

Reversed latitudinal gradients in total density and species richness of birds breeding on Finnish mires

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Latitudinal gradients in the total density and species richness of breeding mire birds were studied on the basis of 72 censuses made on flark fens in middle and northern parts of Finland. Flark fens represent an ornithologically important but common mire type, which support fairly high densities of many species.

It has been shown previously that the average density and species richness of birds breeding on Finnish mires increase towards the north. It is shown here that these “reversed” gradients cannot be attributed to size variation in mire areas studied in different regions. Even after the effect of area on density is removed, species richness increases northwards in samples including the same number of pairs (90 pairs; about 0.9 species more per 100 km north) or areas of the same size (1 km²; about 1.3 spp. more per 100 km north). The northward increase in total density is statistically significant, but largely obscured by the considerable heterogeneity of densities among mires in the same geographical area.

Differences in the proportion of major habitats probably contribute markedly to the northward increasing densities. In particular, flark fens are common in the north (about one-half of the area of treeless mires) but less so in the south (one-fifth or even one-tenth of the area).

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Introduction

Järvinen & Sammalisto (1976; but see also Häyrynen 1970 and Raitasuo 1973) documented that bird density and species richness of breeding birds increase towards the north on Finnish mires (peatlands).

Since the mires studied by Järvinen & Sammalisto (1976) were of different sizes in different parts of Finland, Boström & Nilsson (1983) suggested the possibility that “some of the trends reported ... are effects of size difference of bogs between different regions”. This possibility seems marginal. The three summaries quoted above are based on different data sets but report rather similar trends. Moreover, Järvinen & Sammalisto (1976) did show that species richness increases northwards even when the species-area effect is taken into account. Their equations (based on incomplete counts made largely in the 1950s) predicted about 5 breeding species on a 100-ha mire in southern Finland but over 10 species for northern Finnish mires of the same size. The highest

numbers of species are far above these figures, also in relation to the area of the mire (see Hildén 1967, Väisänen & Järvinen 1977, Häyrynen et al. 1986).

Another problem in the trends reported by Järvinen & Sammalisto (1976) is that treeless mires do not constitute a homogeneous habitat. Indeed, a single mire area, even when one restricts censusing to its treeless parts (as did Järvinen & Sammalisto 1976 and Boström & Nilsson 1983), is actually a complex of different, more narrowly definable habitats, called mire types (see e.g. Ruuhijärvi 1960, 1983, Eurola 1962, Pakarinen & Ruuhijärvi 1978, Eurola & Kaakinen 1979a, 1979b, Reinikainen et al. 1984).

Not unexpectedly, different mire types support different sets of breeding species (Häyrynen et al. 1986, Häyrynen unpubl.), depending on the proximity of forest edges or on the wetness of the habitat (Seiskari 1954, Sammalisto 1955, 1957, Boström & Nilsson 1983, Häyrynen et al. 1986; for data on the relationships between birds and habitat variables on mires, see also Niemi 1983 and Niemi et

al. 1983). Therefore, the observation that species richness and total density increase northwards on Finnish mires is still problematic:

Do reversed latitudinal gradients exist after the elimination of the effect of area on density (Boström & Nilsson 1983)?

Are these gradients largely due to differences in habitat structure between the southern and northern mires (for parallels in island biogeography, see Abbott 1980, Haila et al. 1983)?

Alternatively, can reversed gradients be discerned even after removing the two biases mentioned?

In this paper we will demonstrate that the answer is yes to the first and to the third question, while it is quite probably yes to the second. In addition, the first yes needs qualification: the reversed gradient is very clear in species richness but not so distinct in total density.

Material and methods

In order to answer these questions, a good data set should: (1) be methodologically homogeneous, (2) represent the latitudinal gradient well, (3) represent habitats as homogeneous as possible, and (4) refer to a common habitat (mire) type that is among the most important for mire birds. The data set we analysed fulfils these requirements better than any other data set known to us.

We examined 72 censuses made on flark fens (German: Rimpfiweissmoore; for the botanical terminology, see Pakarinen & Ruuhijärvi 1978, Ruuhijärvi 1983) on Finnish mires by Häyrinen and his co-workers in 1963–84 (Appendix 1). Both early and late censuses are available from southern and northern Finland, so possible long-term trends in bird populations should not obscure the latitudinal gradients.

