The peninsular effect and habitat structure: bird communities in coniferous forests of the Hanko Peninsula, southern Finland

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Raivio, S. 1988: The peninsular effect and habitat structure: bird communities in coniferous forests of the Hanko Peninsula, southern Finland. — Ornis Fennica 65:129–149.

The hypothesis of the peninsular effect predicts that the number of species declines towards the tip of a peninsula, this being attributed to an equilibrium between colonization and extinction.

I tested the hypothesis on the Hanko Peninsula, southern Finland, by collecting quantitative data on birds breeding in pine and spruce forests along the peninsula. I also made habitat descriptions to check whether differences in the number of species and bird densities could be explained by variation in habitat structure.

Rarefaction analysis did not reveal any significant differences in the numbers of bird species between different parts of the peninsula in pine or spruce forests. Nor did the total density of birds in the pooled data, or in the pine forests reveal the expected pattern. The total bird density in spruce forests was highest in the middle of the Hanko Peninsula. This pattern, and also density differences in single species and species groups along the peninsula, could be plausibly explained by habitat structure. Both the analyses of separate habitat variables and DCA ordinations support this conclusion. The most important factor determining bird densities was the luxuriance of the habitat, but the bird communities were also affected by tree species composition and the size class distribution of the trees. It thus appears that habitat differences on a larger scale, e.g. in the proportions of habitat types, also contribute to the diversity gradients observed on many peninsulas.

I discuss scale problems inherent in traditional peninsular studies and the implications of the peninsular effect for conservation policy.

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Introduction

Simpson (1964) was the first to discover that the number of mammal species declined towards the tips of all major North American peninsulas. Simpson called this variation in diversity the peninsular effect, and explained it by the long and narrow geometry of peninsulas. As colonization is possible only from one direction, from the base, the populations at the tip are smaller and thus more vulnerable to extinction (Simpson 1964). MacArthur & Wilson (1967) interpreted the peninsular effect in terms of their theory of island biogeography: the number of species along a peninsula represents an equilibrium between colonization and extinction.

Since Simpson's (1964) work, many studies have been published on peninsular diversity gradients. Cook (1969), Rohwer & Woolfenden (1969) and Tramer (1974) applied Simpson's idea to birds, while Kiester (1971) studied the numbers of reptiles and amphibians. Taylor & Regal (1978) found that the species numbers of small mammals, birds and lizards declined towards the tip of Baja California. Most peninsular studies have been conducted in North America, but there are a few examples from Europe, such as Massa's (1982) study on the number of ants and beetles in Italy and the studies of Busack & Jaksić (1982) and Busack & Hedges (1984) on Iberian reptiles.

The traditional way of studying the peninsular effect is to collect distributional data on a species group from quadrats of a certain size along the entire peninsula. This procedure, however, often involves methodological problems. First, the size of the quadrat affects the gradients observed, as the number of species increases with area (cf. McCoy & Connor 1980). Second, the size and dispersal abilities of the organisms studied have to be considered when de-

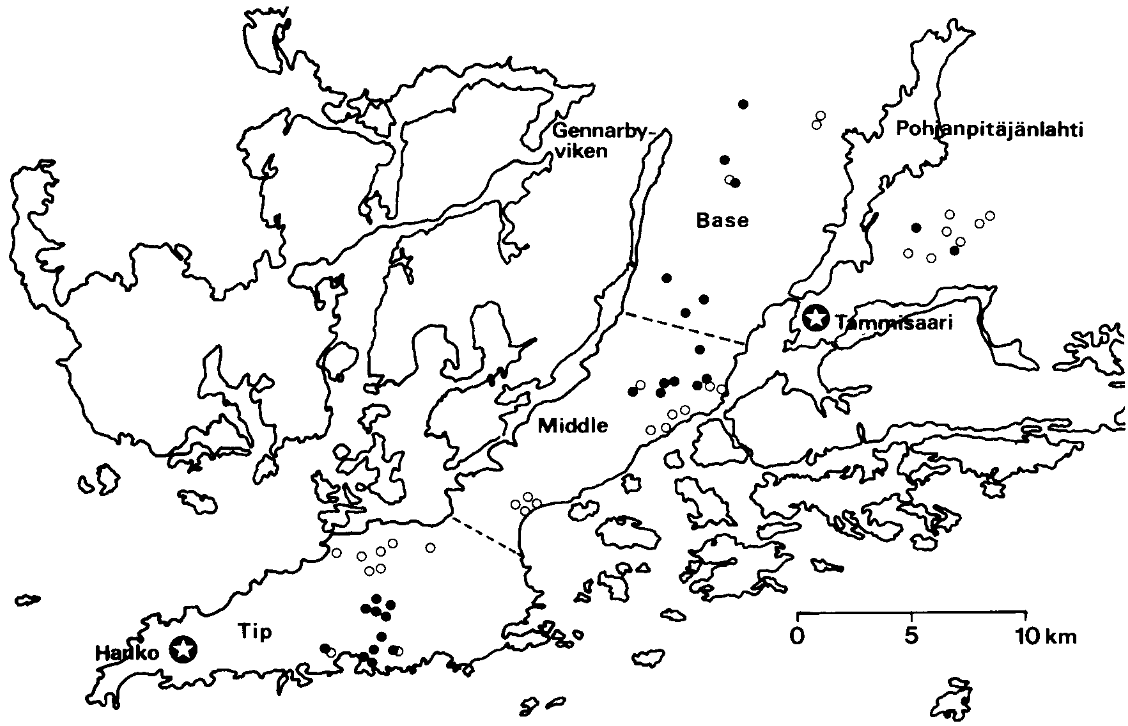


Fig. 1. The study area. Open circles=pine forests, dots=spruce forests.

ciding the area of the quadrats. The spatial distribution pattern of the species also influences the results (McCoy & Connor 1980). Third, the gamma diversity, i.e. the diversity of all habitat types along a peninsula, has been the major concern in most studies, but this can bias the results considerably if the habitat spectrum varies along the peninsula.

Fourth, the use of merely qualitative presence/absence data precludes patterns that could be observed within quantitative data. Emlen (1978) is one of the few who have studied the peninsular effect using quantitative data. He observed that not only did the number of bird species decline towards the tip of the Florida Peninsula, but the densities of different species also decreased.

Along with the traditional explanation of the peninsular effect (Simpson 1964, MacArthur & Wilson 1967, Taylor & Regal 1978), various historical (Cook 1969, Rohwer & Woolfenden 1969, Busack & Jaksić 1982, Busack & Hedges 1984), ecological (Tramer 1974, Wamer 1978, Seib 1980, Busack & Jaksić 1982) and even genetic (Emlen 1978) hypotheses have been suggested (see a review in Brown 1987). In Taylor's (1987) recent model, colonization over water and the orientation of the peninsula were crucial for the occurrence of the peninsular effect. The effects of habitat structure, however, have mostly been neglected.

The questions I address in this study are: (1) Do the number of bird species and the densities of different species breeding in coniferous forests decrease towards the tip of the Hanko Peninsula? (2) How does the habitat structure within coniferous forests along the peninsula affect the patterns observed?

Material and methods

Study area

Hanko Peninsula, located on the southern coast of Finland (59°55′N, 23°15′E), is the largest peninsula in the country, with a length of about 50 km and a width varying between 2 and 10 km. It is bordered on both sides by long and narrow inlets. Archipelagoes extend along the peninsula, so that only the southern tip faces the open sea (Fig. 1).

Table 1. Description of the census data on the peninsula.

		Tip	Middle	Base	Total
Pine forests	Number of pairs	143	152	137	432
	Transect km	18.7	19.8	16.0	54.4
	Area ha	93.4	98.9	79.8	272.0
Spruce forests	Number of pairs	222	220	218	660
	Transect km	15.4	11.0	17.3	43.7
	Area ha	76.9	54.9	86.6	218.4

Table 2. Proportions of different forest types in the habitat description data. n=points described. Area covered by each point 0.4 ha.

Forest type		Tip		Middle		Base	
		n	%	n	%	n	%
Pine forests	CT	40	52.6	21	26.9	7	10.9
	VT	36	47.4	57	73.1	57	89.1
Spruce forests	MT	49	80.3	22	48.9	55	80.9
	OMT	12	19.7	23	51.1	13	19.1

Hanko Peninsula lies in the hemiboreal vegetation zone of Ahti et al. (1968), which is a transition zone between the Central European deciduous forests and the boreal taiga. However, due to edaphic factors, the forests of the study area are mainly coniferous, the dominant tree species being Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) with an admixture of birch (*Betula pendula* and *B. pubescens*) and European aspen (*Populus tremula*). Other deciduous trees are rare. The study area lies in the hemiboreal ornithogeographic zone of Järvinen & Väisänen (1973, 1980).

I divided the study area into three parts; tip, middle and base (Fig. 1). In the base I also included areas of the mainland between the towns of Karjaa and Tammisaari. In each part I censused birds in the two major habitats, pine and spruce forests.

Census methods

Biogeographic studies are usually based on species lists, not on the abundances of different species. However, ecological processes do not necessarily end in extinctions, but they can first be seen in population numbers (Haila 1983). Thus the patterns produced by quantitative and qualitative data can differ considerably (e.g. Bock et al. 1977, 1978, Haila & Järvinen 1981, 1983, Haila et al. 1983, Järvinen & Haila 1984, Haila et al. 1987b, Raivio 1989).

