

Effects of the Introduction of Pied Flycatchers *Ficedula hypoleuca* on the Composition of a Passerine Bird Community

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A nest-box experiment was carried out in rich subalpine birch forests, Swedish Lapland. During a six-year period the passerine bird density in an area (23 hectares) with a surplus of nest-boxes was compared with the density in a control area (29 hectares) without boxes. A large number of the nest-boxes were occupied by one species, the Pied Flycatcher, increasing the bird density in the nest-box area by about 75 per cent. This immigration of the flycatcher did not cause a demonstrable change in the population numbers of the other species. The year to year fluctuations of the flycatcher numbers were in accord with the fluctuations of the other species taken together in the same area and also with the fluctuations of the bird numbers in the control area. The result of this investigation is compared with that of a similar experiment in Southern Sweden.

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INTRODUCTION

It has repeatedly been demonstrated that the introduction of nest-boxes into a forest habitat is followed by an increase in the density of the breeding bird community caused by an immigration of hole-nesting species. In north-European habitats the nest-boxes are occupied mainly by the Pied Flycatcher *Ficedula hypoleuca* and the Great Tit *Parus major* (e.g. von Haartman 1951, Pfeifer 1955, Bruns 1956, Campbell 1968). The rise in the density of the hole-nesting species is often of considerable magnitude. This offers an opportunity to investigate whether the experimentally increased density of one species group, the hole-nesting species, will be followed by a change in the density of the other species in the same area. In other words, the study might involve a test of possible interspecific interactions or interference between the mentioned species groups.

This aspect was considered when the nest-box experiments were incorporated in the long-term ecological studies on the bird community of the subalpine birch forests in Swedish Lapland (Enemar 1966a). The results are presented in this report.

METHODS

The nest-box experiments were carried out at Ammarnäs (65° 58'N, 16° 13'E), Swedish Lapland, in rich subalpine birch forests. Five study plots were established in this area, the first ones in 1963. In 1965 two of the plots were supplied with nest-boxes, plot A5 with 33 and plot A6 with 53 boxes. In 1966 the nest-box numbers were increased to 45 and 76, respectively, and an additional number of nest-boxes were put up outside the same study plots, within about 30 metres from the boundary of the plots. In that way, during the period of

1966 to 1970, the bird community of a total area of 28.9 hectares without nest-boxes could be compared with the community of 23.3 hectares with a large number of nest-boxes.

The size of the stationary populations of most passerine species in the study plots, i.e. the number of permanently maintained territories, was estimated by mapping (Enemar 1959). The number of the breeding pairs of the thrush species was determined by nest counts. A nest-box was considered as corresponding to a breeding Pied Flycatcher when it was occupied by a breeding female for at least one week.

THE BIRD COMMUNITY STUDIED AND ITS HOLE-NESTING SPECIES

The mean density of the bird community for the period 1963–1970 was about 350 stationary males (territories) per square kilometre according to the results of the mapping in study plots. The density fluctuated between years from less than 300 to approx. 450 stationary males per square kilometre.

The composition of the passerine bird community and the average density (pooled values) of the different species are shown in Fig. 1. The fifteen species presented constitute nearly 99 per cent of the whole stationary community. The Willow Warbler *Phylloscopus trochilus* is by far the most common species, making up more than one third of the community. The remaining species are represented by low proportional values (less than 10 per cent), and eight of them have values of about 5 per cent. Two hole-nesting species, the Redstart *Phoenicurus phoenicurus* and the Pied Flycatcher *Ficedula hypoleuca*, belong to this group. The third hole-nesting species, the Willow Tit *Parus montanus*, is regularly but sparsely occurring in this habitat and has a proportional value of less than 2 per cent.

The only hole-nesting species which is of interest in this context is the Pied Flycatcher. As in more southerly habitats its density could be remarkably increased with the aid of nest-boxes in this northern birch woods near the timber line (cf. Meidell 1961). The species

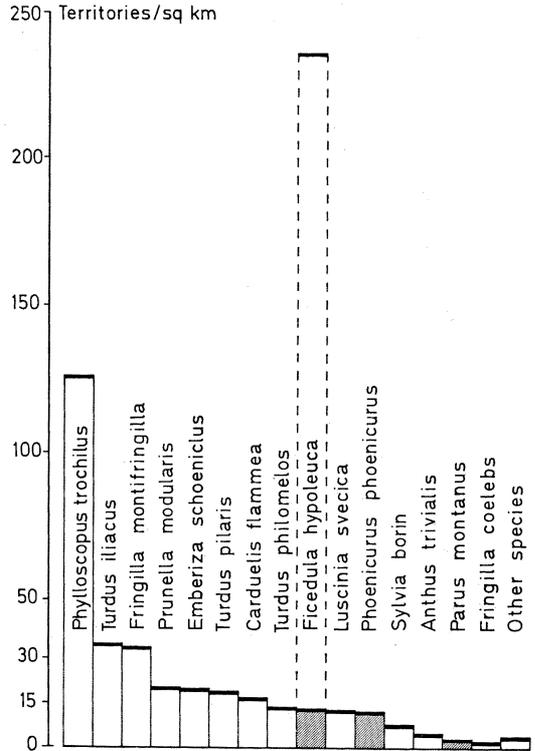


Fig. 1. Diagram showing the densities of the different species in the passerine bird community of the study plots in the rich subalpine birch forest at Ammarnäs, Swedish Lapland (means for the period 1963–1970). The hole-nesting species are represented by hatched columns. The long column (with broken lines) for the Pied Flycatcher *Ficedula hypoleuca* shows the mean density in the nest-box plots (mean for the period 1965–1970).

