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## The effect of the woodland—open peatland edge on some peatland birds in South Finland.

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### Material and methods.

In an earlier paper (SAMMALISTO 1955) I have discussed the results of my bird censuses in South Finland, with particular reference to the so-called edge effect. The data, however, were at that time too meagre for a detailed study of the question; it could only be stated that remarkable differences exist between the commonest peatland birds in this respect. In 1955, the census was continued in the same area as 1954. The material in total consists of 42 bogs in the watershed zone of Suomenselkä, about lat. 63° N and long. 25° E, with a total area of 2100 hectares (8 square miles).

The peatlands of the study area belong to the so-called *open and waterlogged sedge bog complex type*. Each bog complex consists, as a rule, of several types of treeless bogs (neva). Especially characteristic of the study area are the *pale neva-bogs* (»rimpi» neva-bogs), consisting of firmer and mossier peat banks running perpendicular to the course of the water. This type of neva-bog I have classified (SAMMALISTO, op. cit.) together with the *tall-sedge neva-bogs* as »moist» (type A), whereas the *small-sedge neva-bogs* as well as the *Sphagnum fuscum neva-bogs* are »dry» (type B). The drier bogs in this particular peatland complex type are concentrated mainly in the border area between »moist» bogs and the surrounding woodlands. These woodlands are very often *pine peat-bogs*. (For a more detailed description of the Finnish peatland complex types and neva-bog types see AUER 1952 and KUJALA 1952.)

The census method was the conventional sample area method (PALMGREN 1930), in which an attempt is made to count all the breeding birds on a limited area. On neva-bogs the field of view is in general very wide, and therefore the census presents fewer technical difficulties than in woodlands, where many birds escape the watch-

ful eye or ear of the observer. Each neva-bog was therefore censused only once in a breeding season and no correction methods (PALMGREN, op. cit.) were used. However, some bogs censused in May cannot be directly compared with those studied later on, since of certain species the whole population had not yet reached the study area. In calculating the density values, therefore, the data available for these late-arriving species were about 10 per cent fewer than for those migrating earlier.

### The theory of edge effect.

GRINNEL, DIXON and LINSDALE (1930) seem to include in their system of ecologic factors the phenomenon later called edge effect, when they say: »... Physiographic relationships of the section with the surrounding territories, near and far, as affecting or modifying the other factors.» Similarly, SCHIERMANN (1930) points out that when studying the bird fauna of a certain area, one must take into account that possibly more birds breed at the periphery of a woodland district than at its centre. In the thirties, VAN DEVENTER (1936) and LAY (1938) were also aware of the phenomenon; the latter, for example, states that the number of birds in the woodland clearings was nearly twice as great as in the inner parts of the same woodlands. The exact formulation to the problem, however, has been given by BEECHER (1942), when he says: »... the population density of most birds... is proportional to the amount of edge area to unit of area.» According to him, the edge is effective only if its area reaches a certain threshold value. This being the case, the smaller the continuous area of a biotope, the greater the population density in it. Consequently, the density values calculated for different areas of the same biotope cannot be directly compared with each other. The smallest area of a biotope which shows edge effect is called by BEECHER the threshold area of edge effect, this being a unit of area, the threshold of edge effect being a relative value.

The edge effect thus includes the influence of the surroundings of the biotope area and the effect of the size of the biotope area. The significance of the edge has the same ecological basis, however, as the nature of biotopes in general. The concept of edge effect has arisen from the fact that quantitative animal ecology has its background in plant sociology: the intergradation zones between different vegetation types are edges in animal ecology.

Let us for simplicity's sake imagine a biotope characterized by one ecological factor ( $a$ ) only and another characterized by another factor ( $b$ ) only. The edge between these two biotopes can be of three different kinds: 1) No intergradation zone ( $O$ ), 2) a biotope differing from both  $a$  and  $b$  ( $c$ ), or 3) a mixture of  $a$  and  $b$  ( $ab$ ). Let us then imagine one species which demands factor  $a$  only (species  $a'$ ), another which likewise requires  $b$  only (species  $b'$ ), a third which demands both  $a$  and  $b$  (species  $a' b'$ ) and a fourth which requires factor  $c$  (species  $c'$ ). The species, then, inhabiting the different kinds of edges, are as follows:

