefore calculated turnover between years further apart from each other. The result is given in Fig. 1. The turnover for adjacent years is clearly below that between years further apart. In fact turnover increases to a peak for years about 13–14 years apart. Then, interestingly, it declines again. The increase is expected, but the decline is not. Such a decline has not been observed in a number of plots censused over many years in South Sweden. It is still too early, however, to draw any conclusions because the decline is established by comparisons between a small number of years.

3.3. Community and population density

All the estimates of population size are given in Table 2 and 3 for plot K1 and K2 separately.

Since each plot was one km² the figures directly describe the density in pairs (or territories) per km². In plot K1 there were on the average 76 passerines and 18 waders and no regular species of other taxa, making together an average of 94 pairs per year. In plot K2 there were 33 passerines and 7 waders with no other regular species either. The total density thus was about half that of K1 or 40 pairs. The lower density of K2 was mainly due to the fact that half that plot lay on a dry ridge with very poor vegetation. The two plots combined represent fairly well the two dominating habitats in the low alpine region of the area (heaths and bogs) and the density estimates obtained should roughly characterize large areas of the Ammarnäs region. The average density of birds, including both rich and poor habitats, should then be about 70 pairs/km². To this should be added only that neither plot contained any lakes or larger streams. Some alpine areas in the region include such components but it is probable that the overall density would be only slightly different if this is taken into consideration.

In plot K2, where about half of the plot was covered with vegetation more similar to that of K1, we find that the lower, richer half carried 60 pairs/km² (51 passerines and 9 waders) but the upper half only 20 pairs/km² (15 passerines and 5 waders). Thus the density of the lower half was 64 % of that of K1 whereas the density of the upper half was only 21 % of that of K1.

In both plots *Anthus pratensis* was the most abundant species with 38 and 14 pairs per year. *Calcarius lapponicus* was the second most common with 23 and 10 pairs. The third species was different in K1 and K2. In K1 *Phylloscopus trochilus* took this position with 7 pairs and in K2 *Oenanthe oenanthe* took it with 6 pairs. These most abundant species, all passerines, constituted together c. 75 % of all birds.

3.4. Population and community structure fluctuations

The population fluctuations are shown by the coefficients of variation (CV) in Table 2 and 3. In K1 there are two species that differ drastically from the rest: *Luscinia svecica* and *Phylloscopus trochilus*. Both these species are woodland birds that peripherically extend the range up into the lower parts of the alpine
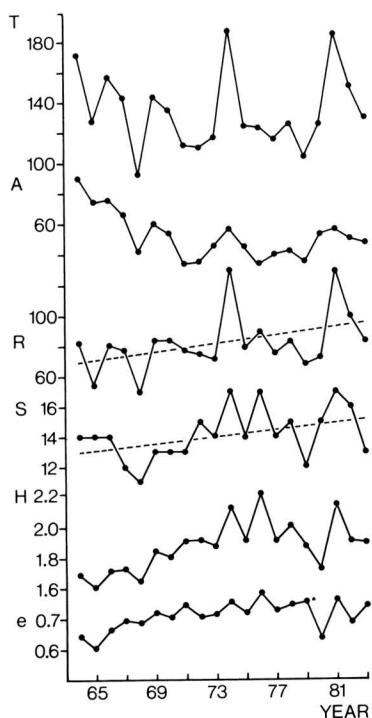
Fig. 2. A number of characteristic variables of the pooled communities of the sample plots K1 and K2. T = total abundance, no. of pairs, A = *Anthus pratensis*, no. of pairs, R = all species except *A. pratensis*, no. of pairs, S = no. of species, H = Shannon's diversity index, e = the eveness index, H/log S.

region. The violent fluctuations probably reflect the fact that the alpine habitats are suboptimal for these species. The fluctuations may be caused by a particularly variable resource in the alpine habitats or, more likely, events in subalpine birch woods (spill-over from an optimal habitat).

