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# Spatial pattern of nest-box occupancy in the Pied Flycatcher *Ficedula hypoleuca* in mountain birch forest

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The spatial pattern of nest-box occupancy of the Pied Flycatcher *Ficedula hypoleuca* was studied in a mountain birch forest in Finnish Lapland using a long-term data set (1967–1991) and spatial autocorrelation techniques (Moran's I and join-count statistic). The study plot consisted of 34 25 × 25 m quadrats with a nest-box in the centre of each quadrat. The plot was heterogeneous in habitat structure and showed evidence of clumping of like forest types (productive vs. unproductive forests). When data for all years were lumped and analysed together, no spatial autocorrelation in nesting area occupancy appeared, i.e. frequencies of pairs/quadrat were arranged at random over the study plot. Furthermore, productivity of the forest area near the nest site played only a minor role in the nest-box selection of the Pied Flycatcher. The results for the individual years indicated either a random or a regular pattern of nest distribution. The Stouffer combined test supported regularity. This result stresses the importance of intraspecific territoriality even in the far north where bird populations are relatively sparse. Regularity of spatial pattern was especially pronounced in high-density years.

## 1. Introduction

Birds in different habitats live under different selection pressures. Thus, differences in habitat selection within a species may lead to local differences in fitness (Partridge 1978). The suitability of a habitat can be estimated from nesting success. Habitat-linked differences in clutch size of the Pied Flycatcher *Ficedula hypoleuca* have been observed in several study areas in southern and central Europe (Järvinen 1989); and in an area in Russia, more nestling Pied Flycatchers died in coniferous than in deciduous forests (cited according to von Haartman 1971; for breeding-success differences between productive and unproductive forests, see Källander et al. 1987).

However, in northern mountain birch forests clutch size and number of fledglings per nest do not depend on habitat productivity (Järvinen 1980, Järvinen & Järvinen 1982), possibly because the populations are relatively sparse here and because any influence that the habitat might have on nesting success would be masked by the stronger influence of adverse weather.

Given the fact that there are no habitat-linked differences in the nesting success of the Pied

Flycatcher in the north, it may be predicted that there are also no clear-cut breeding-site preferences. In this study, based on data for 25 years, I test two hypotheses related to habitat selection of the Pied Flycatcher.

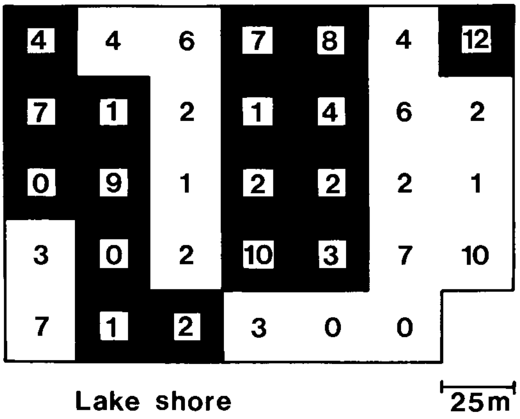
First, an important question: Is spatial autocorrelation in the frequency of breeding occurrences in mountain birch forest revealed by combined analysis of a long-term data set? Strong spatial autocorrelation would mean that values (e.g. frequencies of pairs/quadrat) located near each other are strongly related. If values are simply arranged at random over the map, there is no spatial autocorrelation. Due to environmental heterogeneity (differences in forest density, bush layer, productivity, proximity to a lake shore, etc.), all locations in an area might not be equally likely to receive a breeding Pied Flycatcher pair. This would mean that there are site preferences and thus spatial autocorrelation.

Secondly, since birds tend to be territorial during the breeding season, the spatial distribution of breeding pairs in any one year may be expected to be regular. Therefore, the occupancy of a breeding site by one Pied Flycatcher pair might repulse later-arriving Pied Flycatchers.

## 2. Study area, material and methods

The study was conducted in Kilpisjärvi, northern Finnish Lapland (69°N). The study area was a section of mountain birch forest divided into 34 25 × 25 m quadrats (Fig. 1), with a nest-box in the centre of each quadrat. All boxes were of the same type (entrance hole 32 mm), they faced towards the west or southwest and were 1.5–1.8 m above the ground. Every year boxes in poor condition were replaced with new ones. On one side the plot was bounded by the lake shore, at the other three sides by continuous birch forest (height of birches 5–7 m). Lake Kilpisjärvi consists of two large basins (14 and 23 km$^2$).