Type of edge	O	c	ab
Species			
$a'$	—	—	+
$b'$	—	—	+
$a' b'$	+	—	+
$c'$	—	+	—

In the mixed type of edge there appears a phenomenon called by BARICK (1950) juxtaposition: species with different ecologic demands meet each other and the number of species is thus greater than in the surrounding, »pure», biotopes. On the contrary, »edge preference» is found in all three types of edge; either the species demands a mixture of ecological factors (in type  $O$  there is no actual edge, but the territory of an animal can consist of both biotopes, see PUTKONEN 1942 and MERIKALLIO 1946) or a »new» factor. Thus, there are only two kinds of edge preference, although edge preference appears on all three kinds of edge.

In evaluating the role of the edge effect, the size of the biotope area must be taken into account: one must eliminate those biotope areas which are suspected to be smaller than the threshold area of edge effect. This elimination is, of course, a matter of judgment, since no exact criteria are to be found for the estimation of the size of the threshold area of edge effect.

#### The appearance of the edge effect in the study area.

Regarding only four species are there sufficient data for a study of this kind in my material. Earlier (SAMMALISTO, op. cit.) I have already discussed three of them and found considerable differences

between these species. The following table shows the results of all censuses, except those concerning bogs on which the maximum distance to the nearest trees is under 100 m. (the threshold area of edge effect must be taken into account). The distance in question was about 400 m. on the greatest bog censused by me. This has been divided into eight equally broad zones, and the distance from the nearest trees in the following table increases from left to right. The values mean the number of pairs observed.

<i>Motacilla flava</i> .....	96	6	6	9	1	—	—	—
<i>Anthus pratensis</i> .....	52	44	29	11	10	2	2	—
<i>Saxicola rubetra</i> .....	26	1	—	—	—	—	—	—
<i>Tringa glareola</i> .....	18	16	9	2	1	—	—	—

When compared with the Meadow-pipit and the Wood-sandpiper, the Yellow Wagtail and the Whinchat show a strong edge preference, a fact already established in regard to the Yellow Wagtail by AUER (1916) and FINNILÄ (1915) and in regard to the Whinchat by KALELA (1938). Of the absolute edge preference these statistics reveal nothing, since the zones nearest to the edge are larger than those in the centre.

In seeking the reason for these differences, let us first see the density values of the species in question on different types of neva-bogs. In the following table, A means moist neva-bogs, B 2 *Sphagnum fuscum* neva-bogs and B 1 other dry neva-bogs (see page 81).

	A	B 1	B 2
<i>Motacilla flava</i> .....	5,2	1,9	12,8
<i>Anthus pratensis</i> .....	10,4	0,5	0,4
<i>Saxicola rubetra</i> .....	0,7	0,6	3,4
<i>Tringa glareola</i> .....	3,2	0,1	0,1

As mentioned on page 81, dry neva-bogs are concentrated in the edge zones of the peatland complex: in the two edge zones they represent 46 per cent of the total bog area, whereas in the six centre zones they form only 31 per cent. Therefore it is understandable that species which prefer dry neva-bogs, i.e. the Yellow Wagtail and the Whinchat, are more numerous in the edge zones than in the centre of the bog. The differences between the species, however, are so great that this cannot be the only explanation. In fact, I have previously (SAMMALISTO, op. cit.) suggested that the Yellow Wagtail and the Whinchat need high places for the proclamation of their

territories. The Meadow-pipit has a song flight and for this purpose needs no trees or other high places. SVÄRDSON (1949) assumes that they are needed for watching places; however, there seems to be no great tendency to use them as such in my study area. The Wood-sandpiper is somewhat intermediary between these two extreme types, as is seen later.

Earlier LACK and VENABLES (1939) have noted that the need for high places may be decisive in habitat selection, and KALELA (op. cit.) has also suggested this explanation for the concentration of the Whinchat in the edge zones of neva-bogs. Further evidence in favour of this interpretation is afforded by the distribution of the Yellow Wagtail on *Sphagnum fuscum* neva-bogs.