A similar attempt was made by Boström & Nilsson (1983), who, in order to minimize habitat heterogeneity, studied raised bogs only. This is definitely an improvement, but raised bogs are nevertheless mire complexes, including numerous mire types.

The habitat studied by us is particularly important for mire birds, since bird density on flark fens is higher than on other common mire types (Häyrinen 1970 and unpubl.). Note that there are no flark fens on raised bogs. Flark fens are characterised by numerous ponds and pools, and few or no trees. This habitat is therefore a mosaic of water and *Sphagnum* strings and hummocks.

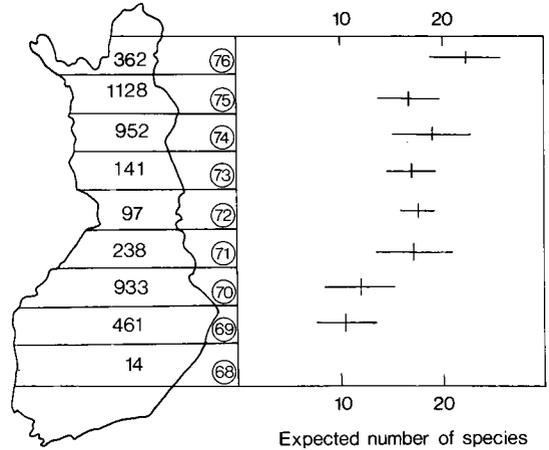


Fig. 1. Left: The distribution of the data, expressed as pairs observed in the censuses, in different 100-km zones of Finland (zone numbers encircled, from 68 to 76). Right: The expected numbers of species ($\pm 95\%$ confidence limits) in rarefaction samples of 1 km² of flark fens in the different zones. The sample size is based on the average density of birds observed in the censuses of flark fens in each zone.

The data were collected in “study plot” censuses. Mire areas were first examined from aerial photographs, which show the different mire types quite well: flark fens in particular are distinct from other mire types. The areas were visited once, which implies that part of the birds were missed, but census efficiency is relatively high on treeless mires (for data, see Svensson 1978, Kouki & Järvinen 1980). The censuses were made in June, during the main breeding season of mire birds, and almost exclusively by Häyrinen, Kouki or observer groups led by Häyrinen.

In order to examine latitudinal patterns in the data, the censuses were grouped according to the 100-km zones of the Finnish uniform grid system (Fig. 1, Table 1). Census effort was fairly constant at between 4 and 11 flark fens per zone excepting the two extremes mentioned above. There is no latitudinal trend in census effort (Fig. 1).

Sample sizes varied between 14 and 1128 pairs per zone, the minimum value coming from the southernmost zone. The minimum being so low, we excluded this zone from all analyses based on the zones (all other zones had at least 97 pairs per zone, and 6 zones out of 9 had more than 200 pairs). The whole data set comprises over 4000 pairs of birds.

Waterfowl were excluded because their censuses in June are unreliable. We included all other species

Table 1. Observed and area-corrected densities (pairs/km²) in different 100-km zones (see Fig. 1). In most cases two zones were pooled in order to avoid zones with less than 10 study areas. The area-corrected densities are based on the regression of observed density upon the inverse of area, and the corrections are equal to the residuals in this analysis.

Zone(s)	Flark fens	Mean area of plot (range)	Observed density		Corrected density	
			Median	Range	Median	Range
68–69 (south)	12	45 (13–102)	87	26–191	69	27–186
70	20	69 (11–295)	69	9–418	66	0–398
71–72	11	65 (16–125)	49	35–87	48	34–75
73–74	14	102 (43–196)	57	21–305	80	19–295
75–76 (north)	15	85 (41–254)	106	21–303	132	14–302

in our analyses, except gull colonies (at least 5 pairs of the same species). We omitted colonies mostly because gulls forage mainly outside mire areas on dump-pits and other human-made habitats. Gull colonies on mires are also capricious, for even a large colony may suddenly disappear (for examples, see Järvinen 1978 and Häyrinen et al. 1986). The data set used by Järvinen & Sammalisto (1976) did not include gull colonies.

In contrast to the data set analysed by Järvinen & Sammalisto (1976), there is a slight northward increase in the area of the study plots in the present data (Table 1).

Total density

No clear relationship between flark fen area and bird density was discernible in our data set. Very small flark fens tended to have high bird densities, but they represented statistical outliers or otherwise single observations having a large influence on the regression between area and density. To make our analysis as conservative as possible, we nevertheless corrected the observed densities using the area-density regression, i.e. we removed the area effect (*sensu* Boström & Nilsson 1983) from our data. The analyses were made separately for waders and passerines, since these taxa were sufficiently common, and separating these taxa permits the comparison of the latitudinal patterns displayed by each.