The fluctuations in K1 and K2 seem to be fairly normal for alpine habitats. The few multi-year studies that are available provide similar coefficients of variation. Moksnes (1973) obtained a *CV* of 22 % for *A. pratensis* and 11 % for the whole community, and the Finse data (Stenseth et al. 1979) gave a *CV* of 32 % for *A. pratensis*. See also Järvinen (1979).

The variation for some community variables are given in Fig. 2. The linear trend of total abundance is almost level. There are three years that deviate particularly much from the rest: 1968, 1974, and 1981. The very low total in 1968 is caused by low numbers in almost all

species and in both plots. The high total in 1974 was caused by unusually high numbers in several species in plot K2. The high total in 1981 reflects high numbers in several species in K1.

If we exclude *Anthus pratensis*, which declined over the first half of the census period, the rest of the community showed an upward trend. Also the number of species increased from an average of 13 during the first 10 years to 15 during the last 10 years. Diversity, the Shannon's *H*, increased, particularly between 1964 and 1976, as did the evenness index, almost exclusively because of the decline of *A. pratensis*. In summary, over the twenty years the community has shown no numerical trend but the birds have become more evenly distributed among a greater number of species.

4. Discussion

4.1. Representativity of the study plots

The question of the representativity of the study plots in relation to the population dynamics of the whole Ammarnäs area will be dealt with in detail in a forthcoming paper. Here we will only compare the species compositon of the study plots with that of the Ammarnäs region in general. A summary is presented in Table 4.

The species have been divided into three categories based on their habitat preferences. The birds of category A, mainly woodland species, are represented in the lower plot by *Phylloscopus trochilus* in most years and by four other species in 5-7 years. Some other species occurred occasionally. The birds of category B, mainly bog and grassland species of alpine, subalpine and boreal distribution, are well represented. Six species bred in at least one of the plots in most years. A few more species of this category occurred occasionally. The birds of category C. the true alpine species, were represented by four species regularly: *Pluvialis apricarius*, *Charadrius morinellus*, *Eremophila alpestris* and *Calcarius lapponicus*.

The reason why some of the other regularly breeding species of the region did not appear regularly in the plots was that their overall density is very low or that there are no suitable habitat or nest sites within the plots. Some of these species were observed as visitors more or

Table 4. General description of the breeding bird fauna of the lower and middle alpine regions of the Ammarnäs area, with comparison with the bird fauna in the study plots (waterfowl and gulls excluded). Explanations: L = low alpine region, M = middle alpine region, x = regular breeder, (x) = occasional breeder, o = no suitable nest site within the plots, + = observed but has not bred in the plot. The figures for K1 and K2 denote the number of years that each species has bred. Category A: Birds belonging to areas below the forest line and more or less regularly extending their ranges into the lower parts of the low alpine region (mainly woodland birds). Category B: Birds belonging both to alpine areas and to areas below the forest line (mainly birds of open lands: bogs, grasslands, etc.). Category C: Birds belonging to alpine habitats exclusively (may extend the range below the tree line but rarely below the forest line).

Category and species	Region		No. of years	
	L	M	K1	K2
A				
Lagopus lagopus	x	–	1	0
Tringa glareola	x	–	7	0
Asio flammeus	(x)	–	0+	0
Alauda arvensis	(x)	–	0+	0+
Motacilla flava	x	–	0+	0
Saxicola rubetra	(x)	–	0+	0
Turdus pilaris	x	–	3	2
T. iliacus	x	–	6	0+
T. torquatus	x	– o	0	0
Luscinia svecica	x	–	14	1
Phylloscopus trochilus	x	–	19	0+
Carduelis flammea	x	–	5	0+
Emberiza schoeniclus	x	–	6	0+
B				
Aquila chrysaetos	x	x o	0+	0+
Buteo lagopus	x	x o	0+	0+
Falco rusticolus	x	x o	0	0
Charadrius hiaticula	x	x	0+	1
Gallinago gallinago	x	x	20	8
G. media	x	–	19	0
Tringa totanus	x	–	0+	0+
T. hypoleucos	x	– o	0	0
Phalaropus lobatus	x	– o	0+	0
Calidris temminckii	x	x	1	7
C. alpina	x	x	20	15
Philomachus pugnax	x	–	20	3
Cuculus canorus	x	x	0+	3
Oenanthe oenanthe	x	x	20	20
Anthus pratensis	x	x	20	20
A. cervinus	(x)	–	1	0
Corvus corax	x	x o	0+	0+
C				
Lagopus mutus	x	x	2	0+
Charadrius apricarius	x	x	20	20
Ch. morinellus	x	x	2	16
Calidris maritima	x	x	0	1
Stercorarius longicaudus	x	x	5	4
Nyctea scandiaca	(x)	(x)	0+	0
Eremophila alpestris	x	x	0	14
Calcarius lapponicus	x	x	20	20
Plectrophenax nivalis	x	x	0	5