The classification of forests was based on a vegetation analysis (for details, see Kalela 1961). Within the plot there were patches of relatively productive and dense forest with herbs in the field layer (meso- and eutrophic forests of Kalela 1961), but also less productive sparse forest patches with shrubs in the field layer (oligo- and oligo-mesotrophic forests). Of the 34 quadrats 17 belonged to the productive and 17 to the unproductive forest type (Fig. 1).



|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 4 | 4 | 6 | 7 | 8 | 4 | 12 |
| 7 | 1 | 2 | 1 | 4 | 6 | 2 |
| 0 | 9 | 1 | 2 | 2 | 2 | 1 |
| 3 | 0 | 2 | 10 | 3 | 7 | 10 |
| 7 | 1 | 2 | 3 | 0 | 0 |  |

Fig. 1. A section of mountain birch forest in Kilpisjärvi, northern Finnish Lapland, divided into 34 25 x 25 m quadrats. Black quadrat = productive forest, white quadrat = unproductive forest. Nest-box in the centre of each quadrat. Numbers within quadrats denote total number of Pied Flycatcher nests in quadrats during 25 years(1967-1991). Moran's coefficient of spatial autocorrelation (I) = -0.100. Expected I for random pattern = -0.030; its standard deviation = 0.129. z score for null hypothesis "no spatial autocorrelation" = 0.532 (2-tailed P = 0.60).

From 1967 to 1991 (n = 25 years) 0–14 Pied Flycatcher pairs nested in the boxes annually. The peak egg-laying period was mid June. Although the plot was a part of a larger nest-box area in Kilpisjärvi (Järvinen 1980), the plot was spatially isolated from the other nest-box areas. In the larger area the number of breeding pairs varied annually between 8 and 57. Population fluctuations in the plot itself paralleled closely those of the larger area (Pearson's correlation coefficient, $r = 0.844$, $n = 25$, $P < 0.001$). Thus, the plot seemed to be a representative sample of the whole Pied Flycatcher population in Kilpisjärvi.

In addition to the 133 Pied Flycatcher pairs, a total of seven Siberian Tit *Parus cinctus* pairs nested in the plot in 1967–91 (maximum 1 pair/year). The occurrence of a few Siberian Tits, however, hardly affected the habitat selection of the Pied Flycatcher, especially because the Pied Flycatcher is a stronger competitor for nest-boxes than is the Siberian Tit (Järvinen 1982).

The distance between the boxes was about 25 m (Fig. 1). The birch trees were not thick enough to provide natural nest sites for the Pied Flycatcher. Since the distance between the nests could not be less than 25 m, distance methods of nest dispersion (e.g. the nearest-neighbour analysis) were not feasible for the analysis of spatial pattern.

I tested the long-term (1967–1991) spatial randomness of breeding-site selection using the I statistics developed by Moran (1950), an appropriate measure for areal data (Upton & Fingleton 1985), which tests the independence of the spatial proximity measure and the similarity measure. Moran's I is thus basically a spatially weighted Pearson's product-moment correlation coefficient. Contiguity of quadrats was defined as their having at least one edge in common (the so-called rook's case).

The calculated (observed) value of spatial autocorrelation (I) is compared with the set of all possible values I can take on, if the number of nestings / 25 × 25 m quadrats are repeatedly and randomly permuted over the set of quadrats. There are n! such values and the expected value of I, E(I), is given by: $E(I) = -[1/(n-1)]$. The difference between the observed and the expected values of I was tested by a normally distributed z statistic: $z = |I-E(I)|/SD$. The standard deviation (SD) of the expected I was derived using a formula in Upton & Fingleton (1985:171). If I is found to be significantly ($P < 0.05$) greater than E(I), the pattern of quadrat values displays positive autocorrelation, i.e. similar values are located near each other (z statistic positive). If I is significantly less than E(I), we have negative spatial autocorrelation (like values are close to unlike ones).

Randomness, clustering or regularity in the spatial distribution of the Pied Flycatcher nests was tested *annually* using the join-count statistic, which is based on the number of 'black' (occupied) and 'white' (unoccupied) quadrats in the study plot (Upton & Fingleton 1985; cf. Fig. 2 in this study). If like quadrats are clustered, there will be relatively few black/white joins; if they are dispersed (regularity), there will be relatively many black/white joins. The test statistic z is calculated in the same way as for the Moran's I test (positive z indicates dispersed pattern; negative z, clustered pattern).

Moran's I test was performed using the randomization option, and the join-count test using the non-free sampling option. When sample sizes are small, these options are a safer choice than the normality and free sampling options (Sokal & Oden 1978, Upton & Fingleton 1985).