normally constitutes less than 5 per cent of the community. This figure was calculated from the extensive field material gathered during the line transects, which have been carried out in the same habitat yearly since 1963 (Enemar & Sjöstrand 1967).

The Redstart also used the nest-boxes, but only in very limited numbers. The Willow Tit entirely refused to breed in the boxes.

RESULTS

The nest-boxes were occupied to a large extent by the Pied Flycatcher as early as the first nest-box year, 1965 (Hanson et al. 1966). This immigration caused a considerable rise in the

total number of birds inhabiting the two study plots. The average density of the flycatcher during the period 1965–70 rose to a level far above that of the Willow Warbler (Fig. 1) and remained high throughout the period, although there were fluctuations between seasons (Table I).

The contents of Fig. 2 indicate that the immigration of the Pied Flycatcher was not followed by a consistent trend in the change

of the total number of the other species populations. To investigate this more accurately a comparison has to be made with the population fluctuations in the box-free study plots. This comparison is also presented in Fig. 2. It shows the density fluctuations of the Pied Flycatcher, and of the total passerine bird community except the Pied Flycatcher for the three box-free plots on the one hand and for the two nest-box plots on the other. The figure

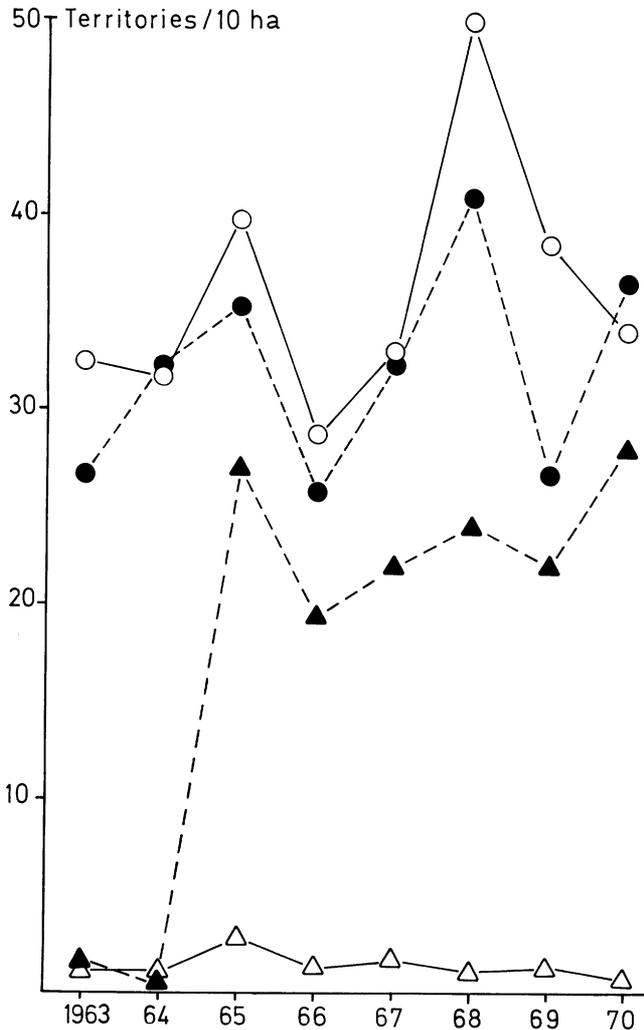


Fig. 2. Density fluctuations of different categories of birds in the study plots during the period 1963–1970.

○ Pooled densities of passerine birds except Pied Flycatcher in three study plots without nest-boxes. Total area 28.9 hectares.

△ The same for Pied Flycatcher.

● Pooled densities of passerine birds except Pied Flycatcher in two study plots with a surplus of nestboxes from 1965. Total area 23.3 hectares.

▲ The same for Pied Flycatcher.

material of these fluctuation curves is presented in Table I and has been treated as follows.

If the induced invasion of the Pied Flycatcher (PF) affects the abundance of other species, this may be revealed through observable differences between plots supplied with nest-boxes and those without in their patterns of density-fluctuations and/or average densities for the period concerned.

