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Colonization of islands in a north-boreal Finnish lake by land birds

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The colonization of the archipelago of Lake Inari (69°N, 28°E) by land birds is analyzed on the basis of census data from 41 islands with a size range of 0.5-885 ha (17 islands censused in two breeding seasons). 43 species of land birds were recorded on the islands. In calculating species-specific expectations of population numbers on the islands, published density estimates from mainland habitats and data on regional abundances were used as a background. Fourteen of the 24 abundant species were observed on the islands in expected numbers, but only one deviating case was not plausibly explained by obvious differences in habitat structure between islands and the mainland (*Anthus trivialis*). Less numerous species on the islands are habitat specialists occurring there in roughly expected numbers. All absences are obviously caused by lack of suitable habitats on the islands — the missing species include specialists of alpine and tundra habitats. Habitat preferences of the species can thus be distinguished as by far the most important factor affecting colonization propensity of land birds in Inari. Communities in different "island type groups" defined on the basis of habitat composition were relatively similar. "Sampling" seems the main factor causing increase in species numbers with increasing island size in Inari, although increasing habitat heterogeneity also has an influence. Frequency patterns in the total pooled data were also compared with distribution types of single species. Successful species on the islands can roughly be divided into three groups: (1) characteristic generalists of forest habitats at the transition between taiga and tundra (4 spp.); (2) characteristic species of the northern taiga, widely distributed in northern Palearctic (11 spp.); and (3) species with an "interzonal" distribution type, i.e. specialized to habitats that are geographically widely distributed but locally patchy (in Inari shores and open, rocky grounds) (2 spp.) Data from the Inari islands support the suggestion that the forest avifauna of Finnish Forest Lapland is impoverished, and a comparison with data from northern Russia and Siberia indicates that this is due to habitat impoverishment: Pine is the only conifer in Finnish northern Lapland, but the richest bird communities reside in spruce forests in the North-Russian taiga.

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1. Introduction

In this paper I analyze the occurrence of land birds in the archipelago of Lake Inari, Finnish Lapland. The area lies at the border between northern boreal (northern taiga) and subarctic (forest tundra) zones (see Sect. 2.1 below). Land birds were censused on 41 islands with a size range of 0.5-885 hectar (17 islands in two years). The physical structure of the study area is similar to that of the Vargskär islands in the Åland archipelago, SW Finland, where land birds were studied in 1976-80 (Haila 1983, Haila & Järvinen 1983, Haila et al. 1983, Järvinen & Haila 1983).

In the Åland archipelago "sampling" seems a proper way of describing the colonization of small islands by land birds, i.e., breeding communities of the islands can be portrayed as samples taken by the islands from a surrounding avifaunal universe (Preston 1948, Haila 1983). The sampling efficiency of each island depends on its area and environmental characteristics. Both community structure on the islands and spatial distribution of breeding pairs in the archipelago (Haila 1983) as well as species-specific colonization patterns (Haila & Järvinen 1983, Haila et al. 1983) support the view.

In this paper I analyze the colonization success of land birds in the Inari archipelago by comparing population numbers of individual species on the islands with expectations derived from census data from the mainland.

Colonization propensity of land birds in the Vargskär archipelago is crucially constrained by the availability of suitable habitats (Haila et al.

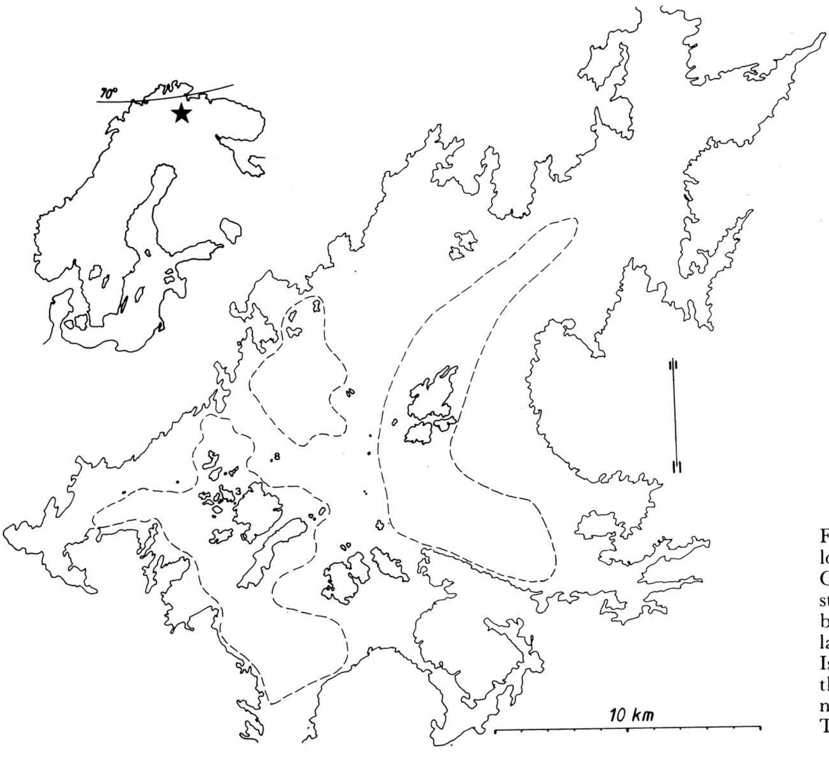

Fig. 1. The study area and its location in northern Fennoscandia. Only the 41 islands included in the study are drawn on the map; broken lines indicate regions in the lake with dense archipelagoes. Islets nos 3 and 8 are indicated in the Figure (because they lack names on topographic maps, see Table 1).

1983). This constraint is *a priori* likely to be important in Inari. The regional species pool comprises about 70 land bird species (Järvinen & Väisänen 1980), but it would be patently unrealistic to expect species of alpine habitats or large, wet subarctic peatlands to be found on the forested islands of Lake Inari.

The analysis of the Åland island land bird communities raised the question of how the structure of the sample (island community) reflects the structure of the universe (pool of colonizing species) (Haila 1983). I shall pursue this question further on the basis of the Inari data by seeking connections between the avifauna of the Inari islands and the biogeographic zones of the northern Palearctic.

Latitudinal zonality in the structure of vegetation and ecosystems, and consequently also in the structure of the fauna, is pronounced in northern areas (a well known fact since the pioneering studies by Middendorf (1869), Severtsov (1874) and Menzbir (1882), see, e.g., Uspenskij (1960), Chernov (1975)). "Fauna" (Mayr 1965, Chernov 1975) is a dynamic whole consisting of species with probably widely differing histories and ecologies but at present living in more or less the same area. Stegman (1931, 1938, 1966) originated the analysis of what he called "faunal types" of Palearctic birds, trying to synthesize within his approach historical and ecological aspects in zoogeography (for a history of the tradition, see Vuilleumier (1975), Voronov (1976), Udvardy (1981)). The approach of Stegman is not purely descriptive, but rather "analytic" (*sensu* Vuilleumier 1975) as it emphasizes ecological adaptations common to species inhabiting a certain biogeographic zone, irrespective of their historical origin (Shvarts 1963, Danilov 1966, Chernov 1975).

Several authors have continued the tradition of Stegman by trying to synthesize data on quantitative distribution and ecological adaptations of birds of the boreal and arctic regions of the Palearctic (e.g. Uspenskij 1960, Danilov 1966, Ravkin 1978, 1983, Ravkin & Shadrina 1980, Brunov 1978, 1980, Kishchinskij 1980a). These studies provide a basis for comparison for the land birds of the Inari islands.

2. Study area

2.1. Biogeographic position

Lake Inari (about 69°N, 28°E) has a water area of 1085 km^2; the lake is shallow; and islands, islets and skerries number about 3000 (total area 300 km^2) (Kallio et al. 1969). Islands in my study number 41 (censused in 1979; 17 also in 1977; see

Table 1), and they are located in the southern parts of the lake (Fig. 1).

Geologic and climatic conditions in the Inari basin have been recently summarized by several authors (Hämet-Ahti 1963, Kallio et al. 1969, Seppälä & Rastas 1980). The acidity of the soil is a critical edaphic factor in the region (Kallio et al. 1969). The ground is mostly covered by coarse moraine material. Mean annual temperature of the lake basin is -0.5°C, mean temperature in July is +14°C, and duration of the thermal summer (10°C-10°C) is 125 days (for detailed data see Kolkki 1966).