I collected quantitative bird census data by the Finnish line transect method (Järvinen & Väisänen 1976, 1977), with the exception that only those observations made on the main belt (25 m on both sides of the transect) were included. To cover the suitable forest patches as efficiently as possible, I censused them along parallel compass lines, the distance between which was at least 50 m. Palmgren (1930) used a similar method on the Åland Islands.

I performed the censuses between 26 May and 18 June 1983, censusing different parts of the study area on successive days, to avoid a phenological bias in the data. I started the censuses a few days earlier than recommended by Järvinen & Väisänen (1976, 1977) for southern Finland, because of the very warm and early spring. The censuses were made only in good weather between 5.00 and 11.00. As I censused only the main belt, it was possible to census longer than recommended without significant effects on the density estimates obtained (for support, see Järvinen et al. 1977). The data consist of 1092 pairs of breeding land birds (Table 1).

Habitat descriptions

The pine forests of the study area represent the *Calluna* (CT) and *Vaccinium* (VT) forest types of Cajander (1949). In these forests the proportion of pine is approximately 90%, the rest is mostly spruce and birch. Extremely barren forests on rock outcrops are not included in the censuses. Forests with at least 75% of spruce were classified as spruce forests. The rest consists of pine and deciduous trees. The spruce forests belong to the *Myrtillus* (MT) and *Oxalis-Myrtillus* (OMT) forest types. The proportions of different forest types in the study area are shown in Table 2.

Because of the marked human impact in the study area, most of the forest areas censused were fairly small, ranging from one to 20 hectares in each part of the study area. The youngest forest patches censused were approximately 40 years old and the oldest about 100 years.

In the period 29 June to 18 August 1983, I described the vegetation at every 250 m along the censused transects. The method used was modified from Tiainen & Väisänen (1982). Each description was made along four 25-m lines at right angles to each other. The width of a line was 4 m. Thus, the area covered by one habitat description was about 400 m^2 and the total area of all 392 descriptions exceeded 15 ha.

I counted the individuals of each tree species (pine, spruce, birch, other deciduous trees) in six size classes (diameters measured at breast height: less than 5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, over 40 cm) and the number of snags (the smallest size class excluded) and bushes (pine saplings, spruce saplings and junipers, deciduous saplings and bushes) along the four lines. I also measured with a hypsometer the height of five randomly chosen canopy trees and estimated the foliage cover at 11 points along the lines. In the understorey I estimated the proportions of different life forms (dwarf shrubs, herbs, mosses, lichens) and the proportions of bare soil and litter with a scale of 0–5 within a circle 10 m in diameter. The corresponding percentages are:

0 = <1%
1 = 1–20%
2 = 21–40%
3 = 41–60%
4 = 61–80%
5 = 81–100%

Statistical methods

It is difficult to compare species numbers in samples of unequal size, as the species number increases with sample size. I used rarefaction (e.g. Simberloff 1978, 1979, James & Rathbun 1981) to overcome this problem.

I used detrended correspondence analysis (DCA; Hill 1979, Hill & Gauch 1980, Gauch 1982) to ordinate the census and habitat data, though the method has recently been criticized by Minchin (1987) and Wartenberg et al. (1987). Methods including linear response models (PCA) were discarded, because of their invalid assumptions.

Results

Numbers of species along the peninsula

The total number of species observed was 41; 25 species in pine forests and 36 species in spruce forests. The species numbers recorded from tip to base were: 19, 18, 20 in pine forests and 28, 24, 25 in spruce forests. According to the rarefaction analysis, in samples of 100 pairs the expected species numbers E(S) ± 2 SD were as follows:

	Tip	Middle	Base
Pine forests	16.3±2.6	15.2±2.6	16.9±2.8
Spruce forests	21.9±3.6	18.8±3.2	20.6±3.0
Pooled data	21.5±4.2	19.5±3.8	20.6±3.8

The rarefaction curves are shown in Figs. 2A–C. The differences in expected species numbers are not significant, as the 95% confidence limits overlap widely. Thus, no peninsular effect *sensu* Simpson (1964) can be observed on the Hanko Peninsula in either of the habitats studied or in the pooled data.

I checked this pattern by counting the number of breeding land bird species in the three 10 × 10 km quadrats used in the Finnish bird atlas (Hyytiä et al. 1983), roughly corresponding to my three study areas on the Hanko Peninsula. The numbers of breeding land birds from tip to base were 111, 93, 85 and those of forest dwelling species 62, 60, 47 — quite opposite to the predictions based on the peninsular effect and thus corroborating the results obtained. As the land area is somewhat smaller at the tip, the sample sizes cannot have biased the results (but inaccuracies in the distribution maps can).

Density differences along the peninsula

The numbers of pairs observed, and the densities and proportions of each species are shown in Appendix 1. The total density of breeding land birds in the pooled data was 222.7 pairs/km^2, which is close to the value obtained from the unpublished line transect data of Järvinen & Väisänen in 1973–77. The density estimate for all pine forests pooled was 158.8 p/km^2 and that for spruce forests 302.2 p/km^2. In pine forests there were no significant differences in total density (tip 153.1 p/km^2, middle 153.7 p/km^2, base 171.8 p/km^2) along the Hanko Peninsula, but in spruce forests the total density was significantly higher (χ^2=25.5, $P<0.001$) in the middle (400.9 p/km^2) than at the tip (288.8 p/km^2) or at the base (251.6 p/km^2). This result (cf. Emlen 1978) also fails to support the existence of a peninsular effect on the Hanko Peninsula, as the lowest density was observed at the base.

I grouped the species according to their systematic relationships, migratory and foraging strategies, diet and nest type (Appendix 2) and compared their observed and expected numbers in the three parts of the peninsula. Only those species and species groups

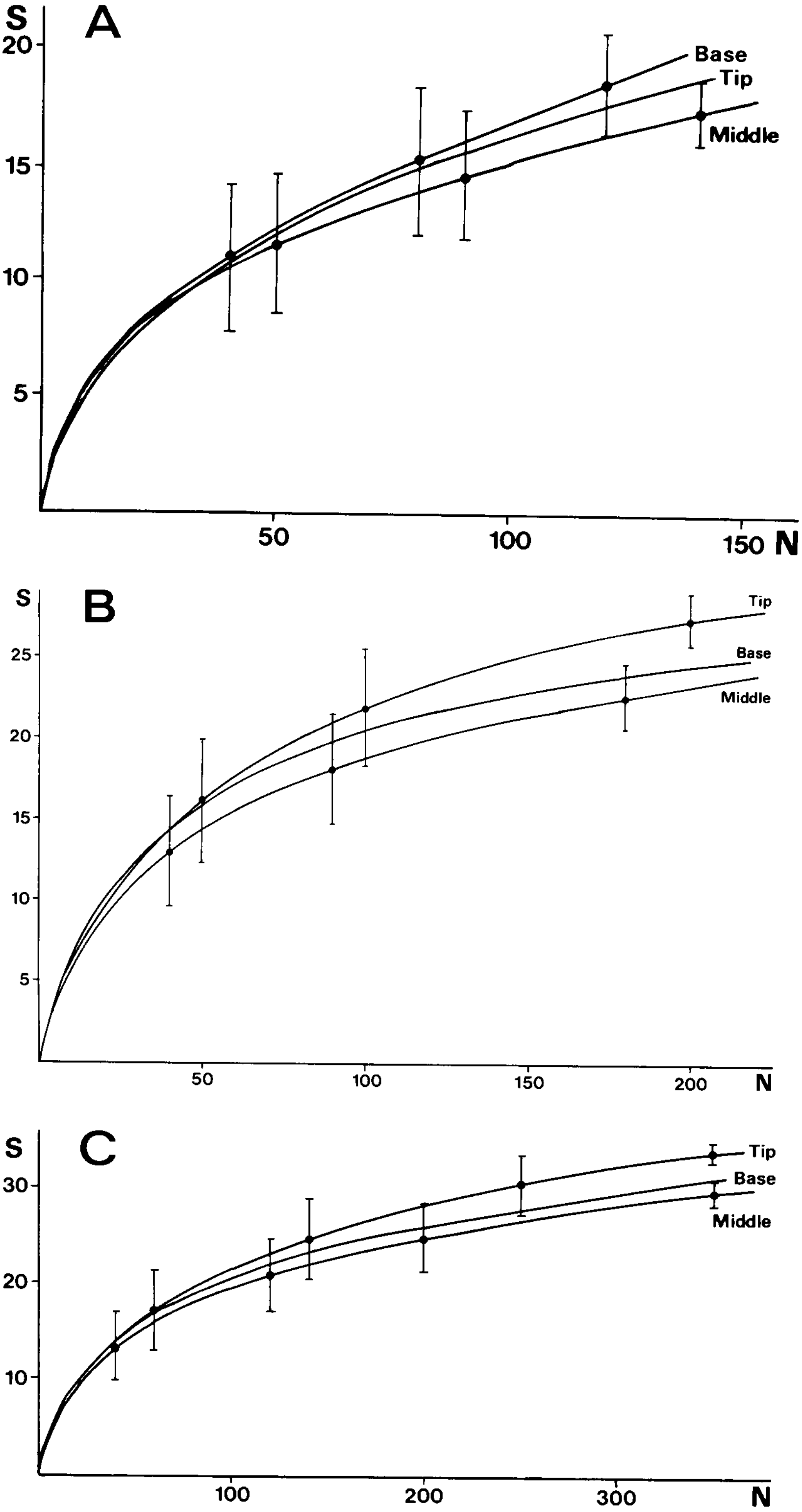


Fig. 2. Expected species numbers (S) estimated by rarefaction as a function of sample size (N) in the three parts of the study area. A. pine forests, B. spruce forests, C. pooled data. Vertical lines indicate ±2 SD.

