

Nest distribution of the Pied Flycatcher *Ficedula hypoleuca* in an area saturated with nest-boxes

Juha Tiainen, Pertti Saurola & Tapio Solonen

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The spatial distribution of nests of the Pied Flycatcher *Ficedula hypoleuca* was studied in a 23-ha forest area in southern Finland in 1969-1983. The study area was supplied with about 500 nest-boxes.

The number of nests varied between 28 and 93. The distribution broadened with increasing population size, but at the same time the density also increased in areas already occupied; the distribution was broader than expected on a random basis. Density-dependent processes, most probably territoriality, restricted clumping at short distances, but on a larger scale the distribution was aggregated.

Population size declined significantly in four subareas from 1969-1976 to 1977-1983, but not in one subarea. At the same time density relations between the subareas changed so that differences between subareas were diminished. There were also less differences in the variabilities of population sizes in different subareas in the latter half of the study period than in the first half. These changes were assigned to differential habitat development and changes in attractiveness of subareas for the Pied Flycatcher (changes in the illumination and spruce density).

Juha Tiainen and Tapio Solonen, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10.

Pertti Saurola, Zoological Museum, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland.

1. Introduction

Male Pied Flycatchers *Ficedula hypoleuca* are territorial, but they defend only small territories around the nest-hole (von Haartman 1956). This leads to a non-random distribution of nests in areas with very high densities of nest-boxes so that occupied boxes tend to be surrounded by empty boxes (Tompa 1967, von Haartman 1972, Alatalo et al. 1983). Normally, the population density is not limited by space, but by the availability of suitable nest sites. At very high densities, the territory size also becomes restrictive (Tompa 1967, von Haartman 1972).

Many Pied Flycatcher males are polygynous (von Haartman 1951, Alatalo et al. 1981, Alatalo & Lundberg 1984). Most males establish new territories when their first mates start laying, but not all males are successful in gaining secondary females (von Haartman 1956, Alatalo & Lund-

berg 1984). Thus, the number of nests corresponds with the number of territories but not with the number of males.

Females select mates. They assess the quality of the male's territory, including the nest-site (von Haartman 1956). The quality of the territory a male is able to acquire depends on his status in the population, which is largely determined by his body size (Lundberg et al. 1981).

These behavioural traits imply that the distribution of nests tells more about site selection by females than by males. In the densest populations, hostility between females (von Haartman 1956) might affect their distribution. This is supported by the fact that females that start nesting later are found in poorer habitats than the early females.

In this paper, we examine the spatial distribution of nests of the Pied Flycatcher in a 23-ha forest area in southern Finland in 1969-1983.

Our study area is supplied with an excess of nest-boxes which the birds accepted without exception as far as we know. The total number of nests was 854 and varied annually between 28 and 93.

We pose the following questions: (1) Does the spatial distribution of nests vary with varying population size? (2) Is the pattern of occupation of the area different in different years?

2. Material and methods

The study was performed at Lammi Biological Station (61° 03' N, 25° 03' E). The study area consists of luxuriant deciduous and mixed forests on fertile soil with smaller amounts of almost pure spruce forest. The amount of edges between forest and open areas is considerable (ca. 2 km). A more detailed description of the study area can be found in Tiainen (1983).

The total number of nest-boxes in our study area was about 500, about 400 of which were of the small size preferred by the Pied Flycatcher. The rest were larger (so-called Starling size) and were only used occasionally. Roughly 350 of the small boxes were available for flycatchers each year, others being occupied by tits *Parus* spp., or in bad condition.

Each nest-box was exactly located on a topographic map with a 50 m grid. The total number of the 0.25-ha squares in the area was 91 (some of them only partly forest). In the grid of 100 × 100 m, the number of squares was 31.

3. Results

3.1. Spatial patterns

Of the 91 0.25-ha squares, 81 contained at least three nest-boxes and 70 at least four nest-boxes; 68 squares contained at least three small boxes (Table 1). There were never more than four nests in a square, but this, and even three nests, was a rare occurrence (Table 2). Most squares with few boxes were situated in habitats which are not much preferred by the Pied Flycatcher. Consequently, during 14 years there were only 22 cases out of 1274 where the single box or both the boxes of a square were occupied by Pied Flycatchers; ten of these cases come from a single square with only one box. In two cases only, no boxes were available in a square for the Pied Flycatcher because the boxes were occupied by tits when the flycatchers arrived.

Thus, it seems to us that the availability of nest-boxes did not affect the distribution of nests much.