less regularly in the plots. In some species the population density in the whole Ammarnäs area varies drastically from year to year, for example in *Carduelis flammea* and *Stercorarius longicaudus*, this being one main reason for their irregular occurrence in the study plots.

Thus, the percentage of the species breeding in alpine habitats in the Ammarnäs region represented regularly in the study plots were for the three categories A, B and C: 33 %, 40 % and 44 %, respectively, and 38 % for all species together. Hence, it seems safe to conclude that the birds breeding in the study plots constitute a fair sample of those occurring in alpine habitats in this part of Sweden. Furthermore, with only three exceptions, none of the species that did not breed regularly within the plots, occur anywhere else in the alpine parts of the Ammarnäs region dense enough to be sampled adequately with plots of two km². The three exceptions are *Charadrius hiaticula*, *Calidris temminckii* and *Plectrophenax nivalis*, which, locally, may breed in rather high numbers in relatively small areas.

4.2. Co-variation between the two study plots

The two study plots are, as mentioned earlier, located only 1 km from each other. One would therefore expect to find the same density changes between the years in both plots.

The correlation coefficients for all species was +0.35 and for all passerines +0.32. The three most abundant passerines common to both plots showed the coefficients +0.68 (*Anthus pratensis*), +0.08 (*Calcarius lapponicus*) and +0.17 (*Oenanthe oenanthe*). *Pluvialis apricarius*, the only regular wader common to both plots, had a coefficient of –0.14. All waders pooled produced a coefficient of +0.49. Of these coefficients, only those of *Anthus pratensis* and the waders were significant.

It is surprising that there was no correlation at all between the two plots for *C. lapponicus* when there was for *A. pratensis*. This is, however, an obvious consequence of the high variation in K2. It can be observed that in 1974 the number of *C. lapponicus* was higher in K2 than in K1 and remarkably higher than in any other year. For this unexpected peak we can find no explanation. In certain areas one can find concentrations of many pairs of *C. lapponicus*, almost loose colonies, but we have not

observed this in our study plots and so shifts of colony location cannot explain the 1974 peak in K2.

The conclusion we must draw is that it is not always safe to make general inferences about population fluctuations from small samples, neither to base a community description on census data from only one or a few years.

4.3. Co-variation between different species

Correlation coefficients were calculated for each of the three pairwise combinations of the three most abundant species in both study plots. They were in plot K1: -0.04 for *C. lapponicus/P. trochilus*, +0.17 for *A. pratensis/P. trochilus*, and -0.14 for *A. pratensis/C. lapponicus*. None of them differed significantly from zero. In plot K2 they were: +0.34 for *C. lapponicus/Oe. oenanthe*, +0.48 for *A. pratensis/Oe. oenanthe*, and +0.27 for *A. pratensis/C. lapponicus*. Only the coefficient for *A. pratensis/Oe. oenanthe* was significantly different from zero.

There was no correlation between *P. trochilus* and *L. svecica* (+0.14), which might have been expected if there were some common factor governing the occurrence of these two woodland species in the alpine habitats.