Table 3. Observed numbers of pairs as percentages of expected numbers in the three parts of the study area. Results are reported only on species and species groups where χ^2 exceeded the $P<0.1$ level.

Species/group	Tip	Middle	Base	P
Pine forests				
Phylloscopus trochilus	62	203	18	P<0.01
Regulus regulus	62	75	175	P<0.05
Paridae	64	109	131	P<0.1
Tit guild	64	96	147	P<0.01
Hole-nesters	66	110	128	P<0.1
Partial migrants	73	69	170	P<0.05
Preferring young trees	46	187	55	P<0.01
Preferring spruce	67	69	177	P<0.01
Foliage insectivores	64	113	126	P<0.05
Spruce forests				
Phylloscopus trochilus	126	147	47	P<0.1
Ph. collybita	42	176	104	P<0.05
Parus cristatus	54	77	155	P<0.1
Fringilla coelebs	92	158	70	P<0.001
Total number of pairs	96	133	83	P<0.001
Total number of pairs (*F. coelebs* excluded)	97	120	89	P<0.05
Passeriformes	96	134	82	P<0.001
Passeriformes (*F. coelebs* excl.)	98	122	88	P<0.05
Sylviidae	99	132	80	P<0.05
Paridae	62	94	137	P<0.05
Fringillidae	96	153	69	P<0.001
Phylloscopus sp.	88	161	72	P<0.01
Conifer tits	49	107	141	P<0.05
Hole-nesters	64	102	130	P<0.1
Open nest	99	135	78	P<0.001
Open nest (*F. coelebs* excl.)	104	122	83	P<0.05
Open nest in tree/bush	100	136	76	P<0.001
Nesting in tree/bush	95	132	84	P<0.001
Ground-nesting	112	124	74	P<0.1
Nest site variable	77	145	92	P<0.05
Strictly resident	62	62	158	P<0.05
Short-distance migrants	93	144	78	P<0.001
Long-distance migrants	93	154	72	P<0.01
Migrants in total	93	147	76	P<0.001
Preferring young trees	99	135	79	P<0.1
Preferring spruce	95	130	85	P<0.01
Foliage insectivores	92	124	92	P<0.1
Feeding mainly on animals	96	124	89	P<0.05

having at least 14 pairs in pine forests and 16 in spruce forests were included in the χ^2-tests. The results are shown in Table 3, where the observed numbers of pairs are presented as percentages of the expected numbers.

Differences in habitat structure and their relations to density variation of birds

The habitat variables with a normal distribution were tested with ANOVA and those with skewed distributions with G-tests to reveal structural differences in habitats along the peninsula. The results are shown in Tables 4A–B.

Pine forests. At the tip of the peninsula, the most typical feature of the pine forests was the abundance of small pines (PIN –5, PIN 5–10) and pine saplings. Other bushes were sparse. Pine was clearly the dominant tree species, accounting for over 98% of all the trees. The proportion of spruce was only 0.5% and that of birch 1.4%. The mean height of the canopy was 13.6 m, which was significantly less than that of the trees at the base of the peninsula (17.6 m). The standard deviation of the canopy height was small in the area. Bare soil and litter were abundant but herbs rare. Thus, the forests at the tip had a fairly simple structure, with an even but low canopy, consisting mainly of pine. Bushes were sparse (except pine saplings) and the field and ground layers poor. The most common forest type was CT.

None of the bird species or species groups were exceptionally abundant at the tip. On the contrary, some species, e.g. the Goldcrest (*Regulus regulus*) and those forming the tit guild, were sparser than expected. Since tits (Paridae), the Treecreeper (*Certhia familiaris*) and Goldcrest are mostly resident, the availability of food in winter could limit the populations in this barren environment.

In the middle of the peninsula, the pine forests consisted of larger trees (PIN 10–20, PIN 20–30) than at the tip. The forests were more diverse, with some medium-sized spruces (SPR 20–30) and birches (BIR 10–20, BIR 20–30). The bush layer was richer; in addition to pine saplings it contained spruce and deciduous saplings. The standard deviations of the canopy height and cover were high. Thus the trees varied clearly in age and there were small openings in the forests.

The Willow Warbler (*Phylloscopus trochilus*) was more abundant than expected in the middle, but sparser at the peninsula base. The Willow Warbler is a typical species of young successional stages, where it prefers forest edges and deciduous trees (e.g. Tiainen et al. 1983). The abundance of small openings and birch in the pine forests of the middle explain the high density of the Willow Warbler. The habitat composition of surrounding areas can also affect the bird densities of a forest island (Haila et al. 1987a). Birch forests were common in the middle of the peninsula, from where surplus individuals could have moved to suboptimal habitats. The high density of the Willow Warbler contributed to the high numbers of species preferring young trees.

The base of the peninsula had the most luxuriant pine forests. Large pines (PIN 20–30, PIN 30–40) and small to medium-sized spruces (SPR –5, SPR 5–10, SPR 10–20) and birches (BIR –5, BIR 5–10) were most abundant in this part of the study area. The canopy height was 17.6 m, significantly higher than in the other parts. Small pines (PIN –5, PIN 5–10) were sparser than elsewhere, but the bush layer was particularly dense.

The Goldcrest was more abundant than expected at the base. The species prefers spruce, the proportion of which increased towards the base. The height of the canopy and proportion of large trees were also greater at the base, which may have contributed to the abundance of the Goldcrest. The numbers of the tit guild were much higher at the base than at the tip, which is explained by the luxuriance of the habitat at the base and the diversity of tree species. In consequence of the high tit numbers, the numbers of foliage insectivores and hole-nesters were also highest at the base.

The abundance of partial migrants and species preferring spruce increased towards the base. These trends can be explained by the increasing proportions of spruce and bushes, as the partial migrants included in this study are chiefly associated with young spruce.

Spruce forests. The peninsula tip was characterized by an abundance of large pines (PIN 30–40) and small birches (BIR 5–10) and other deciduous trees (DEC 5–10). Spruce saplings were also abundant. As in the pine forests, the canopy was lowest (18.2 m) at the tip. The canopy cover varied considerably; there were both small openings and denser areas.

The Willow Warbler was slightly more abundant than expected at the tip, which is explained by the high density of small deciduous trees and the patchiness of the habitat. Tits were sparser than expected; the trend was the same as in the pine forests, but the reason for this is not known.

In the middle of the peninsula, the spruce forests had the greatest proportions of large spruces (SPR 20–30, SPR 30–40, SPR 40–) and birches (BIR 20–30, BIR 30–40). The canopy height (23.7 m) and its standard deviation were significantly higher than elsewhere. The proportion of spruce was higher (82.3%) than at the tip (77.0%) or base (73.4%) and consequently that of pine was exceptionally small. Small birches (BIR –5, BIR 5–10) were rare. The spruce forests of the middle were old and luxuriant; the varying height of the canopy suggested almost natural conditions.

Table 4A. Differences in habitat structure within pine forests of the Hanko Peninsula.

Habitat variable	% of description points with values >0			G	P
	Tip	Middle	Base		
PIN -5	44.7	14.1	10.9	27.12	P<0.001
PIN 5–10	64.5	60.3	39.1	10.11	P<0.01
PIN 10–20	81.6	93.6	89.1	5.35	P<0.1
PIN 20–30	69.7	82.0	98.4	24.59	P<0.001
PIN 30–40	5.3	9.0	17.2	5.39	P<0.1
SPR -5	1.3	10.2	29.7	26.84	P<0.001
SPR 5–10	2.6	11.5	17.2	9.51	P<0.01
SPR 10–20	1.3	17.9	20.3	18.33	P<0.001
SPR 20–30	0.0	14.1	9.4	15.95	P<0.001
SPR 30–40	0.0	1.3	0.0	2.04	ns
SPR 40–		no observations			
BIR -5	7.9	3.8	29.7	21.71	P<0.001
BIR 5–10	3.9	11.5	14.1	5.10	P<0.1
BIR 10–20	3.9	19.2	3.1	14.08	P<0.001
BIR 20–30	0.0	9.0	1.6	11.08	P<0.01
BIR 30–40		no observations			
DEC -5	2.6	0.0	1.6	2.85	ns
DEC 5–10		no observations			
DEC 10–20		no observations			
DEC 20–30		no observations			
DEC 30–40		no observations			
DEC 40–		no observations			
SNAG 5–10	6.6	6.4	10.9	1.16	ns
SNAG 10–20	3.9	5.1	6.3	0.38	ns
SNAG 20–30	1.3	3.8	0.0	3.80	ns
PIN SAPL	38.0	47.4	10.9	24.59	P<0.001
SPR SAPL	9.2	15.4	56.3	44.45	P<0.001
DEC SAPL	8.6	41.0	51.6	38.55	P<0.001
DWARF SHRUBS	90.8	94.9	98.4	4.30	ns
HERBS	27.6	59.0	50.0	16.30	P<0.001
MOSSES	92.1	93.6	89.1	0.94	ns
LICHENS	88.2	84.6	76.6	3.37	ns
SOIL & LITTER	7.9	6.4	0.0	7.94	P<0.05
		Mean		F	P
HEIGHT MEAN	13.6	14.6	17.6	32.87	P<0.001
HEIGHT SD	1.2	1.6	1.4	8.93	P<0.001
COVER MEAN	41.5	40.4	44.8	2.89	ns
COVER SD	26.0	26.9	24.4	3.80	P<0.05

Both the total bird density and the densities of the Chaffinch (*Fringilla coelebs*), Willow Warbler, Chiffchaff (*Phylloscopus collybita*) and sylvids were highest in the middle. Species preferring spruce and young trees and foliage insectivores were more abundant than expected. The high total density contributes to the fact that the groupings based on migratory and nesting strategies also give the highest numbers for the spruce forests of the middle. The high diversity and productivity and the large proportions

Table 4B. Differences in habitat structure within spruce forests of the Hanko Peninsula.