The biogeographic position of northern Fennoscandia is crucially affected by the ameliorating effect of the Gulf Stream, and boreal elements occur higher in the north than in other parts of the Holarctic (Kallio & Sonesson 1979). Phytogeographic zonation of the area is very complex, because the normal north-south temperature gradient is mixed with both a strong moisture gradient extending inland from the Atlantic coast as well as altitudinal effects (see the discussion by Hämet-Ahti 1963, Ahti et al. 1968, Kallio et al. 1969, Eurola 1978). The forests of Inari Lapland comprise two main components: pine forests (*Pinus sylvestris*) dominate the south-eastern parts of the area, including the Inari basin, and mountain-birch forests (*Betula pubescens* var. *tortuosa*) the north-western parts. Hustich (1966) separated these forest types into two different vegetation zones, regarding the mountain birch sections as a Fennoscandian analogue of the forest tundra of northern Russia and Siberia. His distinction was supported by Kallio et al. (1969) who emphasized the pronounced floristic differences between coniferous and birch forests, and included the mountain birch sections of Inari Lapland in the subarctic vegetation zone (Kallio et al. 1969: Fig. 32). According to this terminology my study area in the Inari archipelago belongs completely to the northern boreal vegetation zone that is homologous with the northern taiga of Soviet biogeographers (see Hustich 1979); on the most exposed small islands, however, elements of subarctic vegetation can be found and may even dominate (see Seppälä & Rastas 1980, and below).

In zoogeographic classifications the southern part of Inari Lapland has traditionally been included in the boreal zone ("Forest Lapland") because of the prominence of species connected with coniferous forests in the fauna (reviewed by Voipio 1956, see also Järvinen & Väisänen 1973, 1980). Järvinen & Väisänen (1973, 1980) made an ornithogeographic zonation of Finland based on quantitative bird census data and distinguished a "hemiarctic zone" in southern Inari Lapland as a transitional region between northern taiga and the arctic zone proper dominated by tundra species. They found pronounced differences in faunal composition especially to the north but also to the south of this transitional zone. Their zonation is, however, crucially affected by regional habitat composition; the pine-dominated Inari basin taken separately would be very close to their north-boreal zone (see Järvinen & Väisänen 1980).

Pine is the predominating tree in the coniferous forests of the Inari basin. The spruce (*Picea abies*) occurs in the area only in a few small, isolated stands or as solitary trees (Kallio et al. 1971). In the Kola Peninsula as well as in northern Russia and Siberia spruce (or larch) forms the northern forest limit (Hustich 1966, Gribova et al. 1980).

Table 1. Characteristics of the censused islands. Island names were taken from topographic maps; points of the compass in parentheses indicate the position of censused islands in island groups with a common name. Islets nos 3 and 8 are indicated in Fig. 1 as they lack names on the map. Symbols: A = area (ha), H1-H5 = area of different habitat types (ha) (habitat codes in the text), Censuses = census years, observed species numbers in parentheses.

	A	H1	H2	H3	H4	H5	Censuses
1. Lehtisaari (S)	0.5	0.5	0	0	0	0	1977(2) 1979(2)
2. Vallenkari (SE)	0.5	0.5	0	0	0	0	1979(3)
3. Petäetuluoto	0.6	0	0	0	0	0.6	1977(2) 1979(3)
4. Pietarinlaassa	0.6	0.6	0	0	0	0	1979(2)
5. Vallenkari (NW)	0.6	0.6	0	0	0	0	1979(2)
6. Hirvassaari (SW)	0.6	0.6	0	0	0	0	1979(2)
7. Hirvassaari (W)	0.7	0.7	0	0	0	0	1979(2)
8. Petäjäkari	1.0	1.0	0	0	0	0	1979(2)
9. Ukko	1.5	0	0	0	1.5	0	1979(4)
10. Malkosaari (S)	1.7	0	0	0	1.7	0	1977(4) 1979(5)
11. Liekovuopaja (S)	2.7	0	0	0	0	2.7	1977(4) 1979(2)
12. Lintusaari (SE)	4.4	3.6	0.8	0	0	0	1979(4)
13. Hillasaari (N)	6.4	0	0	0	6.4	0	1979(6)
14. Malkosaari (W)	6.5	0	0	0	6.5	0	1977(6) 1979(6)
15. Hirvassaari (N)	7.4	3.0	3.7	0	0.7	0	1979(7)
16. Liekovuopaja (NE)	8.3	0	0	0	0	8.3	1977(6) 1979(5)
17. Lintusaari (NE)	8.4	8.4	0	0	0	0	1979(6)
18. Hillasaari (S)	9.0	0	0	0	9.0	0	1979(5)
19. Malkosaari (N)	14	0	6	0	8	0	1977(9) 1979(7)
20. Liekovuopaja (N)	17	0	0	0	0	17	1977(6) 1979(5)
21. Lehtisaari (N)	17	4	0	0	13	0	1977(9) 1979(8)
22. Liekovuopaja (SW)	20	0	0	0	0	20	1979(7)
23. Vieppisaari	22	0	0	0	22	0	1979(8)
24. Naarassaari	26	0	12	0	14	0	1979(11)
25. Liekovuopaja (SW)	27	0	1	0	0	26	1979(9)
26. Jänkä Viipassaari	27	0	20	0	7	0	1979(10)
27. Liekovuopaja (SE)	29	0	0	0	0	29	1977(8) 1979(11)
28. Seahasualui	54	0	0	3	0	51	1977(12) 1979(8)
29. Viipassaari	54	0	20	0	34	0	1979(9)
30. Selkä Reposaari	62	0	22	0	40	0	1979(11)
31. Pääsaari	67	0	0	0	0	67	1977(14) 1979(10)
32. Mergamsaari	69	0	0	0	0	69	1977(12) 1979(8)
33. Kärppäsaari	93	0	0	0	37	56	1979(11)
34. Makia Petäjäsaari	99	0	0	0	0	99	1977(10) 1979(13)
35. Keskimm. Reposaari	126	0	13	0	113	0	1979(15)
36. Suovasaari	228	0	0	30	0	198	1979(14)
37. Pieni Jääsaari	290	0	0	10	140	140	1977(18) 1979(16)
38. Hoikka Petäjäsaari	670	0	0	10	0	660	1979(15)
39. Jääsaari	680	0	0	0	480	200	1977(22) 1979(21)
40. Varttasaari	784	0	0	70	518	196	1979(17)
41. Leviä Petäjäsaari	885	0	0	27	0	858	1977(25) 1979(25)

2.2. Island habitats

The Inari basin is floristically impoverished compared with other parts of Inari Lapland, presumably because large parts of the land area of today were submerged for a long period after the glaciation (Kallio et al. 1969); e.g., such common and ubiquitous Lapp herbs as *Filipendula ulmaria* and *Geranium sylvaticum* are very rare in the Lake Inari area (Y. Mäkinen, pers. comm.). Barren pine forest is the dominating habitat element in the Inari archipelago. Birch is common on the islands, however, and in some parts of the archipelago mixed (birch-pine) forests dominate (Seppälä & Rastas 1980: Map). Other deciduous trees occurring in Inari Lapland, e.g. *Alnus incana* and *Populus tremula*, are scarce on the islands for edaphic reasons (Kallio & Mäkinen 1975, 1978). Most of the regionally

Fig. 2. Typical landscapes in Lake Inari (all photos by L. Saraste).

2A. Shore line on an elevated island, dominated by pine (island no 41).

2B. Pine forest (island no 41).

abundant willows (*Salix* spp.) grow on the islands (Kallio & Mäkinen 1975), but are a minor element in the island habitats.

The floristic impoverishment is likely to influence the composition of bird communities in the islands habitats.

Järvinen & Väisänen (1976a) developed a habitat classification of the transition between taiga and tundra based on quantitative bird data. I used their classification in making habitat distinctions on the islands. I identified the following five counterparts to the mainland habitats:

H1. Dry alpine meadow (alpine heath) (B3 of Järvinen & Väisänen 1976a). Open, dry and stony habitat with dwarf shrub and grasses forming the vegetation cover. Alpine heaths dominate a few small exposed islands that lie near broad water stretches in central parts of the lake.

H2. Open subalpine peatland (B6 of Järvinen & Väisänen 1976a). Small bogs with relatively lush vegetation (*Betula nana, Salix* spp. and various herbs and grasses). The habitat type occurs on small islands in northern parts of the lake but is nonexistent on islands dominated by coniferous forests.

H3. Aapa fen in the regio sylvatica (B7 of Järvinen & Väisänen 1976a). Open or semi-open *Sphagnum* peatlands were classified in this habitat type although considerable differences certainly exist between them. Peatlands are small on the islands, however, and a more precise classification is not needed.

H4. Mixed (mountain birch, pine) forest (B10 of Järvinen & Väisänen 1976a). This habitat is widespread in eastern and northern parts of the lake (see Seppälä & Rastas 1980). On a few small and low islands the habitat type actually approaches pure mountain birch forest (B9 of Järvinen & Väisänen 1976a), but these stands cover an insignificant proportion of the study area.