One might draw one conclusion from the fact that we obtained three positive correlations coefficients in K2 but only one in K1: some local factors may be operating with heavier effects in K2 than in K1. The most probable factor is adverse weather conditions: later snow-melting and higher exposure to cold spells late in the season. Regrettably, we have no data on the weather and the early snow conditions for the study plots

4.4. Population variability

We have tested the possibility that population sizes in different years behave as a Poisson variate: the variance should equal the mean. We have tested this for all 27 species of K1 and K2 (Fig. 3).

It can be seen that the variability is rather closely described by the line $s = M^{0.5}$, s being the standard deviation and M the mean population size. Thus the general form of the relation between variability and population size follows the Poisson assumption.
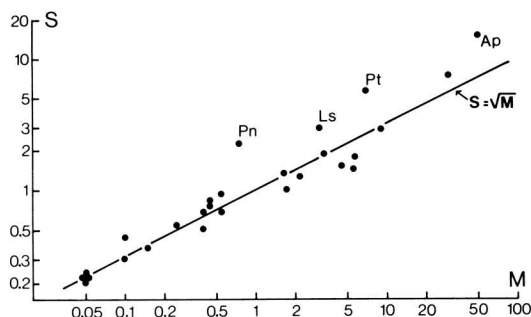

Fig. 3. Standard deviation (s) in relation to mean population size (M) for the whole 20 year period. All 27 species are plotted. Four species with high s are indicated: Pn = *Plectrophenax nivalis*, Ls = *Luscinia svecica*, Pt = *Phylloscopus trochilus*, Ap = *Anthus pratensis*. Both scales are logarithmic.

If there were constrains that limited variability, for example territorial competition, one would expect a number of species to show lower variability. On the other hand if there were important non-random environmental factors operating, the affected species would show higher variability.

The strongest deviations from the line are shown by four passerines: *Anthus pratensis*, *Phyllsocopus trochilus*, *Luscinia svecica* and *Plectrophenax nivalis*. In *A. pratensis* the deviation depends on the high population level during the first four years. If this effect is removed the variability of this species does not deviate appreciably from the straight line. The variability of *P. nivalis* depends solely on high numbers in one single year. The two other species, however, do actually vary consistently much more than they should if their population size were governed by random sampling alone.

There are also deviations to the lower side of the line. These species are waders, so there is a difference between waders and passerines. One assumption is that the waders breed in numbers that may be rather close to the maximum territorial packing whereas this is generally not the case for a majority of the passerines. Differences in longevity and site tenacity could also explain the difference. *P. trochilus* and *L. svecica* breed in much lower numbers in most years than would actually be possible if only local conditions and territory size were considered.

In conclusion we can say that most populations of our study plots behaved as if

there were stable source populations from
which the plots took a random sample every
year.

4.5. The structure and diversity

The structure of the community can be de-
scribed by the dominance curves with the
species in their abundance sequence. Several
different statistical or mathematical 'models'
have been proposed to explain or describe this
structure. Commonly used are the broken-stick
model, the log-normal model and the geo-
metric series model (roughly equivalent to the
log-series model). The broken-stick model was
discussed by MacArthur (1957, 1960) and by
Whittaker (1972). This is, however, a distri-
bution that follows from many different
assumptions. It is a distribution that is com-
paratively even with no pronounced domi-
nation of a few species. The log-normal distri-
bution is a kind of universal outcome if there
are many multiplicative factors (May 1975) or
many different resources that affect the species
of a community more or less independently.
As soon as there are many species in a com-
munity this is likely to be the case. Hence the
log-normal distribution can be understood as
a purely statistical expectation, i.e. a result of
the central limit theorem that says that several
distributions when added or multiplied will
asymptotically approach normality or log-
normality. The geometric distribution de-
scribes a situation when the species of a rela-
tively simple community are governed by a
dominating environmental factor. The species
are said to pre-empt, in some abstract se-
quence, the same fraction of what is left of the
resources by the species already established.
Several authors have compared and con-
trasted the different models (Pielou 1969, 1975,
May 1975). May (1975) provides a brief
summary stressing the fact that the log-normal
distributions is not a result of biological
constraints within a community, whereas the
other two distributions are. But Pielou (1975)
makes it clear that neither model can really
explain anything about the actual causes be-
hind a certain distribution, so they should
perhaps be understood as 'ignorance in
manageable form'.
In Fig. 4 we show the species abundances
(expressed as percent dominance) found in the
Ammarnäs plots K1 and K2. It can be seen that
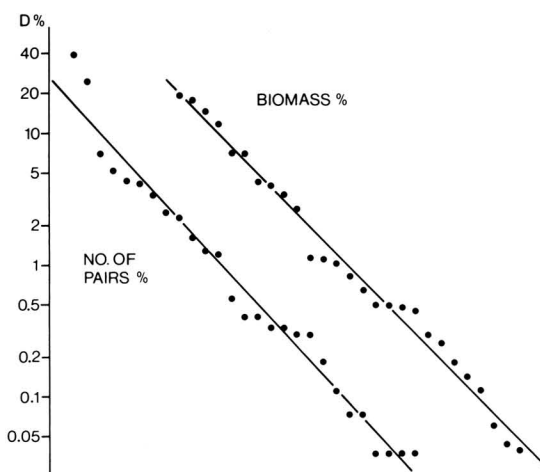there is a good fit with a straight line in the