When combining probabilities for the join-count tests for the individual years, I used the Stouffer method or the inverse normal test: the standard normal deviates (z scores) associated with the probability values (Ps) are added and divided by the square root of the number of years being combined (Hedges & Olkin 1985). Years were considered only when the number of pairs in the plot was at least four ($n = 18$).

## 3. Results

In Fig. 1 the spatial distribution of productive and unproductive birch forest quadrats is shown together with figures for the number of Pied Flycatcher nests in each nest-box in the centre of each quadrat in 1967–1991. There was a tendency for clustering of like forest types in the study plot (Fig. 1; join-count test, $z = 1.881$, 2-tailed $P = 0.060$).

During the 25 years four quadrats of the 34 did not accommodate a single Pied Flycatcher nest, and three quadrats contain 10–12 nests (Fig. 1). However, in the long-term data set there was no evidence of spatial autocorrelation in the observed arrangement of nestings/quadrat; i.e. the pattern of quadrat values over the map was random (Fig. 1; Moran's $I = 0.100$, 2-tailed $P = 0.60$). In addition, there was no selection of productive quadrats over unproductive ones: in 1967–1991 73 nests were in productive and 60 in unproductive quadrats ($\chi^2 = 1.51$, $df = 1$, $P = 0.22$; cf. Fig. 1).

Results of the join-count tests for the individual years appear in Table 1. Fig. 2 shows the distribution of occupied quadrats in 1970 and the analysis of the data for that year. The year 1970 was the only year in which spatial distribution of the Pied Flycatcher nests deviated significantly from randomness ($P = 0.046$).

For several years the number of nests in the plot was low, and, although the observations for the different years are independent, it was not feasible to attach probability values to the individual z scores. However, if the sign of the z scores is considered, plusses (17) clearly outnumbered minuses (7), suggesting a regular (dispersed) rather than a clustered pattern (binomial test, $P = 0.021$). The Stouffer combined test for the years ($n = 18$) involving at least four nests confirmed this ($z = 2.794$, $P = 0.005$).

The spatial pattern of the Pied Flycatcher nests seemed to be related to population density in the plot: regularity was most pronounced in high-density years (Spearman's rank correlation coefficient, $r_s = 0.514$, $n = 24$, $P = 0.010$).

## 4. Discussion

The Pied Flycatcher is a regular migrant to Scandinavia. On average, male Pied Flycatchers arrive at the breeding grounds a week before the females. Each male occupies a small territory consisting of one or several nest holes, which are demonstrated to visiting females. If a prospecting female accepts a box offered, breeding will begin soon. Usually the female lays her first egg within 5–10 days of arrival (Alatalo & Lundberg 1984).

Nest-site quality seems to be of prime importance in the nest-site selection of female Pied Flycatchers (Alatalo et al. 1986). The importance of male quality is smaller in magnitude and is probably observed only in homogeneous habitats (Lifjeld & Slagsvold 1988). In the present study the nest-boxes were of the same quality. Male quality was not studied, and because the habitat was heterogeneous, any effects of male quality on habitat selection were possibly masked by the stronger effects of habitat quality.

According to Moran's I test, when the data for all years were lumped and analysed together, no significant spatial autocorrelation appeared in the pattern of Pied Flycatcher nesting area occupancy, i.e. similar or dissimilar values/quadrat were not situated near each other (Fig. 1). Productivity of the forest area near the nest site also played a minor role in the habitat selection of the Pied Flycather in northern Lapland.

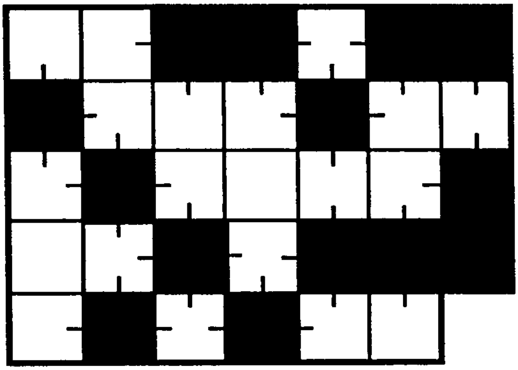


Fig. 2. Fourteen Pied Flycatcher nests in study plot 1970. Black quadrat = occupied, white quadrat = unoccupied. Black/white joins (35) marked with strokes. Expected number of black/white joins for random pattern 27.95 and standard deviation 3.54. Null hypothesis of spatial randomness rejected in favour of dispersed pattern (z score = 1.992, 2-tailed P = 0.046).