Habitat variable	% of description points with values >0			G	P
	Tip	Middle	Base		
PIN -5	4.9	2.2	0.0	4.52	ns
PIN 5–10	13.1	2.2	13.2	5.53	P<0.1
PIN 10–20	42.6	33.3	45.6	1.74	ns
PIN 20–30	57.4	55.6	67.6	2.15	ns
PIN 30–40	21.3	4.4	13.2	6.82	P<0.05
SPR -5	50.8	55.6	63.2	2.05	ns
SPR 5–10	73.8	77.8	61.8	3.85	ns
SPR 30–40	29.5	55.6	26.5	10.88	P<0.01
SPR 40–	0.0	11.1	0.0	13.80	P<0.01
BIR -5	32.8	24.4	45.6	5.60	P<0.1
BIR 5–10	50.8	22.2	39.7	9.16	P<0.05
BIR 10–20	75.4	66.7	58.8	3.99	ns
BIR 20–30	36.1	60.0	33.8	8.56	P<0.05
BIR 30–40	1.6	15.6	1.5	11.18	P<0.01
DEC -5	3.3	0.0	19.1	18.03	P<0.001
DEC 5–10	11.5	0.0	10.3	8.74	P<0.05
DEC 10–20	13.1	4.4	5.9	3.17	ns
DEC 20–30	6.6	0.0	4.4	4.53	ns
DEC 30–40	1.6	0.0	1.5	1.20	ns
DEC 40–	0.0	0.0	1.5	1.87	ns
SNAG 5–10	26.2	40.0	27.9	2.55	ns
SNAG 10–20	18.0	22.2	19.1	0.29	ns
SNAG 20–30	3.3	6.7	1.5	2.10	ns
PIN SAPL	3.3	4.4	0.0	4.07	ns
SPR SAPL	75.4	64.0	54.4	6.21	P<0.05
DEC SAPL	34.4	26.7	61.8	16.50	P<0.001
DWARF SHRUBS	93.4	84.4	94.1	3.31	ns
HERBS	95.1	93.3	98.5	2.28	ns
MOSSES	83.6	62.2	70.6	6.46	P<0.05
LICHENS	1.6	0.0	1.5	1.20	ns
SOIL & LITTER	18.0	2.2	11.8	7.63	P<0.05
		Mean		F	P
SPR 10–20	16.1	12.8	12.4	2.72	ns
SPR 20–30	5.2	8.1	7.5	8.13	P<0.001
HEIGHT MEAN	18.2	23.7	20.4	56.63	P<0.001
HEIGHT SD	1.5	2.2	1.6	8.04	P<0.001
COVER MEAN	61.6	62.9	64.8	1.22	ns
COVER SD	24.0	21.2	20.8	3.59	P<0.05

of spruce and birch have important effects on the densities of many species. Willow Warblers prefer deciduous trees; Chiffchaffs and Wood Warblers (*Phylloscopus sibilatrix*) prefer spruce (Hyytiä et al. 1983). Chaffinches also reach their highest densities in forests rich in large spruces (von Haartman et al. 1963–72).

The density of pine was highest in the spruce forests at the peninsula base, which clearly indicates the barren character of the area. Pines composed almost 13% of all the trees (tip 6.1%, middle 4.8%). Small birches (BIR –5) and other deciduous trees (DEC –5) were also typical. The canopy height was 20.4 m and the bush layer dense.

The only group of species that was more abundant at the base than expected was the tits; the trend was exactly the same as in the pine forests. Accordingly, the density of hole-nesting species was also higher than elsewhere. The abundance of the Crested Tit (*Parus cristatus*) contributed to the high numbers of strictly resident birds. The explanation of the high densities of tits may lie in the mosaic-like structure of the habitat. The spruce forests at the base are rarely continuous, but they are interspersed with rocks and small peatlands bearing pine, in some places also with fields and clear-cuts. Studies performed in Central Sweden (Hansson 1983) and Northern Häme (Haila et al. 1987a) suggest that tits prefer forest edges and patchy habitats.

DCA ordination of the census data

I made two DCA ordinations of the census data: one included all species observed (Fig. 3) and the other only species with at least five pairs (Fig. 4). The latter is probably more reliable, since rare species may distort the ordination. In the ordination of all species I used log-transformation and the option for down-weighting of rare species, to reduce the effects of possible outliers. No transformations were made on the data lacking the rare species.

In both analyses the first axis was interpreted as a gradient from the most luxuriant habitats to the most barren ones. When all species were included, the eigenvalue of the first axis was 0.269 and when rare species were omitted, it was 0.209. In the analysis of the abundant species, the barren end of the axis was characterized by the Redstart (*Phoenicurus phoenicurus*), Tree Pipit (*Anthus trivialis*), Common/Parrot Crossbills (*Loxia curvirostra/pytyopsittacus*), Crested Tit and Spotted Flycatcher (*Muscicapa striata*), while the other end was dominated by the Chiffchaff, Coal Tit (*Parus ater*), Blackbird (*Turdus merula*), Wood Warbler, Wren (*Troglodytes troglodytes*) and Robin (*Erithacus rubecula*). When all species were included, the barren end was additionally characterized by the Black Grouse (*Tetrao tetrix*), Woodcock (*Scolopax rusticola*), Wheatear (*Oenanthe oenanthe*) and Yellowhammer (*Emberiza citrinella*), and the other end by the Goshawk (*Accipiter gentilis*), Blackcap (*Sylvia atricapilla*), Pied Flycatcher (*Ficedula hypoleuca*) and Red-breasted Flycatcher (*F. parva*).

As DCA produces ordinations for species and areas simultaneously, the study areas were ordinated on an environmental gradient according to their bird communities: pine forests at the peninsula tip and spruce forests in the middle were located at the opposite ends of the barren-luxuriant gradient.

The within-habitat differences in bird communities along the Hanko Peninsula were rather small. In pine forests, the tip and the base were furthest away from each other in both analyses. Species preferring barren and light pine forests (Tree Pipit, Spotted Flycatcher, Redstart) were abundant at the tip, while their numbers were smaller at the base. The abundances of species preferring more luxuriant habitats, e.g. the Goldcrest, were considerably higher at the base than at the tip.

The sequence of the spruce forests along the environmental gradient depends on the species set analysed. In both analyses, however, the bird community of the middle was characterized by species abundant in the most luxuriant forests.

The interpretation of the second axis was difficult, because the eigenvalues were small: in the analysis of all species 0.086 and in the other only 0.035. The ordination of all the species shows a vague trend from species preferring large and thus old trees (Goshawk, Pied Flycatcher, Red-breasted Flycatcher) to those frequenting younger trees and bushy areas (Lesser Whitethroat *Sylvia curruca*, Bullfinch *Pyrrhula pyrrhula*, Wood Pigeon *Columba palumbus* and Hazel Grouse *Bonasa bonasia*).

The spruce forests of the peninsula were distributed along the second axis in such a way that the forests of the base and the middle formed the extreme ends of the axis in both analyses. The differences within pine forests along the second axis were small.

DCA ordination of the habitat data

The habitat data analysed with DCA comprised 37 variables (Appendix 3). The data were log-transformed to eliminate distortions by outliers.