If we denote the density corrected with the effect of flark fen area on bird density with D (in pairs/km²) and the 100-km zone with Z (ranging from 68 to 77, see Fig. 1; measured to the nearest 10 km), we observe a consistent northward increase of density:

For waders,

$$D_w = -286 + 4.5 Z \quad (P < 0.01);$$

for passerines,

$$D_p = -245 + 4.1 Z \quad (P < 0.05);$$

and for all species,

$$D_A = -552 + 8.9 Z \quad (P < 0.01).$$

The equations imply that the northward increase in total density is slightly over 4 pairs/km² per 100 km for waders and passerines alike, which makes more than 8 pairs/km² for the two taxa together. These taxa include the bulk of the bird species assemblages of flark fens (excluding the gull colonies) so that the northward increase for all species together is about 9 pairs/km² per 100 km.

In all analyses, two to four observations had particularly large residuals so that the exclusion of these data points from the analyses was considered. Since the slope of the regressions was not decisively affected by the deviating points, they were nevertheless included. In all cases the deviations were due to unusually high density values. Mire areas having large residuals were found both in the south and in the north. This suggests that, for reasons not dealt with in this paper, some mire areas seem to support a very high density of birds in relation to their size and latitudinal location (see also Väisänen & Järvinen 1977, Häyrinen et al. 1986).

The heterogeneity of different mire areas in the same region is also shown by the fact that the above regressions account for no more than 6–9% of the variation in the area-corrected densities. Therefore, there is a significant northward increase in density, but local differences among mires of the same region have a much greater influence on total density than latitude has (Table 1).

Species richness

Species richness on flark fens may increase northwards in two different respects:

First, species number tends to increase with sample size (Palmgren 1930 and many later authors). Since bird density increases northwards on flark fens (above), there may be a northward increase in species richness also when areas of similar size are compared. In order to examine this possibility, we calculated the expected number of species on 1 km² of flark fen in the different 100-km zones. We also took into account the possible effect of area on density (see above) in this calculation using the method of rarefaction (Simberloff 1979).

Second, species richness may increase towards the north because the species-abundance distribution is more equitable on northern than on southern flark fens. In other words, even though we compare samples having the same number of pairs, there may be a difference between northern and southern areas. We examined this, using rarefaction, by comparing random samples of 90 pairs in different 100-km zones. The more even the species-abundance distribution, the greater is the number of species in the samples.

Both analyses gave similar results (Fig. 1, Table 2): a distinct increase in species number towards the north. This can partly be traced to a more equitable species-abundance distribution in the north, i.e. the dominant species are relatively less dominant in the north than in the south. Partly the northward increase in species richness is also due to the effect of greater numbers of pairs per area unit in the north than in the south. These conclusions emerge from the following regressions.

First, the regression between zone (Z) and species richness per 1 km² (S_A) accounts for 69% of the variation in species richness and is statistically significant (P<0.01); about 1.3 species more per 100 km north:

$$S_A = -79 + 1.3 Z.$$

Second, the regression between zone and species richness per 90 pairs (S_P) accounts for about 51% of the variation in species richness (P ≈ 0.01); about 0.9 species more per 100 km north:

$$S_P = -49 + 0.9 Z.$$

It seems best to interpret the regressions cautiously, since they are based on eight zones only. Nevertheless, the results suggest that the effect of low density on species richness is somewhat more important than the effect of differences in the evenness of the species-abundance distribution.

Since the number of flark fens censused in different zones varied from 1 to 20, the pooling of the samples may have increased heterogeneity

Table 2. The northward increase of bird species number on flark fens in Finland. The first column gives the 100-km zones of Finland (see Fig. 1). The second column gives the expected numbers of species (±SD) in rarefaction samples of 90 pairs in each zone.