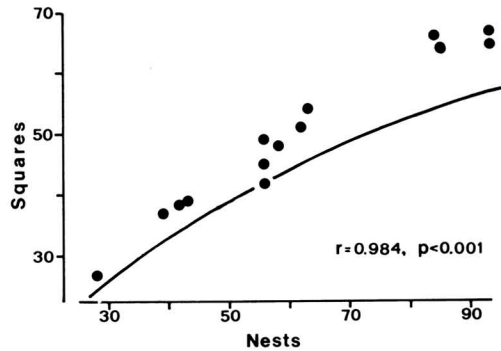


Fig. 1. Relationship between the number of 0.25-ha squares occupied and the number of nests of the Pied Flycatcher during 14 years. Coefficient of linear correlation shown. The continuous line shows the expectation if occupation of squares were a random process.

Table 1. Distribution of 0.25-ha squares with different numbers of nest-boxes. Small boxes with an opening of 32 mm (diameter) are preferred by the Pied Flycatcher. Total of boxes include also those of the so-called Starling size (50 mm diameter opening).

Boxes	Number of boxes/square												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Small	5	18	20	17	14	9	2	5	1	0	1	0	0
Total	1	9	11	13	26	14	4	6	3	3	2	0	1

Table 2. Annual distribution of squares with 1-4 Pied Flycatcher nests (four was the maximum).

Year	Nests/square				Total number of nests
	1	2	3	4	
1969	40	6	2	0	58
1970	-	-	-	-	?
1971	40	20	3	1	93
1972	46	15	3	0	85
1973	57	10	1	1	84
1974	46	16	5	0	93
1975	29	12	1	0	56
1976	42	7	0	0	56
1977	36	3	0	0	42
1978	26	1	0	0	28
1979	35	2	0	0	39
1980	35	4	0	0	43
1981	40	11	0	0	62
1982	46	7	1	0	63
1983	35	9	1	0	56
Total	553	123	17	2	858

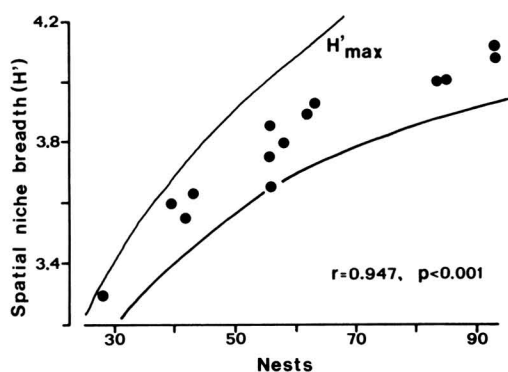


Fig. 2. Relationship between the breadth of distribution and the number of nests during 14 years. The breadth was calculated with the Shannon index ($H' = -\sum p_i \ln p_i$) from the proportion p of the i th square of each year's total population (coefficient of linear correlation shown). The upper curve shows the maximum if each nest were in a different 0.25-ha square. The lower curve shows the expectation if the nests were randomly distributed.

Table 3. Number of years with different distributions of nests of the Pied Flycatcher when the study area was divided into units of different sizes.

Division of the area	N	Pattern of distribution		
		Even	Random	Aggregated
Squares of 0.25 ha	91	11	3	0
Squares of 1 ha	31	2	12	0
Subareas of 4-5 ha	5	0	6	8

The distribution of Pied Flycatcher nests, measured as the number of 0.25-ha squares occupied, broadened quite linearly with increasing population size (Fig. 1). This increase paralleled the statistically expected increase predicted from the Poisson distribution, but at all densities the Pied Flycatchers tended to use a greater number of squares than expected on the basis of a random distribution. The breadth of distribution or usage of the area by the whole population also increased almost linearly with increasing population size (Fig. 2). The number of squares with more than one nest increased as well which resulted in an increasing difference between the observed breadth of distribution and its theoretical maximum. On the other hand, the distribution was broader than expected if the nests had been distributed randomly (Fig. 2).

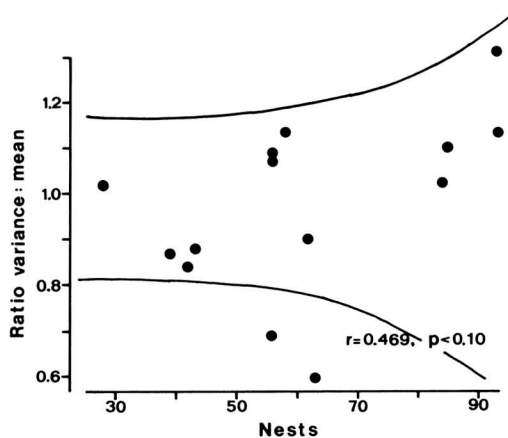


Fig. 3. Relationship between the ratio of variance to mean number of nests in 1-ha squares and the total number of nests during 14 years (coefficient of linear correlation shown). The distribution was never significantly aggregated ($s^2 > \bar{x}$), but was regular in two years ($s^2 < \bar{x}$; the lines show 95% confidence limits for $s^2 = \bar{x}$).