The first axis was interpreted as a gradient from the most luxuriant spruce forests to the most barren pine forests (Fig. 5A), as in the analysis of the census data. The extreme ends of the axis were dominated by all size classes of pine in increasing order and by pine saplings and lichens. All these variables indicate barrenness and dryness of the habitat. At the opposite

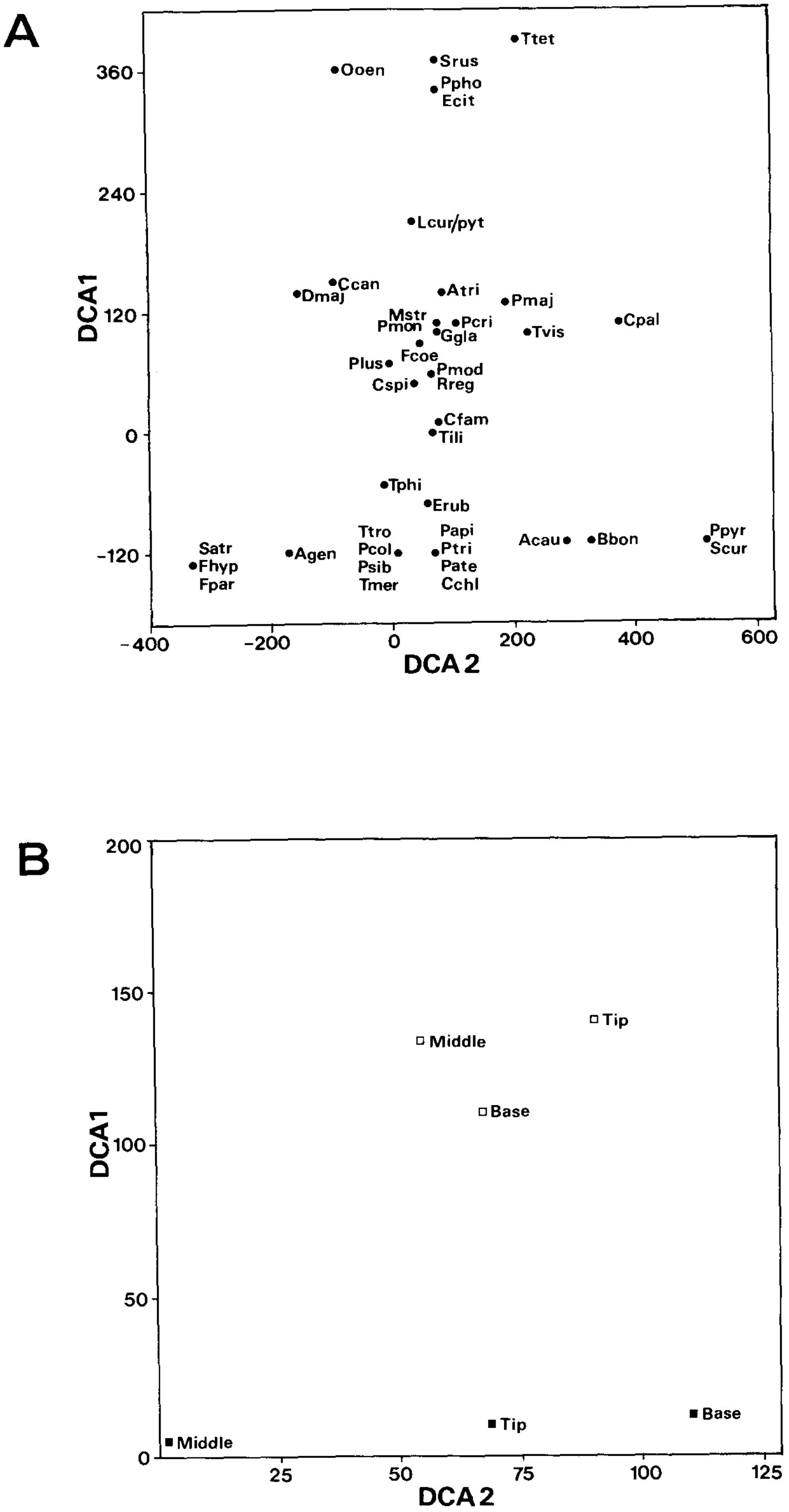
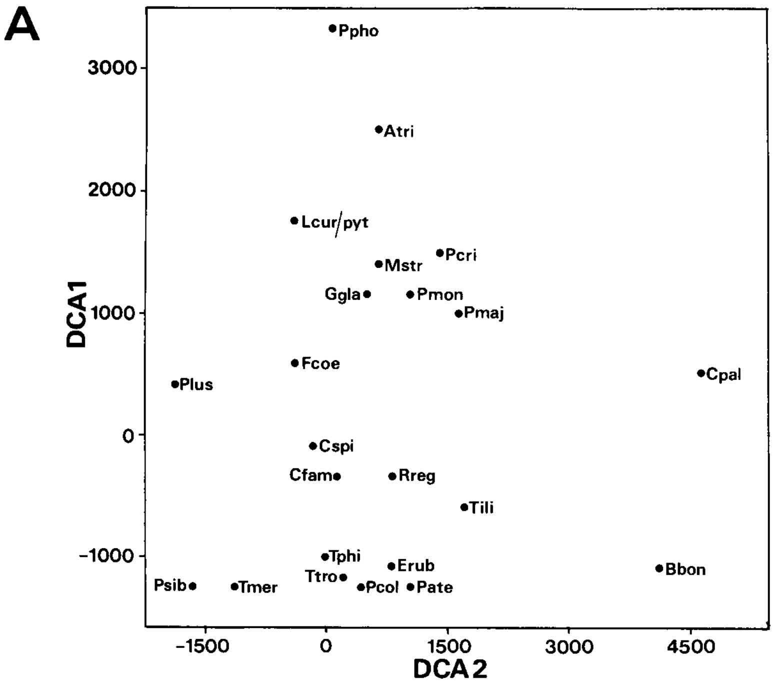


Fig. 3. DCA ordination of all species. A. species (for species abbreviations see Appendix 1), B. study areas: open squares=pine forests, filled squares=spruce forests.



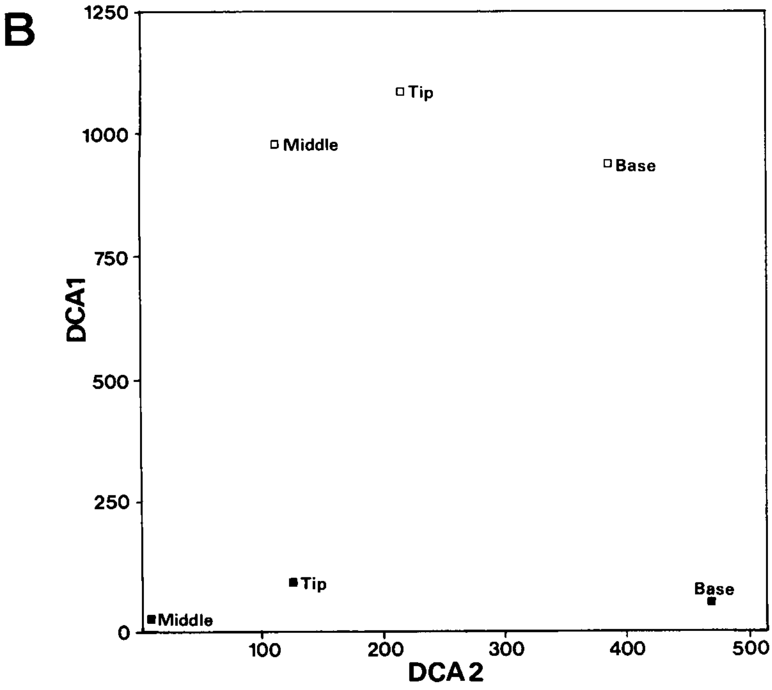


Fig. 4. DCA ordination of the most abundant species. A. species, B. study areas, symbols as in Fig. 3.