H5. Pine forest (B11 of Järvinen & Väisänen 1976a). The predominating habitat on large and elevated islands in the southern part of the lake, typically extremely barren and stony. Even shoreline vegetation is largely made up of pure pine stands.

The proportions of different habitat types on the censused islands (estimated from aerial photographs with the help of the forest type map published by Seppälä & Rastas (1980)), as well as other important island characteristics are given in Table 1. Photographs of the main forest types are shown in Fig. 2.

2C. Mixed forest (island no 39). A relatively lush site (in the island scale), where the mountain birch dominates, but trees are short and bush layer sparse.

2D. Typical shore-line on a small, low island covered by mixed forest (actually similar to alpine birch forests on the mainland) (island no 10).

3. Materials and methods

The censuses were made from 23 June to 2 July 1977 (YH alone), and from 22 June to 1 July 1979 (YH and A. Rönkä), during the period recommended for bird censuses in northern Finland (Järvinen & Väisänen 1976b). Censuses were made in early morning; only on a few small unforested islands were they extended into the afternoon.

As in the censuses in the Åland archipelago, two variants of one-visit censuses were used (see Haila & Järvinen 1981, Haila & Kuusela 1982, Haila 1983, Haila et al. 1983). Small islands (up to 1 km^2) were censused as single study plots, and larger islands by making a transect through the island and using correction coefficients to estimate average densities and population numbers (Järvinen & Väisänen 1977). In Inari considerably larger islands were censused as study plots than in the Åland archipelago. This decision was made because of the low average densities and good detectability of birds in the barren habitats of the islands. Therefore the main results of the methodological test made on Åland (Haila & Kuusela 1982) are probably also applicable to censuses in Inari; i.e., results of one-visit censuses can be used in quantative comparisons. This conclusion is supported by the similarity of the census results in 1977 and 1979.

Thus, in Inari the total breeding community on the 17 islands censused in both years was estimated at 1802 pairs (30 species) in 1977 and at 1898 pairs (31 species) in 1979.

The primary data are published in the Appendix. Species observed in inter-island flight during the censuses are indicated there. As on Åland, these "surplus individuals" presumably do not affect the conclusions, which will be based largely on pooled data of island groups (see Haila et al. 1983).

4. Colonization patterns: Prevalence functions

4.1. Construction of prevalence functions

Prevalence functions are a method of studying colonization patterns of insular populations on the basis of quantitative data (Haila et al. 1983, see also Haila & Järvinen 1981). Islands are

Table 2. Habitat composition (in ha) of the island size classes (see text; habitat codes are given in Sect. 2.2). The 1977 figures (17 islands) in parentheses.

Size class	H1	H2	H3	H4	H5
I	8.1 (0.5)	0.8 (0)	0 (0)	12.2 (1.7)	3.3 (3.3)
II	15.4 (4.0)	50.7 (6.0)	3.0 (3.0)	97.6 (27.5)	220.3 (174.3)
III	0 (0)	47 (0)	147 (37)	1342 (62)	2475 (1364)
Total area	24 (4)	99 (6)	150 (40)	1452 (92)	2699 (1542)

grouped into size classes, the expected population size of each species in the size classes is predicted on the basis of mainland census data, and prevalence in each size class is calculated as observed N divided by expected N. It is important to take into account environmental characteristics of the islands in calculating the expectancies, for regional average densities may result in very unrealistic figures (e.g. Haila & Järvinen 1981).

In an ideal case prevalence expectations can be based on habitat census data from the source area. Unfortunately, in the case of Inari islands, no strictly comparable habitat censuses are available from the mainland. I calculated the expected population sizes from average densities in mainland habitats in the data used by Järvinen & Väisänen (1976: Table 4). It is an advantage that their habitat classification was based on comparisons of bird communities, but there are two other problems in this procedure:

1) The data of Järvinen & Väisänen (1976a) date from a long period (1937-1974) and a relatively wide geographic area. Long-term population changes as well as density gradients within the area covered by Järvinen & Väisänen (1976a) certainly impede the realism of population expectations calculated from their data. I tried to correct this bias by using the results of the Finnish line transect censuses, summarized by Järvinen & Väisänen (1983). (A minor problem is that my line transects made on the islands in 1977 (20 km) are included in Järvinen & Väisänen (1983), but as a tiny proportion of the total data). I also used unpublished original line transect data collected by O. Järvinen and R. A. Väisänen from the Inari basin; a total of 36 km of transects censused in southern parts of the basin in 1977 (the "Inari transects" below) gave valuable background information.

In particular I checked species that have steep density gradients within the area from which the source data of Järvinen & Väisänen (1976a) originated. It is *a priori* likely that this should impede the realism of expectations calculated for the Inari islands. Drastic population changes have been observed in many species in the north since the 1930s, but they are mostly correlated with changes in the areal coverages of different habitats (Järvinen & Väisänen 1983, see also Järvinen & Väisänen 1978c, Järvinen et al. 1977). The island habitats are natural forests, and comparison of bird densities with data that come from similar natural habitats are legitimate despite the relatively long time span.

2) The habitats of the Inari islands are not strictly comparable to the habitats described by Järvinen & Väisänen (1976a), because the islands are edaphically and floristically impoverished (Sect. 2.2). The nearly complete lack of deciduous bushes in the barren habitats of the large islands is a striking feature of my study areas. Differences in habitat structure between islands and the mainland always create an element of uncertainty in comparisons (as emphasized by Abbott 1980, Williamson 1981, Haila & Järvinen 1983, Haila et al. 1983).

I divided the islands into three size classes using observed number of species as the criterion (Table 1). The criteria were: class 1: $S\leq5$, class 2: $5<S\leq10$, class 3: $10<S$ (for islands that were censused in two years I used the mean of the two estimates). Habitat composition of the island size classes is shown in T.able 2.

In the data used by Järvinen & Väisänen (1976a), 49 species were recorded in the five habitats with counterparts on the islands; these 49 species are thus a first approximation of the species pool of the archipelago. 14 of them were not observed on the islands (Sect. 4.3), but 8 other species were recorded there (Sect. 4.3). The total number of species in my data is thus 43.

4.2. Abundant species

Observantions and expectations of 24 abundant species are presented in Table 3, arranged in guild order. In addition, prevalence functions of the four most abundant species are shown in Fig. 3. Variance estimates of the observed population sizes were calculated by assuming the census to be a Poisson process (and variance to equal mean, i.e. observed population size). As discussed by Haila et al. (1983), there are both statistical and ecological reasons why prevalences are usually low in small island size classes. The following

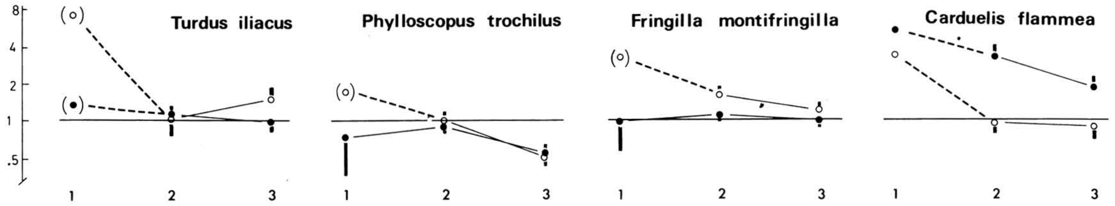

Fig. 3. Prevalence functions of the four most abundant species in the Inari archipelago. The three island size classes are shown on the abscissa, the ordinate gives prevalence values (logarithmic scale). Expectation = 1, marked by a straight line. Circles = 1977, dots = 1979. Observations are bracketed and functions drawn by a broken line whenever expectations are lower than 5 pairs. In size classes with expectations higher than 5 pairs an estimate of the S.D. of the observed population size is indicated by a bar from the lower value downwards and from the higher value upwards.

patterns emerge:

Foliage insectivores (3 spp.). Observations agree with expectations except in *Phylloscopus trochilus*. It is scarcer than expected in the third island size class. The deviation is presumably caused by habitat differences: deciduous bushes are scarce in the island forests (Sect. 2.2, 4.1).

Ground insectivores (9 spp.). Five of the species are as abundant as expected, but four of them have prevalences lower than 1 (*Anthus trivialis, Luscinia svecica, Turdus pilaris* and *Emberiza schoeniclus*). The expectation of *A. trivialis* is probably too high, because the species has a southern distribution and its density shows a steep gradient in the Inari basin; it has also declined in northern Finland (Järvinen & Väisänen 1983). It is surprisingly scarce on the islands, however. Its mainland density was, according to the Inari transects, 1.0 pairs/km^2 in 1977, which gives an expectation of 20 pairs for the islands censused in 1977, but the population estimate was only 6 pairs.