Zone	Species per 100 pairs
69 (south)	11.6±1.4
70	12.9±1.6
71	17.8±1.5
72	17.6±0.6
73	16.5±1.3
74	18.0±1.9
75	16.1±1.5
76 (north)	20.3±1.8

disproportionately in different zones. Therefore, we also examined the northward increase of species richness without merging data from different flark fens. Despite the generally close correlation between the number of species and area of the plot, the geographical location of the study plot was a particularly important predictor of species number. The regression between species number and logarithmic area was highly significant and explained 27% of the variation in species number. However, when Z (south-north location, see Fig. 1) was included, the model improved considerably,

$$S = -67 + 1.8 \ln A + 1.0 Z,$$

where the area (A) is given in hectares. This model explains 55% of the variation in S and is highly significant (P<0.001). This means that species number does increase with area, but there is an even better correlation with the geographical location (Z); one species more per 100 km north after removing the effect of area on species number.

Discussion

An explanation couched in terms of very broadly defined habitats has been proposed for the northward increase in the number of wader species breeding in Fennoscandia. Järvinen & Väisänen (1978) showed that the regional species number of waders tends to increase with the presence of mires, seashore habitats and mountains, all important breeding grounds for several waders. However, they also showed that there is a northward increase in species numbers even if one removes habitat heterogeneity at this level.

In this study we have been able to examine patterns in bird density and species richness in a more detailed way by looking at the patterns within a

clearly defined mire type. The basic patterns are the same as those reported by Järvinen & Sammalisto (1976).

However, the second question posed towards the end of the Introduction still needs to be answered. Briefly, the question is whether the northward increases in bird density and species richness on treeless mires in Finland are more a result of geographical trends observed in the bird species assemblages of a single habitat type (demonstrated in this paper) than a consequence of different proportions of mire types. The latter alternative can only be answered properly when sufficient data are available on bird densities in different mire types in different parts of Finland. Such data are not available now, although Häyrinen's (1970 and unpubl.) data suggest that bird densities on flark fens are higher than on other common mire types in Finland.

Moreover, flark fens are much more common in the north than in the south. Heikurainen (1960) estimated that less than 1% of the mires in southern Finland are flark fens (*Sphagnum* hollow bogs excluded), while their proportion is almost 9% in the north. If we only include treeless mires, the data given by Ilvessalo (1927) suggest that flark fens and similar mire types comprise about 50% of the area of treeless mires in the north, but less than one-fifth, even less than one-tenth in the south. These statements are supported by more recent unpublished data (R. Ruuhijärvi, pers. comm.).

In conclusion, the northward increases in bird density and species richness reported by Järvinen & Sammalisto (1976) probably have two different reasons: the preponderance of rich mire bird habitats, such as flark fens, among treeless mires increases northwards, but density and species richness also increase in flark fens from south to north. Climatological reasons for these trends are discussed in, for example, Ruuhijärvi (1960) and Järvinen & Sammalisto (1976).

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Selostus: Rimpinevojen pesimälinnuston lajimäärän ja tiheyden kasvusta pohjoiseen

Eliöyhteisöissä on yleensä sitä vähemmän lajeja, mitä pohjoisempaan ollaan. Myös populaatiotiheydet ovat pohjoisessa usein alhaisempia kuin etelässä. Soiden pesimälinnusto näyttää

kuitenkin muodostavan selkeän poikkeuksen näistä ekologis-elioämaantieteellisistä säännönmukaisuuksista.

Kirjoituksessa on tarkasteltu pesimälinnuston tiheyden ja lajimäärän alueittaista vaihtelua 72 rimpinevalla, joiden linnusto on laskettu 1963–1984. Aineiston kokonaisparimäärä on yli 4000 (kuva 1).

Yksittäisten koealojen tiheydet olivat lievästi riippuvaisia alan suuruudesta. Tämän vuoksi tiheydet korjattiin pinta-alavaikutuksesta, jotta maantieteellistä vaihtelua voitiin luotettavasti selvittää. Sekä kahlaajien että varpuslintujen tiheys rimpinevoilla kasvaa pohjoiseen (taulukko 1), mutta regression selittävyys on vain 6–9%. Tämä merkitsee sitä, että saman alueen eri soilla tiheydet vaihtelevat suuresti; poikkeavat alueet olivat säännön mukaan epätavallisen runsaslintuisia soita.

Myös lajimäärä kasvaa pohjoiseen (taulukko 2, kuva 1). Lajimäärää verrattiin sekä samankokoisista satunnaisnäytteistä (90 paria) että samoilta pinta-aloilta (1 km²). 90 parin näytteissä lajimäärä kasvaa pohjoiseen noin 0.9 lajia jokaista sataa kilometriä kohti. Neliökilometrin aloilla lajimäärä nousee pohjoiseen noin 1.3 lajia sataa kilometriä kohti.