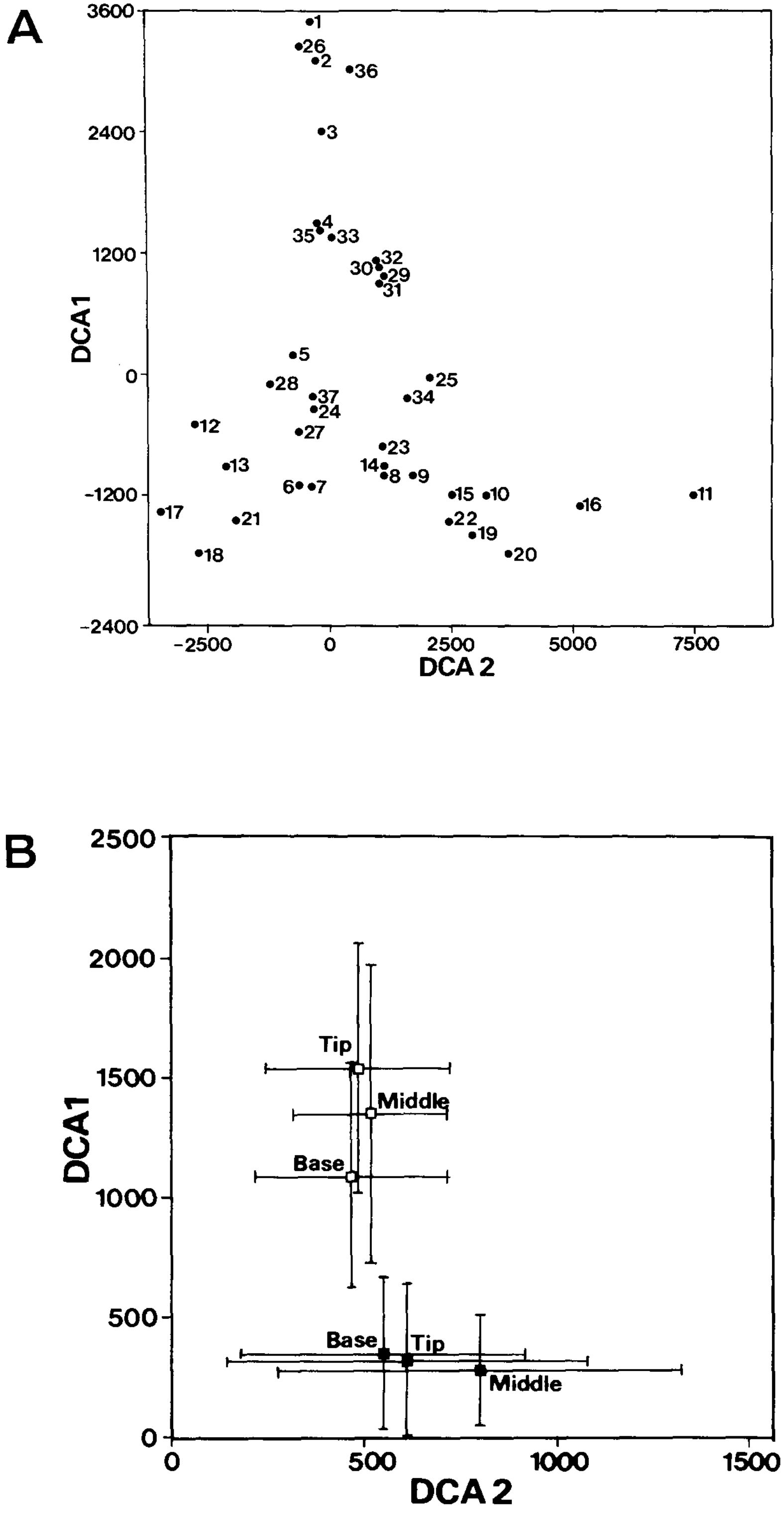


Fig. 5. DCA ordination of the habitat data. A. Habitat variables (for abbreviations see Appendix 3): 1=PIN -5, 2=PIN 5–10, 3=PIN 10–20, 4=PIN 20–30, 5= PIN 30–40, 6=SPR -5, 7=SPR 5–10, 8= SPR 10–20, 9=SPR 20–30, 10= SPR 30–40, 11=SPR 40-, 12= BIR -5, 13=BIR 5–10, 14=BIR 10–20, 15=BIR 20–30, 16=BIR 30–40, 17=DEC -5, 18=DEC 5–10, 19=DEC 10–20, 20=DEC 20–30, 21=DEC 30–40, 22=DEC 40-, 23=SNAG 5–10, 24=SNAG 10–20, 25=SNAG 20–30, 26=PIN SAPL, 27=SPR SAPL, 28=DEC SAPL, 29=HEIGHT MEAN, 30=HEIGHT SD, 31=COVER MEAN, 32=COVER SD, 33= DWARF SHRUBS, 34=HERBS, 35=MOSSES, 36=LICHENS, 37=SOIL & LITTER. B. Study areas: squares (open=pine forests, filled=spruce forests) indicate the mean of the DCA scores for each study area, lines ±2 SD.

end of the axis all size classes of deciduous trees (other than birch) were dominant. The eigenvalue of the first axis was 0.268.

As 392 habitat descriptions were included in the ordination, it was difficult to locate the different parts of the study area along the gradient. To surmount this, I calculated the mean and two standard deviations for each part on the basis of their DCA scores on the first and second axes (Fig. 5B). The pine forests of the tip and the spruce forests of the middle then formed the opposite ends of the first axis. The pine forests of the peninsula were distributed on a much larger area along the gradient than those of spruce; the spruce forests of the Hanko Peninsula thus resembled each other more than did the pine forests.

The pine forests of the tip were the most barren and those of the base the most luxuriant. This trend is due to the increase in the proportions of spruce and birch towards the base. The densities of both spruce and deciduous saplings also increased towards the base. The differences between spruce forests were negligible as the variation within an area was greater than that between the areas. The spruce forests of the base and middle were furthest away from each other.

The eigenvalue of the second axis was only 0.054. However, a weak gradient can be observed from large spruces and birches to smaller trees and bushes. The extreme ends of the axis were dominated by spruces, birches and other deciduous trees at least 20 cm in diameter on the one hand, and birches and other deciduous trees less than 10 cm in diameter on the other. This gradient could be observed only in the spruce forests, because of the tree species concerned. The differences within spruce habitats were negligible, since the 95% confidence limits overlapped widely. The spruce forests of the base and middle formed the opposite ends of the second DCA axis.

The DCA ordinations of the bird census and habitat data correspond with each other extremely well. The same gradient from the most barren forests to the most luxuriant ones can be observed in the two analyses. The tree species composition and the productivity of a forest have a clear influence on its bird community. The structural differences within each habitat correspond well to those observed in the bird communities; the extreme ends of the axes were the same in the two DCA ordinations.

When the DCA scores for the study areas along the first DCA axis of the census and habitat data were correlated, Spearman's r_s was significant for all species ($r_s=1.00$, $P<0.01$, $n=6$) and for the most abundant species ($r_s=0.94$, $P<0.05$, $n=6$).

Although the eigenvalues of the second DCA axis were small in both analyses, the same trend in the size class distribution of spruces and birches can be observed.

Discussion

The significance of habitat variation along peninsulas

The peninsular effect was not observed on the Hanko Peninsula: There were no significant differences in the number of species. The total density of birds in the pooled data and in the pine forests did not show any trends along the peninsula. The total density in spruce forests and the densities of certain species did deviate from the expected numbers, but in most cases in a manner not predicted by the hypothesis of the peninsular effect. These density differences could mostly be explained by differences in habitat structure along the peninsula. This is shown clearly by the correlation between the DCA ordinations of the bird census and habitat data.

Peninsular studies carefully examining the effects of habitat structure are virtually non-existent, but the proportions of different habitat types have been studied by some authors. Wamer (1978) studied the relations between avian diversity and the proportions of habitat types in Florida. He demonstrated that the number of bird species depended on the vegetation, especially on the amount and structure of the canopy. The proportion of forested habitats declined markedly towards the tip of the peninsula, which explained the smaller number of species at the tip.

In their study of reptiles and amphibians, Means & Simberloff (see Simberloff & Abele 1984) also concluded, that the changes in habitats along the Florida Peninsula explained the lower number of species at the tip.

In contrast, the study of Busack & Jaksić (1982) on the Iberian herpetofauna did not show any consistent correlations between species diversity and variables of the climate, vegetation, soil or area.

Scale problems in peninsular studies

What constitutes a peninsula for a group of species depends on the size and dispersal abilities of the organisms. A few kilometres is enough for species with poor dispersal abilities, such as land snails, while this short a distance does not affect birds.

Hanko Peninsula is very small compared with Baja California, the length of which exceeds 1 000 km, or Florida (ca. 600 km). Most of the peninsular studies published have been performed on these two long peninsulas. Differences in species number along these two north-south oriented peninsulas are to be expected, because large changes in the climate and vegetation occur along a distance of nearly 1 000 km. The fact that structural differences in habitats can be found on a considerably finer scale, on the Hanko Peninsula, supports this conclusion. If the peninsular effect was a universal phenomenon, it should be observable in all groups of species and on all peninsulas, even on finer scales (cf. Simberloff 1974).

The western Palearctic taiga forms a peninsula on a much larger scale. In a study based on qualitative and quantitative data derived from the literature, Haila et al. (1987b) found that the number of bird species breeding in coniferous forests did not decline from the Ural Mountains towards the southwest when the quantitative data were analysed with rarefaction. In contrast, the presence/absence data showed a decreasing, albeit irregular, trend in species number from north to south.

The peninsular effect has traditionally been studied by collecting presence/absence data from quadrats of fixed area. However, the diversity gradients obtained by this method vary considerably, depending on whether small or larger quadrats or latitudinal zones are sampled over the peninsula (McCoy & Connor 1980). Large quadrats can also partly include sea, especially at the tip of the peninsula. In such a case, the species number of the tip is smaller due to reduced sample size. However, Simpson (1964) claimed that this does not affect his results; the number of species is less at the tips of peninsulas than in land areas of equal size at the bases. The spatial distribution of species also affects the diversity gradients obtained (for details, see McCoy & Connor 1980).

Most peninsular studies (e.g. Simpson 1964, Cook 1969, Kiester 1971, Tramer 1974) discuss the total diversity, i.e. the gamma diversity of peninsulas. However, if a certain habitat type is missing from the tip of the peninsula, or its proportion is significantly less than at the base, these areas are not comparable, because each habitat usually has its specific fauna. In such a case the peninsular effect is merely a consequence of varying proportions of habitat types. Thus, it seems more efficient to study species numbers within one or a few carefully defined habitat types. On the other hand, if a peninsular effect is observed within a single habitat, this does not necessarily mean that it is present in other habitats or on the peninsula as a whole (cf. Wiens et al. 1986). Thus, the results obtained from the coniferous forests of the Hanko Peninsula cannot be generalized for the whole peninsula (or for other groups of species).

Field data are usually collected during rather short periods, often covering only one season, like the material of this study. Chance may then greatly affect the results (Wiens 1981, 1986, Wiens et al. 1986). Changes in population size are not necessarily simultaneous or of the same order of magnitude in all parts of a peninsula, particularly if large areas are concerned. Likewise, the occurrence of naturally rare species in a sample depends greatly on chance (e.g. Wiens 1981). However, Taylor & Pfannmuller (1981) concluded that if the peninsular effect is a universal phenomenon, it should be evident even in data collected during only one season.

Conservation and the peninsular effect

On the basis of the peninsular effect, Wilson & Willis (1975) suggested that long and narrow nature reserves are poorer than, for example, circular reserves, because of the higher extinction rates due to the high proportion of edges. The least suitable shape would be an area resembling a star, which consists entirely of peninsulas (Willis 1984). These ideas have been widely used and they are included in the World Conservation Strategy (IUCN 1980).