Habitat impoverishment on the islands is a plausible explanation for the scarcity of the other three species. *Emberiza schoeniclus* mostly breeds in low bushes on peat bogs and marshlands, but they are scarce on the islands (Sect. 2.2). *Turdus pilaris* is relatively abundant in northern Fennoscandia up to the arctic coast (Järvinen & Väisänen 1978a, 1983), but it occurs sporadically in northern Lapland and is mainly restricted to lush habitats (von Haartman et al. 1963-72, Järvinen & Väisänen 1978a). The regional density of *Luscinia svecica* in the Inari basin is about 1 pair/km^2 (Järvinen & Väisänen 1983), and in the Inari transects its density estimate was 1.6 pairs/km^2; this gives an expectation of 36 pairs for the 1977 islands, but the only records (2 pairs) of the species were made on two small, bushy islands in 1979. Scarcity of deciduous bushes in the island habitats is the most plausible explanation for its low numbers.

Sallying flycatchers (3 spp.). All three species are scarcer than expected. All three have a southern distribution with a steep gradient in regional densities in the Inari basin (Järvinen & Väisänen 1983), and the expectations are thus too high. The scarcity of lush birch woods on the islands probably contributes to the low numbers of *Ph. phoenicurus* and *F. hypoleuca*; in the Kilpisjärvi region both species breed in this habitat (A. Järvinen 1978, 1980, see also Järvinen & Väisänen 1978a). *Ph. phoenicurus* has declined (Järvinen & Väisänen 1983), but, interestingly, its average densities observed in the island pine forests were similar to those in earlier data from natural pine forests (Järvinen & Väisänen 1976).

Seed eaters (3 spp.). Observed on the islands in expected numbers.

Other species (6 spp.). Two species (*Lagopus lagopus* and *Bombycilla garrulus*) are scarcer than expected, and one (*Tringa glareola*) is more abundant than expected. *L. lagopus* is scarcer than expected, presumably because the islands are mostly covered by barren, monotonous forests. Winter conditions, in particular, may be too harsh on the islands where shrub bogs are scarce. *B. garrulus* is known for its irregular occurrence and great population fluctuations in Finnish Lapland (von Haartman et al. 1963-72). Its density estimate from the Inari transects in 1977 was 0.3 pairs/km^2, which gives an expectation of 7 pairs for the 1977 islands, and the population estimate was 3 pairs. Obviously the prevalence expectation of the Waxwing is too high. The small, forested bogs on the islands may be relatively more fabourable for *Tringa glareola* than large, open peatlands.

4.3. Scarce species

In the following tabulation I present a list of the 11 species that were observed on the islands in low numbers (and were included in the habitat data of Järvinen & Väisänen 1976a):

	Expectation (the set of 41 islands)	Population estimate (17 islands in 1977, 41 in 1979)
Falco columbarius	17	1979: 1
Bonasa bonasia	8	1977: 1
Charadrius apricarius	1	1979: 2
Calidris temminckii	5	1979: 2
Philomachus pugnax	13	1979: 6
Lymnocryptes minimus	3	1979: 1
Gallinago gallinago	6	1977: 2, 1979: 1
Numenius phaeopus	1	1979: 2
Cuculus canorus	45	1977: 5, 1979: 3
Dendrocopos minor	4	1979: 1
Saxicola rubetra	1	1979: 6

Most of the species are habitat specialists, e.g. peatland waders, that were observed on the islands in roughly expected numbers (note that most of the waders were recorded on small islands with alpine heaths (H1) (Appendix)). The three exceptions are only apparent and due to unrealistic prevalence expectations. The regional density of *F. columbarius* is less than 0.06 pairs/km^2 (Järvinen & Väisänen 1983), i.e. similar to that observed in the archipelago. *B. bonasia* is a southern species and occurs in the Inari basin occasionally (von Haartman et al. 1963-72, Järvinen & Väisänen 1983). The range of *C. canorus* reaches the arctic coast, but a steep density gradient is situated in Forest Lapland (Järvinen & Väisänen 1983). Its density estimate derived from the Inari transects in 1977 was 0.2 pairs/km^2, which results in a population expectation of 4 pairs for the 1977 islands, and the estimate was 5 pairs.

The following eight species were observed in the island censuses but not in the censuses Järvinen & Väisänen (1976a) used as their sources; expectations were calculated by multiplying regional density estimates (Järvinen & Väisänen 1983) by the total area of the 41 censused islands:

	Expectation	Population estimate	
	(the set of 41 islands)	1977 (17 islands)	1979 (41 islands)
Buteo lagopus	2	2	2
Tringa nebularia	5	0	9
Actitis hypoleucos	(2)	19	14
Strix nebulosa	-	1	1
Motacilla alba	(40)	36	107
Corvus corone	10	7	2
C. corax	2	3	4
Carduelis spinus	-	0	9

A. hypoleucos and *M. alba* are habitat specialists of shores and islands (von Haartman et al. 1963-72, Järvinen & Väisänen 1983), and expectations based on regional densities are therefore misleading. The same is true of *C. corone,* mostly confined to habitation in the north but also breeding and feeding along shores even at the arctic coast (e.g., Bianki et al. 1967). Otherwise observations match expectations.

The following list includes species recorded in the island habitat counterparts in the data of Järvinen & Väisänen (1976a) but not observed on the islands; expectations for the total set of 41 islands are given in parentheses after each species name; the symbol (G) indicates species with a steep density gradient in the Inari basin (Järvinen & Väisänen 1983): *Charadrius morinellus* (<1), *Tringa erythropus* (7), *Phalaropus lobatus* (<1), *Apus apus* (G) (7), *Eremophila alpestris* (<1), *Anthus cervinus* (4), *Prunella modularis* (G) (9), *Turdus viscivorus* (G) (7), *Sylvia borin* (G) (14), *Phylloscopus borealis* (9), *Parus montanus* (G) (9), *Lanius excubitor* (G) (10), *Calcarius lapponicus* (3) and *Plectrophenax nivalis* (<1). The four species with expectations lower than 1 pair are obviously absent because of rarity (relative to the available habitats) (see Haila & Järvinen 1983, Järvinen & Haila 1983). For another set of six species the expectations are highly misleading because of density gradients; rarity is a sufficient reason for their absence (again relative to the regional habitat composition — some of them occur regularly in northern Norway in lush deciduous woods, e.g. Järvinen & Väisänen (1978a)). This leaves four species that have relatively high regional densities in the Inari basin but were absent from the islands:

Ph. borealis is presumably absent because of habitat impoverishment; it occurs most frequently in lush habitats (von Haartman et al. 1963-72, see also Vladimirskaya 1948, Novikov 1952a, 1958). *T. erythrinus* and *A. cervinus* favour open, wet subarctic peatlands (Järvinen & Väisänen 1978a, 1978b), but this habitat type is absent from the archipelago. The absence of *C. lapponicus* is presumably also due to habitat scarcity. Its North-Norwegian favoured habitat, "Calcarius heath" (Järvinen & Väisänen 1978a) is almost non-existent on the islands. The Lapland Bunting has greatly increased in southern parts of its range in recent decades, and it is relatively abundant in alpine habitats in southern Inari Lapland (Järvinen & Väisänen 1983); the Inari transects in 1977 gave a mainland density estimate of 6.1 pairs/km^2. A realistic prevalence expectation should be based on detailed data on the habitat distribution of the species in southern parts of its range, but these data are lacking.

4.4. Population changes

Prevalence functions of four species show obvious differences between the two census years (Table 3):

Lagopus lagopus was not observed in 1977 but was recorded on seven islands in 1979, three of which were also censused in 1977. The data are thus small, but the species is known for its great

Table 3. Observed (above) and expected (below) population numbers of 24 abundant species in the three island size classes in 1977 (17 islands) and 1979 (41 islands), arranged in guild order.