The spatial variation of density, measured by the coefficient of variation (SD/\bar{x}) in 1-ha squares, decreased with increasing density because squares uninhabited at lower densities were filled up.

We next examined the spatial pattern of distribution using the annual ratios of variance to mean number of nests per square. In 1-ha squares the annual mean density varied between 0.90 and 3.00 nests/square. The distribution was random (the variance and mean did not differ significantly) in all years but two, when it was even (Fig. 3). The ratio increased significantly with an increasing number of nests, although the variation was large. The pattern of distribution was not random on all scales, however. When the spatial unit was small (0.25 ha), the distribution was mostly even; and when the spatial unit was large (4-5 ha), the distribution was mostly aggregated (Table 3).

The above analyses showed that the distribution of nests depended on population size but was not random. However, they do not reveal whether there are any density-dependent processes behind the pattern of distribution. Taylor et al. (1978, 1980) have shown that the relationship between spatial variance and mean population density fits the power function in hundreds of animal species of many different

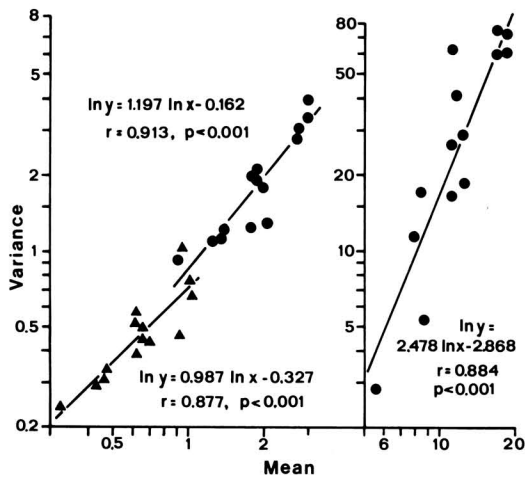


Fig. 4. Dependence of variance to mean number of nests during 14 years. The regression coefficient was less than 2, when squares of 0.25 ha (triangles) or 1 ha (dots left) were used as areal units, showing density dependence, but not when the five Subareas A-E (4–5 ha; right) were used.

taxa, among them more than 100 bird species (Taylor's power law; Taylor 1961). Hanski (1982) showed that the exponent of the power function, or the regression coefficient in the log-transformed form of the function, takes the value 2 if the distribution is density-independent and values < 2 if the distribution is density-dependent.

The relationship of the variance to the mean number of nests per square depended on the scale. In grids of 0.25 and 1 ha, the regression coefficient was < 2 (Fig. 4). This indicates density-dependence: with increasing population size nests get more widely distributed and the density in aggregations does not grow freely. However, the regression coefficient did not deviate significantly from 2 when areas of 4–5 ha were used (Fig. 4), which indicates that the aggregations were located independently of each other.

3.2. Temporal patterns

Next we examined the similarity of distributions in the 0.25 ha squares in different years. Pairwise indices of percentage similarity ($PS_{jk} = \sum \min(p_{ij}, p_{ik})$ where p is the proportion of nests in a square i in years j and k ; see e.g. Hurlbert 1978)

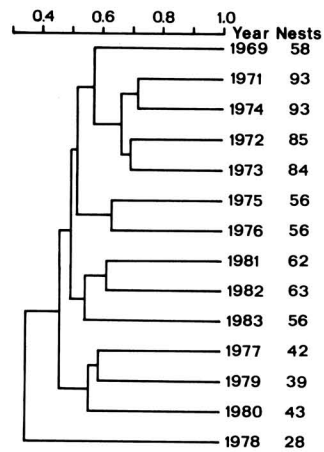


Fig. 5. Similarity of annual distributions of nests in 0.25-ha squares. Years with similar numbers of nests were largely grouped together with few exceptions.

were calculated and the resulting matrix was subjected to a cluster analysis (the simple group average method explained by, e.g., Cody (1974) was used).

The years were grouped almost in a chronological order, each cluster consisting of successive years (exception: 1978; Fig. 5). This result suggests that the study area has changed because of succession of the vegetation to such an extent that this has had an impact on the Pied Flycatcher. However, years with similar population sizes were also largely grouped together which suggests that the whole analysis is sensitive to population size.

The former alternative was further examined by dividing the study area into five subareas and looking at population trends in each of them separately. The division of subareas was fairly natural so that each of them was more or less uniform in habitat type and also different from the others.

Population size was significantly larger in 1969–1976 than in 1977–1983 as were the subpopulations in four subareas. In Subarea A, however, the number of nests did not change significantly (Table 4, Fig. 6). Mean density was much more variable between subareas in 1969–1976 than in 1977–1983. In the first period, the low density in Subarea D was more variable from

Table 4. Number and density of nests of the Pied Flycatcher in different subareas during the first and second half of the study period, respectively. Differences in population sizes and variabilities (*CV* in %) were tested with *t*-test and *F*-test, respectively. In 1969–1976, the population size in Subarea D was more variable than that in B, C, or E, and in A more variable than in B, and in 1977–1983 in C less variable than in other subareas ($P < 0.05$).