Table 1. Joins-count tests for individual years (1967-1991; z scores) and number of Pied Flycatcher nests within study plot (see Fig. 1).

| Year | z score | No. of pairs |
|---|---|---|
| 1967 | +0.582 | 4 |
| 1968 | – | 0 |
| 1969 | –0.233 | 5 |
| 1970 | +1.992 | 14 |
| 1971 | +0.014 | 10 |
| 1972 | +0.100 | 6 |
| 1973 | +0.582 | 4 |
| 1974 | +0.787 | 12 |
| 1975 | +0.971 | 6 |
| 1976 | +0.497 | 3 |
| 1977 | –0.353 | 2 |
| 1978 | –1.262 | 2 |
| 1979 | +0.258 | 5 |
| 1980 | +1.545 | 8 |
| 1981 | +1.153 | 4 |
| 1982 | –0.353 | 2 |
| 1983 | –0.889 | 3 |
| 1984 | +0.536 | 6 |
| 1985 | –1.214 | 5 |
| 1986 | +0.971 | 6 |
| 1987 | +0.451 | 8 |
| 1988 | –0.196 | 3 |
| 1989 | +1.153 | 4 |
| 1990 | +1.240 | 5 |
| 1991 | +0.971 | 6 |

No forest area is completely homogeneous, but is a mosaic of patches with different physiognomy and plant species composition. Hence we would expect to find varying numbers of bird nests in different parts of a forest area. Despite the fact that the mountain birch forest in the study plot was not homogeneous and showed evidence of clumping of like forest types, the spatial pattern of Pied Flycatcher nests was not clumped in any one year but either random or regular (Table 1, Fig. 2). The binomial test and the Stouffer combined test for the years with at least four nests suggested a regular pattern (see Results).

Regularity means that occupied quadrats are spaced out more than would be expected from random occupation of the available quadrats. This result stresses the importance of intraspecific territorial behaviour in shaping the structure of a bird community even in the north where populations are relatively sparse. The Pied Flycatcher is a territorial species, but its aggressiveness is restricted to the vicinity of the nest-hole (v. Haartman 1956). According to my observations, Pied Flycatchers also forage outside the 25x25 m area around the nest-box, but, at least during the nestling period, they obtain a considerable amount of their food near the nest-box.

The density of Pied Flycatchers in the plot followed that of the larger study area. When the number of breeding pairs rose, fewer empty boxes were available both in the plot and elsewhere. In high-density years regularity of spatial pattern was more pronounced than in low-density years. This may reflect the fact that when the number of nests/area increases there is less free space for foraging and other activities, and under such conditions birds are more territorial than in low-density years in trying to secure their "own" area for themselves.

From 1967 to 1991 four quadrats did not receive a single Pied Flycatcher nest, and two of these quadrats were situated near the lake shore (Fig. 1). Järvinen (1984) showed that in the Pied Flycatcher population if the date of laying is late at Kilpisjärvi, birds avoid the icy shoreline. Further away from the shore seasonal processes (plant growth) are ahead of those near the shore. In "late" seasons, habitats near the shore lag behind the other habitats more than in "early" seasons. However, near the shore the number of fledglings per nest is about the same as further away (Järvinen 1982). Probably due to swarming insects, success in the later stages of breeding seem to compensate near the shore for the late start of breeding and relatively small clutches (Järvinen 1982).

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## Selostus: **Asuttujen kirjosieponpönttöjen tilajärjestys tunturikoivikossa**

Asuttujen kirjosieponpönttöjen tilajärjestystä tutkittiin Kilpisjärven tunturikoivikossa 25 vuoden aineiston ja spatiaalisten autokorrelaatiomenetelmien avulla. Tutkimusalue koostui 34 25 × 25 m ruudusta, joiden keskustassa oli linnunpönttö. Ruudut jaettiin kahteen kasvillisuustyyppiin, karuihin ja reheviin koivikoihin. Kun kaikkien vuosien aineisto yhdistettiin, ruutujen asutustiheydessä ei havaittu merkitsevää autokorrelaatiota eli tiheysarvot/ruutu olivat tutkimusalueella satunnaisesti (Kuva 1). Myöskään ruudun kasvillisuustyypillä ei ollut vaikutusta siepon pesäpöntön valintaan. Yksittäisinä vuosina asuttujen pesien sijainti viittasi joko satunnaiseen tai satunnaista tasavälisempään tilajärjestykseen (Taul. 1, kuva 2). Ns. Stoufferin yhdistelmätesti puhui tasavälisyyden puolesta. Pohjois-Suomen suhteellisen harvoissakin sieppopopulaatioissa voi siis esiintyä territoriaalisuutta erityisesti runsaan pesimäkannan vuosina.

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