This type neva-bog occurs very frequently in the intergradation zone between neva-bog and pine peat-bog. Its typical feature is a more or less continuous *Sphagnum fuscum* cover, which is also typical of a great number of pine peat-bog types. Usually the *Sphagnum fuscum* neva-bogs are not entirely treeless: here and there one can see a small birch or pine. The number of trees is, of course, greatest in the zones nearest to the woodland edge; therefore some edge preference should be found, according to the interpretation mentioned above, even on *Sphagnum fuscum* neva-bogs.

The following table shows a comparison of the distribution of the Yellow Wagtails between neva-bogs which consist wholly or almost wholly of *Sphagnum fuscum* neva-bog and all the other neva-bog types studied. In an intraspecific comparison one must allow for the fact that the greatest possible distance to the nearest trees varies according to the size and form of the sample area. Therefore, each neva-bog must be separately divided into zones, the number of which is the same for all the bogs and then the values of representative zones can be added to each other. In the following table the distance from the nearest trees increases from left to right, as in all subsequent tables.

	Number of pairs			
<i>Sphagnum fuscum</i> neva-bogs	22	7	3	2
All the other neva-bogs	73	7	2	2

The difference is statistically significant ( $\chi^2 = 9.98$ ) and strongly suggest that on *Sphagnum fuscum* neva-bogs the Yellow Wagtail is less dependent on the woodland edge than on other types of neva-

bogs. The other possible explanation is that the greater concentration in the edge zone on these other types of neva-bogs is due to the fact that they are often surrounded by a narrow belt of *Sphagnum fuscum* neva-bog. I consider, however, that the density value on *Sphagnum fuscum* neva-bogs is not sufficiently great to explain so great a difference in edge preference as the statistics show. Nor is it likely that microclimatic factors are involved, since it is supposed that the intermediary form between *Motacilla flava flava* and *M. f. thunbergi* (which inhabits the neva-bogs of my study area) is fairly well adapted to the microclimatic conditions of neva-bogs (SAMMALISTO 1956). The Yellow Wagtail thus obviously favours *Sphagnum fuscum* neva-bogs because these offer the best combination of the required ecological factors, namely openness and high places. The Whinchat seems to be even more restricted to the edge than the Yellow Wagtail. In this case the reason may be that it cannot persist in the very unfavourable microclimatic conditions prevailing in the central parts of neva-bogs. This explanation is supported by the fact that I have only once seen the Whinchat on the edge of a wooded islet in the central parts of a neva-bog, whereas the Yellow Wagtail is very common in such places.

From the table on page 84 (top) we cannot decide whether the Meadow-pipit is dependent on trees or not: firstly, the areas of the zones are different, and secondly, the percentage of moist bog is different in different zones. Since the density on dry neva-bogs is minute, I have omitted them in the following comparison. The expected (= random) distribution is therefore calculated according to the area of moist neva-bog in each zone. Only the distance to the nearest continuous woodland has been measured, since the woodland islets are fairly evenly distributed and their influence cannot, therefore, essentially alter the result. The zones are 100 m. broad.

Area of moist neva-bog in hectares .....	441	289	163	68	8
Observed .....	65	56	22	15	—
Expected .....	72	48	27	11	—

The edge zone shows a lower density than the following zone towards the centre; the difference, however, is not significant ( $\chi^2 = 3.63$ ).

When judged from the table on page 84, (top) the distribution of the Wood-sandpiper seems to be rather similar to that of the Meadow-pipit. However, a more detailed analysis shows that the true state of affairs is not so. In the following table a similar comparison as above in the case of the Meadow-pipit is represented in regard to the Wood-sandpiper. Here, owing to meagreness of data, the zones are 200 m. broad.

Observed .....	42	3
Expected .....	35	10

The difference is significant ( $\chi^2 = 6.30$ ). The Wood-sandpiper seem to be not so dependent on the neighbourhood of the trees as the Yellow Wagtail; however, the following facts probably completely level out the difference: 1) In the case of the Wood-sandpiper the dependence on trees is greater than the above statistics show, since the wooded islets have been omitted, 2) the Wood-sandpiper favours areas of open water (SAMMALISTO 1955) which most frequently occur in the central parts of the bogs, and 3) the territory of the Wood-sandpiper is larger than that of the Yellow Wagtail. In all, it seems obvious that the Wood-sandpiper is dependent on trees. This is already suggested by GROTE (1939), who has noted that the species starts its song flight from the top of a tree.