Long and narrow areas are obviously poorer on very fine scales, when the whole "peninsula" will consist of edges, but this is not true on larger scales, such as the Hanko Peninsula. Simberloff & Abele (1984) attack the recommendations, because none of the studies so far published have proved that the peninsular effect resulted from the equilibrium between colonization and extinction. Blouin & Connor (1985) also demonstrated that the shape of an island or a peninsula does not have any effect on species diversity. Much more important from the conservation point of view is to study local conditions, especially habitat structure and the proportions of different habitats in the area concerned, in addition to the animal species and their ecological requirements. Of particular importance (Järvinen 1982) is the presence of habitats that support unusually many endangered or rare species.

Acknowledgements. I owe special thanks to Olli Järvinen for many fruitful discussions, criticism and advice during this long project, which started as my M.Sc. thesis. Yrjö Haila, Pekka Helle, Antero Järvinen and Staffan Ulfstrand made useful comments on the manuscript. Financial support from the Alfred Kordelin Foundation and the Finnish Cultural Foundation is greatly appreciated.

Selostus: Hankoniemen havumetsälinnusto: ei niemimaavaikutusta, vaan elinympäristön rakenne-erot selittäjänä

Saarten lajimäärä pienenee etäisyyden kasvaessa mantereeseen ja saaren pinta-alan pienentyessä, mutta on myös havaittu, että lajimäärä usein vähenee kohti niemimaiden kärkiosaa. Myös lintutiheyden on havaittu laskevan kohti niemimaan kärkeä. Selitykseksi tälle ns. niemimaavaikutukselle on yleensä esitetty niemen kärkiosan vähäistä saavuntaa hävintään verrattuna. Sen sijaan elinympäristöjen rakenteellisia eroja ei niemen kärjen ja tyven välillä ole yleensä otettu huomioon.

Tutkimuksen tarkoituksena on selvittää: (1) Voiko Hankoniemen havumetsälinnustossa havaita niemimaavaikutusta? (2) Kuinka mahdolliset erot elinympäristöjen rakenteessa vaikuttavat lajimäärän ja tiheyden eroihin?

Aineisto on kerätty linjalaskennoin (vain pääsaran havainnot) mänty- ja kuusimetsistä kolmelta Hankoniemen vyöhykkeeltä; kärjestä, keskiosasta ja tyveltä. Havaintoja kertyi 1092 lintuparista. Laskentareittien varrelta on 250 m:n välein määritetty 37 muuttujaa, jotka kuvaavat biotoopin rakennetta.

Niemimaavaikutusta ei voitu havaita Hankoniemellä. Samankokoisissa satunnaisnäytteissä lajimäärä ei laskenut kohti niemimaan kärkeä kummassakaan biotoopissa. Linnuston kokonaistiheys ei vaihdellut tilastollisesti merkitsevästi, kuten ei myöskään mäntymetsien linnuston tiheys. Sen sijaan kuusikoissa tiheys oli selvästi korkein tutkimusalueen keskiosassa. Myös tiettyjen yksittäisten lajien ja lajiryhmien tiheydessä havaittiin kummassakin biotoopissa joitakin merkitseviä eroja. Nämä tiheyserot voidaan pääosin selittää biotooppien rakenteessa havaituin eroin (mm. puuston kokoluokkajakauma, puulajisuhteet ja pensaskerroksen tiheys). Sekä linnustosta että biotooppiaineistosta tehdyt DCA-oordinaatiot vastaavat hyvin toisiaan; metsien rehevyys sekä kuusen ja koivun kokoluokkajakauma olivat tärkeimmät selittävät tekijät kummassakin analyysissä.

Tulokset viittaavat siihen, että niemimailla havaitut lajimäärä- ja tiheyserot johtuvat ensi sijassa biotooppien määrän ja rakenteen eroista.

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Received 14 September 1988, accepted 4 October 1988

Appendix 1. Bird census data from the different parts of the Hanko Peninsula; number of pairs (n), density (pairs/km²) and proportion among all pairs observed (%).

Pine forests	Tip			Middle			Base			Total		
Species	n	p/km²	%	n	p/km²	%	n	p/km²	%	n	p/km²	%
Pernis apivorus (Papi)	–	–	–	–	–	–	–	–	–	–	–	–
Accipiter gentilis (Agen)	–	–	–	–	–	–	–	–	–	–	–	–
Bonasa bonasia (Bbon)	–	–	–	–	–	–	–	–	–	–	–	–
Tetrao tetrix (Ttet)	1	1.1	0.7	–	–	–	–	–	–	1	0.4	0.2
Scolopax rusticola (Srus)	1	1.1	0.7	1	1.0	0.6	–	–	–	2	0.7	0.5
Columba palumbus (Cpal)	2	2.1	1.4	–	–	–	–	–	–	2	0.7	0.5
Cuculus canorus (Ccan)	1	1.1	0.7	–	–	–	1	1.3	0.7	2	0.7	0.5
Dendrocopos major (Dmaj)	–	–	–	1	1.0	0.6	1	1.3	0.7	2	0.7	0.5
Picoides tridactylus (Ptri)	–	–	–	–	–	–	–	–	–	–	–	–
Anthus trivialis (Atri)	24	25.7	16.8	19	19.2	12.5	19	23.8	13.9	62	22.8	14.4
Troglodytes troglodytes (Ttro)	–	–	–	–	–	–	–	–	–	–	–	–
Prunella modularis (Pmod)	–	–	–	–	–	–	1	1.3	0.7	1	0.4	0.2
Oenanthe oenanthe (Ooen)	–	–	–	1	1.0	0.6	–	–	–	1	0.4	0.2
Turdus merula (Tmer)	–	–	–	–	–	–	–	–	–	–	–	–
T. philomelos (Tphi)	–	–	–	2	2.0	1.3	–	–	–	2	0.7	0.5
T. iliacus (Tili)	–	–	–	1	1.0	0.6	1	1.3	0.7	2	0.7	0.5
T. viscivorus (Tvis)	1	1.1	0.7	–	–	–	1	1.3	0.7	2	0.7	0.5
Sylvia curruca (Scur)	–	–	–	–	–	–	–	–	–	–	–	–
S. atricapilla (Satr)	–	–	–	–	–	–	–	–	–	–	–	–
Phylloscopus sibilatrix (Psib)	–	–	–	–	–	–	–	–	–	–	–	–
Ph. collybita (Pcol)	–	–	–	–	–	–	–	–	–	–	–	–
Ph. trochilus (Plus)	4	4.3	2.8	14	14.2	9.2	1	1.3	0.7	19	7.0	4.4
Regulus regulus (Rreg)	7	7.5	4.9	9	9.1	5.9	17	21.3	12.4	33	12.1	7.6
Muscicapa striata (Mstr)	12	12.9	8.4	8	8.1	5.3	7	8.8	5.1	27	9.9	6.2
Ficedula parva (Fpar)	–	–	–	–	–	–	–	–	–	–	–	–
F. hypoleuca (Fhyp)	–	–	–	–	–	–	–	–	–	–	–	–
Erithacus rubecula (Erub)	–	–	–	–	–	–	1	1.3	0.7	1	0.4	0.2
Phoenicurus phoenicurus (Ppho)	2	2.1	1.4	2	2.0	1.3	1	1.3	0.7	5	1.8	1.2
Aegithalos caudatus (Acau)	–	–	–	–	–	–	–	–	–	–	–	–
Parus montanus (Pmon)	4	4.3	2.8	9	9.1	5.9	8	10.0	5.8	21	7.7	4.9
P. cristatus (Pcri)	11	11.8	7.7	17	17.2	11.2	17	21.3	12.4	45	16.5	10.4
P. ater (Pate)	–	–	–	–	–	–	–	–	–	–	–	–
P. major (Pmaj)	1	1.1	0.7	3	3.0	2.0	3	3.8	2.2	7	2.6	1.6
Certhia familiaris (Cfam)	1	1.1	0.7	–	–	–	2	2.5	2.2	3	1.1	0.7
Garrulus glandarius (Ggla)	3	3.2	2.1	1	1.0	0.6	1	1.3	0.7	5	1.8	1.2
Fringilla coelebs (Fcoe)	63	67.5	44.0	60	60.7	39.5	49	61.4	35.8	172	63.2	39.8
Carduelis chloris (Cchl)	–	–	–	–	–	–	–	–	–	–	–	–
C. spinus (Cspi)	3	3.2	2.1	1	1.0	0.6	4	5.0	2.9	8	2.9	1.8
Loxia curvirostra/ pytyopsittacus (Lcur/pyt)	–	–	–	2	2.0	1.3	1	1.3	0.7	4	1.5	0.9
Pyrrhula pyrrhula (Ppyr)	–	–	–	–	–	–	–	–	–	–	–	–
Emberiza citrinella (Ecit)	1	1.1	0.7	1	1.0	0.6	1	1.3	0.7	3	1.1	0.7
Total	143	153.1	100	152	153.7	100	137	171.8	100	432	158.8	100