Pohjois-Suomen suolinnuston yleiseen runsauteen vaikuttaa rimpinevojen lintutiheyksien kasvun ohella myös rimpinevojen suhteellisen osuuden selvä kasvu pohjoiseen.

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Appendix 1. The numbers of pairs observed on the flark fens censused. The fens have been grouped according to the 100-km zones shown in Fig. 1. Gull colonies are omitted.

Species	Zone							
	69	70	71	72	73	74	75	76
<i>Falco columbarius</i>	–	–	1	–	–	–	–	–
<i>F. peregrinus</i>	–	1	–	–	1	1	–	–
<i>Lagopus lagopus</i>	–	1	1	–	–	–	–	4
<i>Grus grus</i>	1	5	1	1	1	9	4	–
<i>Charadrius hiaticula</i>	–	–	–	–	–	4	5	2
<i>Pluvialis apricaria</i>	5	3	6	4	–	1	17	28
<i>Vanellus vanellus</i>	32	81	25	10	6	7	2	–
<i>Calidris temminckii</i>	–	–	–	–	–	–	1	1
<i>C. alpina</i>	–	–	–	–	–	–	–	9
<i>Limicola falcinellus</i>	1	6	3	3	3	14	85	1
<i>Philomachus pugnax</i>	58	78	15	11	9	82	178	22
<i>Lymnocyptes minimus</i>	–	4	–	1	2	10	31	3
<i>Gallinago gallinago</i>	16	39	11	2	6	63	58	16
<i>Limosa lapponica</i>	–	–	–	–	–	–	–	2
<i>Numenius phaeopus</i>	5	15	12	3	–	4	–	2
<i>N. arquata</i>	4	10	8	2	3	5	–	–
<i>Tringa erythropus</i>	–	1	5	3	5	63	29	12
<i>T. nebularia</i>	14	49	12	4	3	13	3	2
<i>T. glareola</i>	65	128	20	9	14	104	128	27
<i>Phalaropus lobatus</i>	–	–	–	–	–	64	23	10
<i>Stercorarius longicaudus</i>	–	–	–	–	–	–	–	4
<i>Larus minutus</i>	–	–	3	–	–	–	–	–
<i>L. ridibundus</i>	–	1	–	–	–	5	–	5
<i>L. canus</i>	–	–	8	–	–	1	–	2
<i>L. fuscus</i>	–	–	1	1	–	–	–	–
<i>L. argentatus</i>	1	11	–	–	1	–	–	–
<i>Sterna hirundo</i>	–	–	–	1	–	–	–	–
<i>S. paradisea</i>	–	–	–	–	–	14	–	11
<i>Asio flammeus</i>	–	–	–	–	–	–	–	1
<i>Alauda arvensis</i>	2	–	–	1	–	–	2	–
<i>Anthus trivialis</i>	1	–	–	–	–	3	–	–
<i>A. pratensis</i>	158	277	58	14	40	162	175	23
<i>A. cervinus</i>	–	–	–	–	–	–	17	1
<i>Motacilla flava</i>	83	185	29	24	37	183	191	37
<i>M. alba</i>	10	26	1	–	1	23	–	–
<i>Luscinia svecica</i>	–	–	–	–	–	10	49	35
<i>Saxicola rubetra</i>	4	5	4	–	–	1	–	–
<i>Turdus pilaris</i>	–	5	–	–	–	–	–	–
<i>T. iliacus</i>	–	–	–	–	–	11	8	1
<i>Acrocephalus schoenobaenus</i>	–	–	1	–	–	–	–	1
<i>Phylloscopus trochilus</i>	–	1	–	–	4	38	38	29
<i>Muscicapa striata</i>	1	–	–	–	1	–	–	–
<i>Fringilla coelebs</i>	–	–	–	–	–	2	–	–
<i>F. montifringilla</i>	–	–	1	–	1	2	–	–
<i>Carduelis flammea</i>	–	–	–	–	–	1	5	7
<i>Calcarius lapponicus</i>	–	–	–	–	–	–	15	62
<i>Emberiza citrinella</i>	–	–	–	–	–	2	–	–
<i>E. pusilla</i>	–	–	–	–	–	1	–	–
<i>E. schoeniclus</i>	–	2	12	3	3	49	64	1
Total	461	933	238	97	141	952	1128	362
Total area (km ²)	5.1	13.8	5.6	1.6	4.0	10.3	8.8	4.1