Sub-area	Area (ha)	1969–1976				1977–1983				Tests			
		Mean	<i>SD</i>	<i>CV</i>	Pairs/ha	Mean	<i>SD</i>	<i>CV</i>	Pairs/ha	<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>
A	4	9.3	3.40	36.6	2.32	10.9	4.89	44.9	2.72	0.53	NS	1.50	NS
B	5	21.4	4.86	22.7	4.28	11.6	3.41	29.4	2.32	4.81	***	1.68	NS
C	4	10.3	2.84	27.6	2.57	6.0	0.88	14.7	1.50	2.73	*	3.53	*
D	5	12.6	6.04	48.1	2.52	7.4	2.85	38.3	1.48	2.06	o	1.58	NS
E	5	21.4	6.17	28.8	4.28	11.7	4.57	39.0	2.34	3.34	**	1.83	NS
Total	23	74.7	18.81	25.2	3.25	47.6	14.12	29.7	2.07	3.05	**	1.39	NS

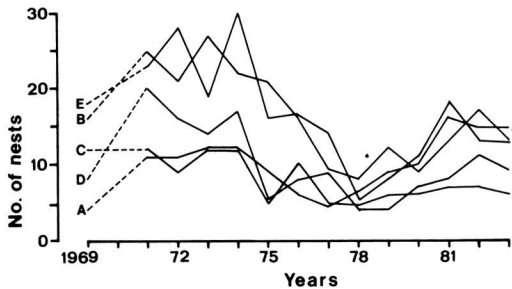


Fig. 6. Annual variation of the number of nests in the five Subareas A–E. Data of 1970 were incomplete and omitted. There was a significant decline in the number of nests in Subareas B–E from 1969–1976 to 1977–1983, but not in Subarea A.

one year to another than was the density in other subareas; also, density in Subarea A was quite variable. Only in Subarea C did variability of density decrease from the first period to the second; at the same time the density became less variable than in other subareas.

4. Discussion

Territoriality of the Pied Flycatcher has a different expression from most other passerine bird species. As nest-sites are the most limiting resource for this species, and suitable sites are normally sparse, the Pied Flycatcher has evolved to defend small territories just around the nest-site (von Haartman 1956, 1972).

Our results can be interpreted from this basis; territoriality acts as a spacing mechanism at small distances but Pied Flycatchers tend to clump together over larger areas. Consistent with

this idea, (1) the number of small squares occupied was higher than expected on a random basis (Fig. 1); (2) the whole area was used more broadly than expected on a random basis, though not maximally (Fig. 2); (3) even though the variance-to-mean ratios were usually approximately 1, indicating randomness, the ratio nevertheless tended ($P < 0.1$) towards low values when population size was small, indicating an even dispersion pattern; and (4) the distribution was even and the number of nests density-dependent in small spatial units, but aggregated and density-independent in larger units (Fig. 4, Table 4). Alatalo et al. (1983) experimentally demonstrated that Pied Flycatcher males searching for territories orient themselves towards already singing males and settle down in their vicinity if nest-sites are available.

To understand the possible role of territoriality in the overall nest distribution and different density trends in the Subareas A–E (Table 4), differences in the development of vegetation must be known. Subarea A has been kept quite similar throughout the study years. In Subareas B, C, E, and half of D, the development of vegetation has been natural (except that seedlings of spruce have been removed from B) and the forest has become more closed and darker. Spruce is common in Subarea C and is the main tree species in much of its area. Half of Subarea D is almost pure spruce forest which was dense until thinning in 1977; spruce is also common elsewhere in the area. Subareas A, B, and E are mainly dominated by deciduous trees.

The results in Table 4 can now be interpreted as follows. In 1969–1976, Subareas B and E were probably most attractive for the Pied Flycatcher,

as the densities were highest. The variability of density was low probably because of the damping effect of territoriality. Subarea D was marginal; density was low and variability high. In 1977-1983, Subareas A, B, and E were of equal value for the Pied Flycatcher (or perhaps B was most attractive; variability was somewhat lower there than in other subareas, probably indicating some territorial effect). The population had now probably declined so much that territoriality did not affect the distribution as much as it had before, as there is no such consistency in the variabilities. The low variability of Subarea C remains unexplained.

The differences between Subareas A-E demonstrate the necessity of including several

habitats in studies of the dynamics of local populations. Results from single sites may not be representative because of spatial heterogeneity and because patterns in different habitats may differ depending on the study year (cf. Tiainen 1983). In other words, spatio-temporal scaling problems must be seriously considered in studies of population dynamics (Wiens 1981).

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