	1977			1979		
	I	II	III	I	II	II
Foliage insectivores						
Phylloscopus trochilus	2	40	267	4	72	553
	1	41	482	6	81	968
Parus cinctus	0	2	40	0	1	39
	0	2	29	0	4	59
Fringilla montifringilla	4	56	581	6	85	958
	1	37	484	6	77	983
Ground insectivores						
Anthus trivialis	0	0	6	0	0	0
	0	6	50	0	8	91
A. pratensis	0	3	0	8	34	98
	0	5	29	1	29	96
Motacilla flava	0	4	0	0	14	150
	0	3	28	0	10	80
Luscinia svecica	0	0	0	1	1	0
	0	1	7	0	3	17
Oenanthe oenanthe	1	8	24	3	6	30
	0	1	12	0	2	25
Turdus pilaris	0	1	2	0	0	12
	0	1	16	0	3	32
T. philomelos	0	3	28	0	0	65
	0	3	26	0	4	48
T. iliacus	3	14	217	2	26	287
	0	13	144	2	23	285
Emberiza schoeniclus	0	0	0	0	11	9
	0	2	18	0	9	46
Sallying flycatchers						
Phoenicurus phoenicurus	0	2	63	0	6	127
	0	10	118	1	19	235
Muscicapa striata	0	1	43	0	2	39
	0	7	68	0	11	129
Ficedula hypoleuca	0	1	6	0	0	9
	0	4	40	0	6	78
Seed eaters						
Carduelis flammea	1	15	120	5	78	511
	0	15	135	1	24	257
Loxia curvirostra	0	1	17	1	5	40
	0	1	8	0	1	15
Pinicola enucleator	0	1	26	0	1	39
	0	0	7	0	1	16
Other species						
Lagopus lagopus	0	0	0	1	2	14
	0	2	21	0	4	42
Tetrao urogallus	0	0	59	0	2	42
	0	3	22	0	4	41
Tringa glareola	0	1	27	0	0	89
	0	1	2	0	3	12
Picoides tridactylus	0	0	2	0	0	1
	0	1	5	0	1	9
Bombycilla garrulus	0	0	3	0	0	4
	0	2	17	0	3	33
Perisoreus infaustus	0	1	32	0	0	55
	0	2	21	0	3	41

population fluctuations in the north (von Haartman et al. 1963-72).

Anthus pratensis and *Motacilla flava* were more abundant in 1979 (prevalence close to 1) than in 1977. On the 17 islands censused in both years the population estimates were 3 (1977) vs. 25 (1979) for *A. pratensis* and 4 (1977) vs. 19 (1979) for *M. flava*. In 1977 all records of both species were made in habitats H1 and H2 on small islands, but in 1979 they also occupied peatland habitats on large islands (H3) (Appendix). A probable explanation for the scarcity of the two species in 1977 is offered by an exceptionally cold period with heavy snowfall that occurred in Lapland in mid-June 1977. In NE Lapland (150 km SE of Lake Inari) the ground was covered by snow from 21 to 24 June, with a maximum depth of 25 cm, and several bird species suffered heavy nest losses (Pulliainen 1978). In late June I observed in Inari several high-flying *Motacilla* spp. individuals that obviously had left their breeding grounds. Possibly the pairs observed in the open habitats in 1977 tried to raise a new brood, which is known to occur even in the Subarctic (e.g. Hildén 1967, von Haartman et al. 1963-72, Pulliainen 1978).

Carduelis flammea was more abundant in 1979 than in 1977, population estimates of the islands censused in both years being 136 (1977) vs. 312 (1979). The species is known for marked population fluctuations, and it also often changes breeding area during the summer between the first and the second brood (Peiponen 1957, 1962).

4.5. Conclusions: Habitat preferences and island colonization

Because of the heterogeneity of the mainland data and the differences in the habitat structure between the islands and the mainland (Sect. 4.1), a conservative evaluation of the observed patterns is necessary. 43 species were observed in the island censuses, and prevalence functions could be constructed for 24 abundant species. Nine were scarcer than expected. In eight of the cases, however, the obvious explanation is in the habitat structure on the islands, and the low prevalence of only one species (*Anthus trivialis*) is not easily explainable by the habitat differences. The remaining 19 less abundant species were all observed in numbers roughly agreeing with expectations derived from mainland densities. I regarded density gradients in Inari basin as an explanation for observations lower than expectations in several species with a southern distribution. The explanation applies to all "gradient species" included in the background data of Järvinen & Väisänen (1976a), which makes it plausible. Most absences from the islands were obviously due to lack of suitable habitats; only one of the missing species (*Calcarius lapponicus*) had high enough regional densities in the Inari basin to be expected to occur on the islands, but even in this case differences in habitat

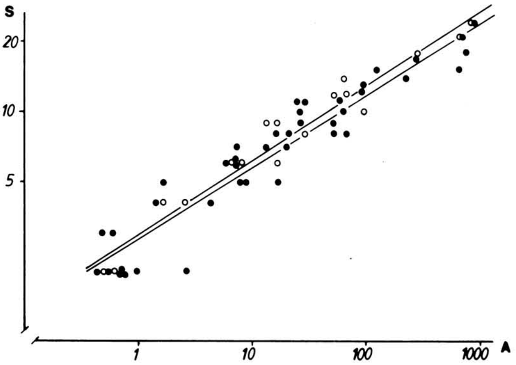

Fig. 4. Species-area regressions in the two data sets (with logarithmic transformations on both axis) (circles = 1977, dots = 1979) (regression equations: 1977, $y = 0.323x + 0.467$; 1979, $y = 0.311x + 0.449$).

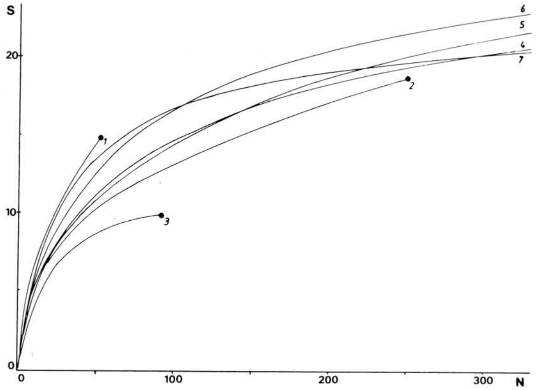

Fig. 5. Rarefaction curves calculated from the pooled data of the island type groups (see text for the group codes).

structure may be a plausible explanation for the absence.

The only species with observed population numbers higher than expected was *Tringa glareola*, but better background data are needed for this peatland wader. In other words, there were no traces of "density compensation" (e.g. MacArthur et al. 1972, Wright 1980) in my study area in Inari. On the small, bushy islands population estimates were close to expectations, but the small island habitats are probably similar to their mainland counterparts. Habitat preferences seem to be of overriding importance in determining the colonization propensity of land birds in Inari.

5. Species numbers

Fig. 4 shows the species-area regressions (logarithmic scale) in the data set of both census years. Correlations are highly significant in both cases (1977, 95 % of the variance explained; 1979, 90 % of the variance explained). The slopes are also similar (z=0.32 and z=0.31 in 1977 and 1979, respectively). There were no significant differences between the two data sets when the 17 islands censused in both years were compared (pairwise t-test, t=1.38, df=16, n.s.).

Rarefaction is a more informative method of studying variation in species number because the effect of varying sample size can be removed (Simberloff 1978, 1979, Engstrom & James 1981, James & Rathbun 1981). I divided the islands into groups according to proportions covered by different habitats on each island ("island type groups"), and pooled the data of all islands and both years in each group. (For a justification of the procedure, see Haila (1983)).

Island type groups were defined as follows (island codes in Table 1):

Group 1. Small islands dominated by alpine heaths (H1) (islands 1, 2, 4, 5, 6, 7, 8, 12, 15, 17).

Group 2. Islands with subalpine peatlands (H2) and with mixed forests (H4) as an important secondary habitat (islands 19, 24, 26, 29, 30).

Group 3. Small, low islands covered by homogeneous mixed forests (H4) (islands 9, 10, 13, 14, 18, 23).

Group 4. Islands covered by pure pine forests (H5) (islands 3, 11, 16, 20, 22, 27, 31, 32, 34).

Group 5. Islands where mixed forests dominate but other habitats also occur (islands 21, 35, 39).

Group 6. Islands where pure pine forests dominate but other habitats also occur (islands 25, 28, 36, 38, 41).

Group 7. Large, heterogeneous islands with mixed and pine forests in roughly equal proportions (islands 33, 37, 40).

Rarefaction curves (James & Rathbun 1981) based on the pooled data of the island type groups are shown in Fig. 5. There is only one statistically significant difference in species numbers between the groups; group 3 has lower S than the others. This is presumably a consequence of the barren character of the group 3 islands; in fact, the habitat found there is structurally close to the barren B9 of Järvinen & Väisänen (1976a) (mountain birch forest; see Sect. 2.2).

In other words, species number increases with increasing sample size at a similar rate on all forested island types. The conclusion can be investigated further by comparing the pooled "communities" of the island type groups 4–7 (forested islands) (Table 4). Average density in the pine dominated groups is about 70 pairs/km^2, as compared with about 90 pairs/km^2 in the other

Table 4. Pooled communities in forested island type groups (4–7); overall characteristics and Ddiff matrix; see text.