#### The methodological importance of the edge effect in bird ecology.

SEISKARI (1954) has studied the birds of the neva-bogs in southernmost Finland, an area characterized by peatland complexes of the *raised bog* type (see AUER 1952). The density values calculated by him are based on a considerable body of data (2600 hectares of neva-bog) and comparison with my results thus seems justified. In regard to the species discussed above the comparison is as follows:

	Raised bogs	Suomenselkä
<i>Anthus pratensis</i> .....	7.7	6.7
<i>Motacilla flava</i> .....	3.5	5.6
<i>Saxicola rubetra</i> .....	0.4	1.1
<i>Tringa glareola</i> .....	0.7	1.8

The differences are almost entirely explained by methodological differences: I have always censused the whole neva-bog, whereas Seiskari (personal communication) has studied only certain parts

of each bog in such a way that proportionally more edge zone than central zone has been omitted. Only in regard to the Wood-sandpiper does a real difference probably exist, which is natural, because we are dealing with a northern species.

### Summary.

The concept of the so-called edge-effect has arisen from the fact that quantitative animal ecology has its background in plant sociology: the intergradation zones between vegetation types are edges in animal ecology. Edges can be mixtures of two biotopes. In this case there occurs a phenomenon called juxtaposition: the edge satisfies the demands of the species inhabiting the surrounding biotopes. Some species may prefer the edge zone, either because of the mixture of ecological factors or because the edge has a special edge vegetation.

On the neva-bogs studied in the Suomenselkä watershed, the Yellow Wagtail and the Whinchat are to a high degree bound to the neighbourhood of trees, since they must have at hand high places to proclaim their territory. The Meadow-pipit has a song flight and is thus in no need of such places. The song flight of the Wood-sandpiper is started from the top of a tree, and therefore the species is dependent on trees, although other ecological factors tend to obscure this condition.

The density values obtained for Suomenselkä differ considerably from those obtained by earlier workers for the raised bogs, but — except probably in regard to the Wood-sandpiper — this is obviously in part due to methodological differences. In comparisons concerning density and dominance values one must always take into account the proportion of edge to the total study area.

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### Selostus: Metsän ja nevan reunavyöhykkeen vaikutuksesta eräiden nevalintujen esiintymiseen Etelä-Suomessa.

Reunavaikutuksen käsite on saanut alkunsa siitä, että kvantitatiivisessa eläin-ekologiassa yleensä käytetään perustana kasvivyhdyskuntia: kasvillisuustyyppien vaihteluväyhykkeet ovat eläin-ekologiassa saaneet reunavyöhykkeen nimen. Reuna voi olla kahden kasvillisuustyyppin sekoittumisen tulos. Tällöin ilmenee ns. rinnakkainjoutumista: reuna tyydyttää molemmilla ympäröivillä biotoopeilla asustavien lajien elinpaikkavaatimukset. Toiset lajit taas suosivat reunavyöhykettä (reunansuositinta), joko ekologisten tekijäin sekoittumisen takia tai siksi että reunaan on muodostunut erikoinen reunakasvillisuus.

Suomenselän vedenjakajaseudun nevoilla keltavästäräkki ja pensastasku ovat suuressa määrin puiden läheisyydestä riippuvaisia, koska ne tarvitsevat pesimäpiirinsä ilmoittamiseen ympäristöä korkeamman paikan. Niittykirvisellä on laulento eikä se sen vuoksi tarvitse puita. Myös lirolla on laulento, mutta laji lähtee sille puun latvasta, joten se on riippuvainen puusta vaikka muiden ekologisten tekijäin vaikutus on omiaan peittämään tämän asiantilan. Tutkimuksissa saavutettujen tiheysarvojen erot Suomenselän soiden ja kohosoiden välillä johtunevat muiden e.m. lajien kuin liron osalta tutkimusmenetelmien erosta. Alueellisisa vertailuissa on aina otettava huomioon reuna-alan osuus koko tutkimus-alueesta.