Fig. 4. Dominance in percent for the 27 species ordered in
sequence of abundance and biomass. Vertical scale loga-
rithmic.

semi-log plot. This is the property of the geo-
metric series. The plot of number of pairs
shows, however, a pronounced overabundance
for the two commonest species. If instead the
plot is based on biomass, the fit is still better
and also the two most important species (not
the same) fall on the line. This indicates that
the apparent overabundance of the two most
common species was caused by their small size
(*Anthus pratensis* and *Calcarius lapponicus*)
and their lesser share of the total energy flow.
We have also made the same semi-log plot of
the birds in K1 and K2 separately. There is a
better fit with a straight line for the birds of K2
than for those of K1. This is agreement with
Whittaker's (1965) statement that the geo-
metric series is most often found in pioneer
and ephemeral communities and in those
which have rigorous environments and rela-
tively few species.
We also made the same comparison between
the passerine and wader parts of the com-
munity. The passerines showed a better fit to a
straight line than the waders, which also is in
lien with Whittaker's (1965) interpretation: the
environment must be considered to be harsher
for the passerines than for the waders.
In summary it can be concluded that the re-
sources channeled through the birds in the
alpine region of the Ammarnäs area are parti-
tioned among the species according to a
geometric series model. If Whittakers (1965)
opinion is correct one would expect the
community to be governed by some domi-

nating environmental factor. A good guess seems to be the adverse climatic conditions giving a small and poorly diversified energy base for the birds. Also, the alpine habitats could be considered to be a kind of pioneer community, permanently remaining in a kind of pioneer state by these adverse conditions.

4.6. Increase of the species number in time and space

An average of 14 species bred each year but 27 species bred at least once during all the 20 years. It is reasonable to assume that more species will be added to the list in the future. How fast will they be added?

The increase in the number of species (when all the years are combined in all possible sequences and the mean increase per year is calculated) followed very closely a straight line in a log–log diagram. The regression equation was $\log(\text{no. of species}) = 0.2 \log(\text{no. of years}) + \log 14$. The slope 0.2 is close to the one expected from, among several other models, Preston's (1962) canonical hypothesis for species-area relations.

If the sample plots are representative of a much larger area and if there are no important trends in the composition and abundance of the community in time, the space and time dimensions ought to be freely exchangeable. Twenty years of census in our $2\,\text{km}^2$ plots would correspond to one year within $40\,\text{km}^2$. Within the next 80 years eight species should be added to the list of our plots giving a total of 35 species after 100 years of census. This figure is very likely to be approximately correct subjectively considering the potential breeders not yet found. This is in accordance with the previous observation about the Poisson character of the variation.

It seems safe to conclude, then, that reliable information about the species structure of a large area can be obtained by using information obtained in a small area over many years, provided of course that the habitat in the small area is representative of the larger one. This question has also been discussed by Haila (1983).

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