	4	5	6	7
Number of pairs	410	1372	1978	1375
Number of species	22	33	33	24
Density (p/km^2)	67.1	90.3	70.5	94.4
Ddiff	4	5	6	
5	0.02			
6	0.12	0.08		
7	0.24	0.11	0.06	

groups. I also compared the composition of the pooled communities by the index Ddiff (Järvinen & Väisänen 1977), based on pairwise comparisons of the communities. The differences are relatively small, the largest being 0.24 units between groups 4 and 7. For a comparison, the two birch forest variants defined by Järvinen & Väisänen (1978a) in northern Norway differed by about 0.18 units. Furthermore, varying proportions of peatlands in the island type groups certainly affect the differences. I conclude that community composition is relatively similar on different types of forested islands; Järvinen & Väisänen (1976a) similarly emphasized the similarity of bird communities in different forest habitats in Inari Lapland.

Connor & McCoy (1979) discussed alternative meachanisms leading to the commonly observed regular increase in S with increasing island area. On the Åland Islands their habitat diversity hypothesis and sampling hypothesis received support (Haila 1983). As the forest habitats on the islands of Inari archipelago seem to be very similar to each other as regards birds, the sampling hypothesis is the best candidate as an explanation for the regularity, i.e., large islands should have higher species numbers than small ones because the total number of individuals is greater, and scarce species are more probably included in the community. I checked this prediction by first pooling the data of all forested islands larger than 2 km^2 (island type groups 4–7), then calculating a rarefaction curve from this "community" and using this curve to predict species numbers on smaller islands (and combinations of them). The result is shown in Fig. 6. The expectation does not hold true. There is a clear tendency towards lower than expected species numbers on small islands. The same tendency is true also of single islands. In censuses on islands within the size range of 30 ha–2 km^2 (Table 1, Appendix), observed species number was lower than expected in 9 cases, and higher in 3 cases.

One reason for the deviation is certainly that habitat heterogeneity is, after all, greater on large islands because of peatlands (Table 1). Another reason is that birds actually colonize single islands and not island groups. That is why prevalence functions of single species often dip at the lower end of the island size scale (Haila et al. 1983), but similarly it means that an ecologically realistic expected species number for pooled small island data is lower than that derived by rarefying large island communities.

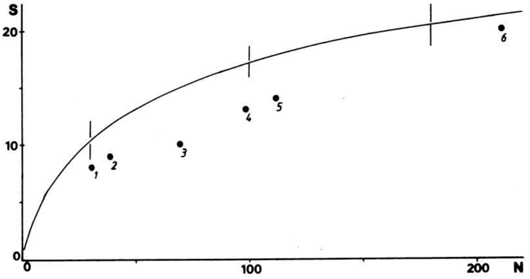

Fig. 6. A rarefaction curve calculated from the pooled data of forested islands larger than 2 km^2 (with bars indicating ± 1 S.D.), compared with observed species number in pooled small island data. Codes: (1) islands with pine forests, smaller than 15 ha; (2) islands with mixed forests, smaller that 15 ha; (3) all forested islands smaller than 15 ha; (4) islands with mixed forests, smaller than 30 ha; (5) islands with pine forests, smaller than 30 ha; (6) all forested islands smaller than 30 ha.

To conclude, increasing habitat heterogeneity certainly affects the increase of species number with island area on the Inari islands, but "sampling" seems a factor of cardinal importance.

6. Where do the colonizers come from?

6.1. On zonal connections of the Inari avifauna

Fig. 7 shows the species-abundance distribution in my pooled data (population estimates of all islands, both years, *N*=5528), arranged in Preston's (1948, 1962) octaves but without excluding any of the single pair populations. It is obvious that no simple statistical distribution fits the data. I also checked the species-abundance distributions of different sub-sets of the total island data set (island type groups, different years) but they looked no less irregular than the distribution in Fig. 7. On the basis of the distribution, the Inari island colonizers can be divided into three abundance classes:

1) The four dominants (>512 pairs/species, making up 68 % of the total) are *Turdus iliacus, Phylloscopus trochilus, Fringilla montifringilla* and *Carduelis flammea.*

2) The "hump" in the middle comprises 13 species with 64≤N<256: *Tetrao urogallus, Tringa*

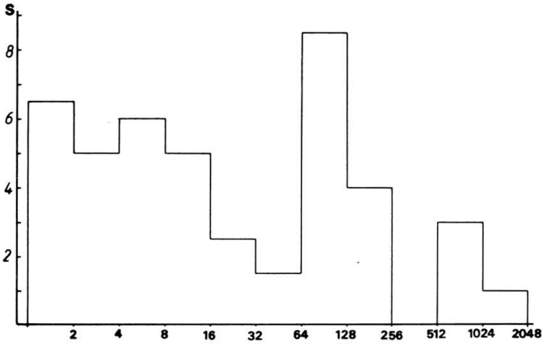

Fig. 7. Species-abundance distribution in the total pooled data (N=5528), arranged in "Prestonian" octaves (intervals: 1-2, 2-4, 4-8, 8-16, ...; species with exactly 2^n pairs in the data were halved between neighbouring octaves).

glareola, Anthus pratensis, Motacilla flava, M. alba, Phoenicurus phoenicurus, Oenanthe oenanthe, Turdus philomelos, Muscicapa striata, Parus cinctus, Perisoreus infaustus, Loxia curvirostra (including *L.* spp.) and *Pinicola enucleator.*

3) The tail to the left comprises 26 scarce species with less than 64 pairs/species. The most numerous among them were *Actitis hypoleucos* with 33 pairs, and *Emberiza schoeniclus* with 20 pairs.

Species-abundande distributions are usually assumed to have some regular from (e.g. May 1975, Pielou 1975, Engen 1978; for additional references, see Haila 1983). The irregular shape of the distribution in my data is not due to any bias in the sampling process, as the island habitats are represented in approximately correct proportions in the study area. Rather, a background for the irregularity might be found in the structure of the faunal universe from which the island bird communities are "sampled" — in a sampling process, the species-abundance distribution is created conditional upon the underlying abundance vector of the component species (Engen 1977; see also Hengeveld 1979, Haila 1983). In the following I shall inspect the abundance and distribution patterns of the Inari colonizers in a wider geographical scale.

Chernov (1975: Fig. 32) presented a schematic illustration of the relation between ranges of single species and biogeographic zones. He assumed that distributional patterns of individual species are mainly determined by habitat preferences and can be classified into three main types: (1) *Zonal distribution* is typical of species that are specialists of habitats prevailing in a certain biogeographic zone (e.g. taiga species or tundra species). (2) Species with more flexible environmental requirements often have *zonal-interzonal distribution*, i.e., the center of the range lies within a specific zone, but margins reach mixed habitats in neighbouring zones. (3) Species with *interzonal distribution* have a wide range that reaches over several biogeographic zones; the species are often adapted to very specific, widely distributed but locally restricted environmental conditions (e.g. shores or wetlands; many synanthropic species can also be included in this group).

Using Chernov's (1975) terminology, the following components can be identified in the land birds of the Inari islands:

1) The four dominants are very widely distributed and abundant in the northern taiga and forest tundra of the Palearctic (*T. iliacus* to the Kolymy river and *Ph. trochilus* to the Anadyr basin in the east; *C. flammea* has a Holarctic distribution; e.g. Danilov (1966)). An interesting fact is the good agreement between expected and observed population numbers of these species in the Inari archipelago (Fig. 3) despite the heterogeneity of the background data (Sect. 4.1). They are the zonal dominants of the forest habitats in the transition zone between taiga and tundra in the western Palearctic (Uspenskij 1960, Danilov 1966, Järvinen & Väisänen 1976a, 1978a).

2) The bulk of the second abundance group is made up by specialists of the northern taiga (*T. urogallus, P. cinctus, P. infaustus, L. curvirostra* and *P. enucleator*), three characteristic species of open habitats in the northern taiga zone (*T. glareola, A. pratensis* and *M. flava*), and three forest passerines common in the northern taiga but with their center of distribution in more southern forests (*Ph. phoenicurus, T. philomelos* and *M. striata*). Expected and observed population numbers of all the northern species coincide well (Table 3); all characteristic species of the northern taiga (Stegman 1931, 1938, Brunov 1978, 1980) included in the species pool were observed on the islands in expected numbers. Two of the southern species have prevalences lower than 1, but the deviations may be caused by unrealistic expectations.

An indication that the colonization propensity of the southern faunal element may be impeded in Inari is given by the low prevalence of *Anthus trivialis* (although the specific mechanism causing the deviation remains obscure). The species occurs up to the forest tundra in several parts of the western Palearctic (e.g. Novikov 1958, Danilov 1966, Estaf'ev 1981), but is scarcer than expected in the apparently favourable open forests of the Inari islands (Sect. 4.2).