Spruce forests	Tip			Middle			Base			Total		
Species	n	p/km^2	%	n	p/km^2	%	n	p/km^2	%	n	p/km^2	%
Pernis apivorus (Papi)	1	1.3	0.4	–	–	–	–	–	–	1	0.4	0.2
Accipiter gentilis (Agen)	1	1.3	0.4	1	1.8	0.4	–	–	–	2	0.9	0.3
Bonasa bonasia (Bbon)	2	2.6	0.4	–	–	–	4	4.6	1.8	6	2.7	0.9
Tetrao tetrix (Ttet)	–	–	–	–	–	–	–	–	–	–	–	–
Scolopax rusticola (Srus)	–	–	–	–	–	–	–	–	–	–	–	–
Columba palumbus (Cpal)	–	–	–	–	–	–	4	4.6	1.8	4	1.8	0.6
Cuculus canorus (Ccan)	–	–	–	1	1.8	0.4	–	–	–	1	0.4	0.2
Dendrocopos major (Dmaj)	–	–	–	1	1.8	0.4	–	–	–	1	0.4	0.2
Picoides tridactylus (Ptri)	1	1.3	0.4	–	–	–	–	–	–	1	0.4	0.2
Anthus trivialis (Atri)	6	7.8	2.7	2	3.6	0.9	3	3.5	1.4	11	5.0	1.7
Troglodytes troglodytes (Ttro)	3	3.9	1.4	1	1.8	0.4	1	1.2	0.4	5	2.3	0.8
Prunella modularis (Pmod)	1	1.3	0.4	–	–	–	–	–	–	1	0.4	0.2
Oenanthe oenanthe (Ooen)	–	–	–	–	–	–	–	–	–	–	–	–
Turdus merula (Tmer)	2	2.6	0.9	3	5.5	1.4	2	2.3	0.9	7	3.2	1.1
T. philomelos (Tphi)	8	10.4	3.6	10	18.2	4.5	9	10.4	4.1	27	12.4	4.1
T. iliacus (Tili)	4	5.2	1.8	2	3.6	0.9	5	5.8	2.3	11	5.0	1.7
T. viscivorus (Tvis)	1	1.3	0.4	–	–	–	1	1.2	0.4	2	0.9	0.3
Sylvia curruca (Scur)	–	–	–	–	–	–	1	1.2	0.4	1	0.4	0.2
S. atricapilla (Satr)	–	–	–	2	3.6	0.9	–	–	–	2	0.9	0.3
Phylloscopus sibilatrix (Psib)	9	11.7	4.0	9	16.4	4.1	5	5.8	2.3	23	10.5	3.5
Ph. collybita (Pcol)	5	6.5	2.2	15	27.3	6.8	14	16.2	6.4	34	15.6	5.2
Ph. trochilus (Plus)	12	15.6	5.4	10	18.2	4.5	5	5.8	2.3	27	12.4	4.1
Regulus regulus (Rreg)	47	61.1	21.2	34	62.0	15.4	42	48.5	19.3	123	56.3	18.6
Muscicapa striata (Mstr)	6	7.8	2.7	5	9.1	2.3	6	6.9	2.8	17	7.8	2.6
Ficedula parva (Fpar)	–	–	–	1	1.8	0.4	–	–	–	1	0.4	0.2
F. hypoleuca (Fhyp)	–	–	–	1	1.8	0.4	–	–	–	1	0.4	0.2
Erithacus rubecula (Erub)	13	16.9	5.8	12	21.9	5.4	14	16.2	6.4	39	17.8	5.9
Phoenicurus phoenicurus (Ppho)	–	–	–	–	–	–	–	–	–	–	–	–
Aegithalos caudatus (Acau)	2	2.6	0.9	–	–	–	1	1.2	0.4	3	1.4	0.4
Parus montanus (Pmon)	2	2.6	0.9	5	9.1	2.3	8	9.2	3.7	15	6.9	2.3
P. cristatus (Pcri)	5	6.5	2.2	5	9.1	2.3	16	18.5	7.3	26	11.9	3.9
P. ater (Pate)	2	2.6	0.9	4	7.3	1.8	5	5.8	2.3	11	5.0	1.7
P. major (Pmaj)	4	5.2	1.8	–	–	–	3	3.5	1.4	7	3.2	1.1
Certhia familiaris (Cfam)	3	3.9	1.4	4	7.3	1.8	3	3.5	1.4	10	4.6	1.5
Garrulus glandarius (Ggla)	2	2.6	0.9	1	1.8	0.4	1	1.2	0.4	4	1.8	0.6
Fringilla coelebs (Fcoe)	68	88.5	30.6	84	153.1	38.2	59	68.1	27.1	211	96.6	32.0
Carduelis chloris (Cchl)	1	1.3	0.4	–	–	–	–	–	–	1	0.4	0.2
Carduelis spinus (Cspi)	9	11.7	4.0	7	12.8	3.2	5	5.8	2.3	21	9.6	3.2
Loxia curvirostra/ pytyopsittacus (Lcur/pyt)	2	2.6	0.9	–	–	–	–	–	–	2	0.9	0.3
Pyrrhula pyrrhula (Ppyr)	–	–	–	–	–	–	1	1.2	0.4	1	0.4	0.2
Emberiza citrinella (Ecit)	–	–	–	–	–	–	–	–	–	–	–	–
Total	222	288.8	100	220	400.9	100	218	251.6	100	660	302.2	100

Appendix 2. Groups of species used in χ^2-tests. For species abbreviations see App. 1.

Sylviidae: Satr, Scur, Plus, Pcol, Psib, Rreg

Paridae: Pmon, Pcri, Pate, Pmaj

Fringillidae: Fcoe, Ppyr, Cchl, Cspi, Lcur/pyt

Tit guild: Rreg, Pmon, Pcri, Pate, Pmaj, Cfam

Conifer tits: Pmon, Pcri, Pate

Hole-nesters: Dmaj, Ptri, Fhyp, Ppho, Pcri, Pmon, Pate, Pmaj

Open nest: All others excluding hole-nesters and Mstr, Fpar, Cfam, Ooen

Open nest in tree/bush: Papi, Agen, Cpal, Ggla, Satr, Scur, Rreg, Acau, Fcoe, Ppyr, Cchl, Cspi, Lcur/pyt

Nesting in tree/bush: Species with open nest in tree/bush and hole-nesters including Mstr, Fpar, Cfam

Ground-nesting: Ttet, Bbon, Srus, Atri, Plus, Psib, Erub, Ecit

Nest site variable: Ccan, Ttro, Pmod, Pcol, Tmer, Tili, Tvis, Tphi, Ooen

Strictly resident: Ttet, Bbon, Pcri

Partial migrants: Rreg, Tmer, Cchl, Cspi, Ppyr, Ecit

Short-distance migrants: Srus, Cpal, Ttro, Pmod, Erub, Tili, Tphi, Tvis, Fcoe

Long-distance migrants: Papi, Ccan, Atri, Satr, Scur, Plus, Pcol, Psib, Fhyp, Fpar, Mstr, Ooen, Ppho

Migrants in total: Short- and long-distance migrants

Preferring young trees: Satr, Plus, Pmod, Erub, Tili, Tphi, Tmer, Ppyr

Preferring spruce: Pmod, Pcol, Psib, Rreg, Erub, Tphi, Cfam, Ppyr, Cspi, Pate

Foliage insectivores: Ccan, Scur, Satr, Psib, Pcol, Plus, Rreg, Pmon, Pcri, Pate, Pmaj, Acau

Feeding mainly on animals: Foliage insectivores and Atri, Pmod, Erub, Ooen, Tmer, Tphi, Tili, Tvis, Ecit, Ttro, Ppho, Mstr, Fhyp, Fpar, Papi, Agen, Srus, Ptri, Cfam

Appendix 3. Habitat variables determined.

The number of pines whose diameter at breast height is

PIN -5	less than 5 cm
PIN 5–10	5–10 cm
PIN 10–20	10–20 cm
PIN 20–30	20–30 cm
PIN 30–40	30–40 cm

The number of spruces whose diameter at breast height is

SPR -5	less than 5 cm
SPR 5–10	5–10 cm
SPR 10–20	10–20 cm
SPR 20–30	20–30 cm
SPR 30–40	30–40 cm
SPR 40–	over 40 cm

The number of birches whose diameter at breast height is

BIR -5	less than 5 cm
BIR 5–10	5–10 cm
BIR 10–20	10–20 cm
BIR 20–30	20–30 cm
BIR 30–40	30–40 cm

The number of other deciduous trees whose diameter at breast height is

DEC -5	less than 5 cm
DEC 5–10	5–10 cm
DEC 10–20	10–20 cm
DEC 20–30	20–30 cm
DEC 30–40	30–40 cm
DEC 40–	over 40 cm

The number of deciduous and conifer snags whose height is at least 1 m and diameter at breast height

SNAG 5–10	5–10 cm
SNAG 10–20	10–20 cm
SNAG 20–30	20–30 cm

PIN SAPL The number of pine saplings (height 0.5–2.5 m)
SPR SAPL The number of spruce saplings and juniper bushes (height 0.5–2.5 m)
DEC SAPL The number of deciduous bushes and saplings (height 0.5–2.5 m)

HEIGHT MEAN The mean height of five canopy trees
HEIGHT SD The standard deviation of the height of five canopy trees
COVER MEAN The mean canopy cover (11 measurements)
COVER SD The standard deviation of the canopy cover

DWARF SHRUBS Proportion of dwarf shrubs (scale 0–5)
HERBS Proportion of herbs (scale 0–5)
MOSSES Proportion of mosses (scale 0–5)
LICHENS Proportion of lichens (scale 0–5)
SOIL & LITTER Proportion of bare soil and litter (scale 0–5)