3) Two of the species in the second abundance class have inter-zonal distributions, *Oenanthe oenanthe* and *Motacilla alba* (e.g. Danilov 1966, Chernov 1975). Both are specialists of open, stony grounds, *M. alba* also favouring shores. Both

species are abundant on small rocky islands in Inari (Appendix), as well as on the Åland islands (Haila et al. 1983). Not unexpectedly, they are also successful colonizers of islands in the Arctic Ocean (Tugarinov 1936, Gerasimova & Skokova 1959, Karpovich & Kohanov 1967, Kohanov & Skokova 1967). A few species in the third abundance class also have a typical inter-zonal distribution, but they are scarce because of habitat and/or food limitations (*Actitis hypoleucos, Corvus corone, C. corax*).

4) There are three interesting cases in my data that are regarded as characteristic species of the Palearctic forest tundra by Uspenskij (1960) and Danilov (1966) and are considerably scarcer on the Inari islands than expected, *Luscinia svecica, Turdus pilaris* and *Emberiza schoeniclus* (Fig. 3). The probable explanation is habitat impoverishment on the islands. These three species are specialized to lush (wet) deciduous scrub habitats and forest islands in the Subarctic, and are scarce in monotonous forest habitats (Sect. 4.2, see also von Haartman et al. 1963-72, Järvinen & Väisänen 1976a, 1978a).

5) Species in the third abundance class are specialists of habitats that are scarce in the archipelago, and "casual breeders" (Williamson 1981, Haila 1983), i.e. species that occur irregularly on the islands. The group is heterogeneous; some of the species are scarce because they require large breeding and feeding territories although they may breed in the area yearly (e.g. predators), but a few species occurring occasionally in Inari Lapland are also included in my data (*Bonasa bonasia, Carduelis spinus*).

The peculiar frequency structure of the breeding land birds of the Inari islands, shown in Fig. 7, thus seems to reflect the structure of the avifauna of the surrounding areas. Zonal dominants are abundant, and the effect of southern faunal elements is slight. The classification of distribution types should not be taken too literally, however. It is rather a methodological suggestion that emphasizes specific ecological adaptations of species showing different distribution patterns (Chernov 1975).

6.2. Faunal impoverishment?

Järvinen & Väisänen (1976a, 1980) suggested that the forests of Inari Lapland have an impoverished avifauna, reflected in the similarity of community structure in birch and pine forests. They regarded "peninsular effect" as a possible cause of this impoverishment, i.e. the fact that the coniferous forests of northern Fennoscandia are a "peninsula" of the northern taiga, separated from the North-Russian and Siberian taiga by the White Sea.

Bird communities are relatively similar in the different island type groups in the Inari archipelago (Sect. 5), and the high degree of dominance in the pooled data (Fig. 7) is also an indication of impoverished faunal structure. The increasing similarity of bird communities in different habitats toward the north is no speciality of Finnish Lapland, however. The same trend has also been observed in Western Siberia (Ravkin 1978, 1983, Ravkin & Shadrina 1980). Therefore the possibility that the faunal impoverishment in Inari reflects changes in habitat structure should be ruled out before biogeographic processes can be accepted as an explanation.

Solution to the problem can be sought by comparing the Inari avifauna with other regions in the northern Palearctic taiga. For the comparison I used faunistic data from the Kola Peninsula (mostly originating from the Lapland Natural Reserve, about 68°N, 32°E; Vladimirskaya 1948, Novikov 1952a, 1952b, 1958), and census data from the Pechora basin (about 66°N, 56°E; Estaf'ev 1981) and Ob basin (about 67°N, 65°E; Vartapetov et al. 1980). Here, however, a new problem immediately presents itself: Are the habitats similar? The answer is no — pine is the only conifer in the Inari basin, but from the Kola Peninsula to the east spruce (or larch) makes up the northern forest limit (Sect. 2.1). This is *a priori* likely to yield a difference in the birds as well; as, e.g., Novikov (1952a) But'ev (1969) and Estaf'ev (1981) emphasized, spruce stands support the richest bird communities in the North-Russian taiga.

The comparison should thus provide an answer to two questions: (1) Is the avifauna richer in northern areas with richer habitat structure than in Inari Lapland? (2) Is the avifauna richer in other northern areas in habitats comparable to those found in Inari Lapland?

Vladimirskaya (1948) and Novikov (1952a, 1952b, 1958) gave a list of 16 species that breed in spruce dominated habitats in the Kola Peninsula but that are occasional or do not occur at all in Inari Lapland (although 13 of the species were characterized as "rare" or "relatively rare", the exceptions being *Accipiter gentilis, Bonasa bonasia* and *Parus montanus*). Six of them belong to the Siberian faunal type of Stegman (1938) (*B. bonasia, Tarsiger cyanurus, P. montanus, Pyrrhula pyrrhula, Loxia leucoptera* and *Emberiza rustica*). Thus it seems that the presence of spruce in the northern taiga of the Kola Peninsula in the close vicinity of Inari Lapland considerably increases the diversity of the bird fauna residing there, and the first question can be answered in the affirmative.

I tried to eliminate the effect of different regional habitat composition according to the following method: By using the habitat census data of Estaf'ev (1981) and Vartapetov et al. (1980) from their study areas in the Pechora and Ob basins, respectively, I constructed expected breeding communities for the 41 Inari islands included in my study. Pure pine forests were included in the censuses in both areas. As the counterpart of mixed forest (H4, see Sect. 2.2) I chose subalpine birch forest in the Pechora data (censused at the northwestern slopes of the Ural Mountains), and light spruce-larch forest in the Ob data. This means that habitat differences are in reality greater in the two other areas than in Inari, and the comparison is conservative. Counterpart habitats to my habitat types H1 and H2 were censused by Estaf'ev (1981) on the Ural Mountains, but they are absent from the Ob basin; however, owing to small areas, their contribution to the total communities is small.

The results, compared with expectations derived from the habitat data of Järvinen & Väisänen (1976a), look as follows:

Expected community characteristic	Inari	Pechora	Ob
Number of pairs	4174	4584	4116
Number of species	44	42	43
Degree of dominance:			
1st sp.	26 %	27 %	14 %
1st+2nd sp.	51 %	35 %	26 %

The comparison suggests that (1) average densities in the counterpart habitats in the three areas approximate each other, and (2) species numbers in the three expected breeding communities are practically identical. There is a difference in the degree of dominance; it is higher in the Inari expectation than in Pechora or Ob. The similarity of species numbers in the three expectations suggests, however, that the avifauna of the Inari basin is not impoverished compared with regions with similar habitat composition.

Thus there are no reasons to evoke a hypothesis of "peninsular effect" to explain the faunal impoverishment of the Inari Region. Regional habitat impoverishment is a more probable cause. Interestingly, "peninsular" or "insular" effects have also been suggested as an explanation for the avifaunal paucity of Kamchatka, at the other end of the Palearctic taiga; but in the light of quantitative data, habitat differences are a more plausible explanation (Kishchinskij 1980b). The same mechanism, actually, works in another scale in the relationship between Inari islands and the regional species pool: the island habitats are impoverished compared with the mainland (Sect. 2.2), but so too is the avifauna (Sect. 4.2 and 4.3).

7. Is the North different?

As a conclusion I compare the results of the Inari studies with the colonization patterns observed on the Åland Islands (Haila 1983, Haila & Järvinen 1983, Haila et al. 1983, Järvinen & Haila 1983). A crucial problem often encountered in insular studies is how to define realistically the pool of colonizing species (see, e.g., Grant & Abbott 1980, Williamson 1981). On Åland it was necessary to distinguish between mainland species pool and the pool of actual colonizers, constrained by habitat availability on different island types (Haila 1983). The same distinction is also necessary in Inari: An important component of the avifauna of Inari Lapland consists of species residing in alpine habitats and subarctic peatlands, but they must be excluded from the pool of actual colonizers of the forested islands. There is also an important difference, however. On Åland different "island type groups", separated on the basis of habitat composition, showed statistically significant differences in species richness of the bird communities (Haila 1983); but this is not true of the Inari islands (Sect. 5). This is due to the increasing similarity of forest habitats in the north as regards birds, noticed by Järvinen & Väisänen (1976a, 1980), Ravkin (1978, 1983) and Ravkin & Shadrina (1980).

On Åland, 64 of the 82 species observed in the island censuses (78 %) occurred in the archipelago in expected numbers (the minimum estimate was 56 species, 68 %). Of the 43 species in my Inari island data, 33 (77 %) were as abundant as expected. Because of the heterogeneity of the background data the estimate is certainly conservative, but the general picture seems similar in both archipelagoes. Most of the deviations in the Åland data were explained by differences in habitat microstructure between islands and the mainland, and the same explanation is plausible in Inari as well (Haila et al. 1983 and Sect. 4.5).

Haila et al. (1983) gave a suggestive list of factors influencing the colonization propensity of different species on the Åland Islands. Habitat availability was the most important among them, and the same is certainly true of the Inari avifauna. Other factors listed by Haila et al. (1983) were: (1) The principle that "generalists get a headstart" in colonizing patchy habitats of the islands, (2) edge effect, (3) predation, (4) interspecific competition, (5) lowered wintering opportunities, and (6) specific food resources (although the additional factors concerned only relatively few species each). In Inari, on the contrary, additional factors seem unnecessary — habitat requirements of the species are an almost exclusive determinant of colonization ability. The only puzzling case in Inari is the low prevalence of *Anthus trivialis* (Sect. 4.5).

These conclusions suggest that the "sample" nature of island land bird communities (Sect. 1) is even more conspicuous in Inari than in Åland. Harsh environmental conditions in the north probably accentuate the stochasticity of the actual colonization events by single pairs. Wiens (1983) suggested that avian communities should be compared with each other along an equilibrium — nonequilibrium gradient. Communities in the high north certainly lie closer to the nonequilibrium end of the spectrum; e.g. Järvinen (1979) found evidence that northern bird communities in Fennoscandia are less stable than those farther south. Danilov et al. (1981) published data indicating that populations in the forest tundra of the Ob basin (67°N) vary greatly in numbers from year to year, and the variations, furthermore, are unsynchronized between different species and even between different areas.

The emphasis on habitat requirements implies that autecological adaptations of the species are important for subsistence and island colonization in the north. Autecology and biotic interactions are not contradictory concepts, however; but ecological adaptations of single species always include biotic interactions. The problem is whether the most important among them are those between different bird species or those between birds and their biotic environment. Thus, e.g., the structure of food webs varies between different latitudinal zones in the north, and this certainly affects the biotic connections of birds residing in different zones (e.g. Sdobnikov 1958, Brunov 1978, 1980).

As an example I present two apparent cases of "colonization shifts" (i.e. different colonization patterns in two regions, see Diamond & Marshall 1977) between Åland and Inari. *Turdus iliacus* and *Phylloscopus trochilus* occur on considerably smaller islands in Inari than in Åland, relative to the total colonizing fauna (Sect. 4.2 and Haila et al. 1983). One might seek an explanation for the difference in the presence or absence of other bird species on small islands. Prevalences of both species in both areas are close to 1, however. They occur on the small islands in expected numbers. The apparent regional difference in colonization patterns is thus a consequence of a difference in the position of the two species in local faunas, relative to available habitats and ecological resources. There are no immediate reasons why interspecific interactions among birds should be the main factor causing this difference.

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Appendix. Primary data from the Inari island censuses in the years 1977 and 1979. Island codes are given in Table 1. Figures in brackets refer to observations made during additional excursions on islands that were censused by line transects (transect lengths: island 36, 1979: 2.3 km; 37, 1977: 4.0 km, 1979: 3.0 km; 38, 1979: 6.0 km; 39, 1977: 7.0 km, 1979: 8.1 km; 40, 1979: 6.0 km; 41, 1977: 9.0 km, 1979: 7.9 km). Symbol (i) indicates species that were observed in interisland flight during the censuses.

	1		2	3		4	5	6	7	8	9	10		11		12	13	14		15	16		17	18	19		20	
	77	79	79	77	79	79	79	79	79	79	79	77	79	77	79	79	79	77	79	79	77	79	79	79	77	79	77	79
Buteo lagopus (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Falco columbarius (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bonasa bonasia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lagopus lagopus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Tetrao urogallus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pluvialis apricaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Calidris temminckii	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philomachus pugnax	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Lymnocryptes minimus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gallinago gallinago	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Numenius phaeopus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
Tringa nebularia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. glareola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Actitis hypoleucos (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Cuculus canorus (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-
Strix nebulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dendrocopos minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Picoides tridactylus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthus trivialis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. pratensis	-	1	1	-	-	1	-	1	1	1	1	-	-	-	-	1	2	-	2	4	-	-	4	-	2	4	-	-
Motacilla flava	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	1	-	4	1	-	-
M. alba (i)	-	1	1	1	1	1	1	1	-	1	1	-	1	-	-	-	1	1	1	2	2	1	1	1	1	1	1	1
Bombycilla garrulus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Luscinia svecica	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-
Phoenicurus phoenicurus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saxicola rubetra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oenanthe oenanthe (i)	-	-	-	-	1	-	-	-	-	-	1	1	1	-	-	-	-	1	-	-	1	-	1	-	1	1	-	-
Turdus pilaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. philomelos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. iliacus	1	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	2	2	-	-	1	1	-	1	1	-	3	2
Phylloscopus trochilus	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	3	3	2	1	2	1	-	4	6	6	5	3
Muscicapa striata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficedula hypoleuca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parus cinctus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Perisoreus infaustus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corvus corone (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. corax (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fringilla montifringilla (i)	1	-	-	1	1	-	-	-	-	-	1	1	1	1	1	-	3	4	3	1	4	3	-	2	4	4	9	7
Carduelis spinus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. flammea (i)	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	3	2	2	2	-	3	-	4	1	1	2	5
Loxia curvirostra (i)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Pinicola enucleator	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Emberiza schoeniclus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	2	2	3	2	3	2	2	2	2	2	4	4	5	4	2	8	14	13	11	18	11	9	9	12	21	18	21	18

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21		22	23	24	25	26	27		28		29	30	31		32		33	34		35	36	37		38	39		40	41		Total
77	79	79	79	79	79	79	77	79	77	79	79	79	77	79	77	79	79	77	79	79	79	77	79	79	77	79	79	77	79	
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-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-	7
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-	-	-	-	-	-	-	-	-	-	-	-	2	2	1	-	-	2	-	-	1	-	1	2	5	3	2	11	4	2	38
1	1	-	1	-	-	-	-	-	-	-	-	1	-	1	1	-	1	3	2	-	-	1	1	-	1	-	-	1	(1)	19
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	(1)	1	1	1	9
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1	1	-	-	7	1	6	-	-	-	-	10	7	-	-	-	-	7	-	-	10	2	-	-	-	-	1	6	-	2	87
-	-	-	-	3	1	1	-	-	-	-	3	12	-	-	-	-	2	-	-	3	(1)	-	-	1	-	-	10	-	2	52
2	2	1	2	1	3	-	1	1	1	1	1	3	2	2	1	1	-	3	2	3	1	1	3	1	2	(1)	1	(2)	2	71
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	2
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-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
2	-	-	-	-	1	-	1	-	1	1	-	1	1	1	1	2	-	-	1	2	-	2	2	1	(1)	1	-	2	(4)	37
-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	1	-	(1)	1	-	-	-	1	-	-	6
-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	1	-	-	-	1	-	3	2	1	3	3	3	6	4	2	32
3	2	3	2	6	2	2	1	1	1	2	4	1	1	1	2	3	3	4	3	5	3	13	3	8	22	22	16	21	9	186
1	3	1	5	15	3	9	6	2	6	4	25	11	11	8	11	4	11	15	8	22	20	18	10	2	39	70	22	25	26	451
-	-	1	-	-	-	-	-	1	1	-	-	-	2	-	-	-	1	-	-	-	-	3	-	-	(1)	4	-	3	1	18
-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	(1)	-	5
-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	1	-	-	-	1	(1)	(1)	1	1	2	3	1	16
-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	2	-	-	2	1	2	1	-	1	1	1	13
-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	(1)	-	-	3	1	10
1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	(1)	1	-	-	-	1	-	1	1	7
4	4	7	7	9	6	3	8	5	11	7	10	5	12	18	12	15	13	20	16	10	29	51	27	32	59	91	44	104	82	773
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1	4	9	10	5	8	6	3	2	4	7	5	9	6	13	2	11	16	3	11	20	10	13	33	41	24	60	29	22	36	450
-	-	1	-	-	-	-	-	1	1	-	-	1	1	-	-	3	3	-	1	1	(1)	4	1	2	5	6	7	4	7	51
-	-	-	-	-	-	-	1	1	-	-	-	-	1	-	-	-	1	1	3	-	-	-	-	4	-	(1)	-	4	1	18
-	-	-	-	9	1	8	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20
16	18	23	29	58	26	38	22	18	31	26	61	53	43	52	35	40	61	52	52	82	76	123	93	116	176	279	164	229	206	2522