To evaluate the degree of association of density-patterns, the passerines except Pied Flycatcher (PePF) were grouped each year (1966–1970) according to whether they belonged to box-plots or not. The log likelihood ratio test (G-test, Sokal & Rohlf 1969) was used to test whether the observed frequencies varied independently of year of sampling. It resulted in a G-value = 4.94, $df = 4$, and $P \simeq 0.20$. As the proportion of PePF in the box-plots did not change significantly during the years of study, whereas the total number of PePF did (143 to 239 pairs), we are justified in concluding that the patterns of fluctuation were not different in the two types of plots.

The same test was performed on the numbers of Pied Flycatcher in box-plots as proportions of all passerines in the same plots during the years 1965–1970. We obtained $G = 2.35$, $df = 5$, $P > 0.50$. This does not permit us to reject the hypothesis stating that frequencies of PF are independent of sampling year. Again, as the proportion of PF is reasonably constant while the total numbers of birds are fluctuating, we regard the patterns of fluctuation of PF and of PePF as equal.

The differences in average density of PePF between plots were considered by applying two non-parametric, distribution-free tests. This type of test was chosen because we judged that the assumptions for relevant parametric tests were not supported by the material.

The Kruskal-Wallis test for difference of location in ranked data grouped by single classification (Sokal & Rohlf op. cit.) was worked out with the density-values arranged in 5 groups (plots). Of these, 4 yielded 6 samples each, and one 5 samples (years). The test statistic H , distributed approx. as $\chi^2_{[a-1]}$,

showed a value of 2.76, which should be compared with the critical $\chi^2_{0.05[4]}$ of 9.49. Thus, there is no significance for difference of location on the 5 % level.

The non-parametric multiple comparison by simultaneous test procedure (Sokal & Rohlf op.cit.) effects comparisons of location between all possible pairs of plots. To obtain equal sample size(s), which is demanded by this test, two alternatives were tested: a) the values from the box-free plot that was established in 1966 were omitted, b) the four values from the year 1965 were omitted. Both alternatives resulted in values of the test statistics that were remote from the critical values on the 5 % level of significance. So, neither test, although based on different test criteria, gave us any reason to reject the null hypothesis of no difference in density between plots.

As shown by the presented test results, the bird densities summed over all species do not show (demonstrable) differences between the two types of plots. However, this does not tell us anything about the fluctuations of the individual species. They can, obviously, vary in totally different ways in the two types of plots without affecting the totals. To consider the variation patterns of each species in box-plots versus box-free plots, we used a rather general model. This model does not, however, permit calculations of coefficients of correlation. It merely serves as a method to summarize and visualize the fluctuations of individual species.

The underlying assumptions may be expressed as

$$E(x_{ijk}) = a_{ij} + b_{ik} \text{ where}$$

$i = 1, 2.$ type of plot
 $j = 1, \dots 6.$ year (1965–1970)
 $k = 1, \dots 13.$ species (all those presented in Fig. 1 except PF and Redstart)
 x_{ijk} = the density in plot i , year j of species k .

The expected value of x_{ijk} depends on i , j , and k as well as combined effects of these. We assumed that the combination of type of plot and year as well as type of plot and species could be of importance, while the combination of year and species was disregarded. Further, any correlation between x_{ijk} and $x_{i'jk}$ was as-

sumed to be due only to type of plot; that is $Q_{ijk}, i'jk = Q_{i,i'}$.

Since

$$E(\bar{x}_{ij.}) = a_{ij} + b_{i.},$$

$$E(\bar{x}_{i.k}) = \bar{a}_{i.} + \bar{b}_{i.k},$$

$$+ \bar{x}_{i..} = \bar{a}_{i.} + \bar{b}_{i.}$$

we can estimate $(a_{ij} + b_{ik})$ by

$$E(\bar{x}_{ij.} + \bar{x}_{i.k} - \bar{x}_{i..}) = a_{ij} + b_{ik}.$$

The data was corrected with regard to the combined effects by putting $x_{ijk} - \bar{x}_{ij.} - \bar{x}_{i.k} + \bar{x}_{i..} = y_{ijk}$. Obviously, $E(y_{ijk}) = 0$. We studied these residuals for all pairs of species and years in the two types of plots by plotting y_{1jk} versus y_{2jk} (see Fig. 3). The resulting scatter gives a strong impression of a positive correlation between variation patterns of species in two types of plots.

The most deviating points (encircled) refer to Redwing and Fieldfare in 1968. These species are most often colony-breeders. Their patchy spatial distribution makes their densities in the plots largely due to mere chance. There is no reason to suspect that the PF has

any influence on the localization of thrush colonies.

As the statistical tests show that there are no significant deviations between the fluctuation patterns of the different population categories, the results can be summarized as follows:

1. The fluctuation pattern of the nest-box population of the Pied Flycatcher does not differ significantly from that of the other species taken together in the same plots.
2. The fluctuation pattern of all species taken together (except the Pied Flycatcher) in the plots with nest-boxes does not deviate from that of the box-free plots.
3. None of the species seems to have different patterns of fluctuation in box plots compared with the box-free plots.

DISCUSSION

The problem of competitive interactions between co-existing species has been analyzed by a large number of ornithologists based on

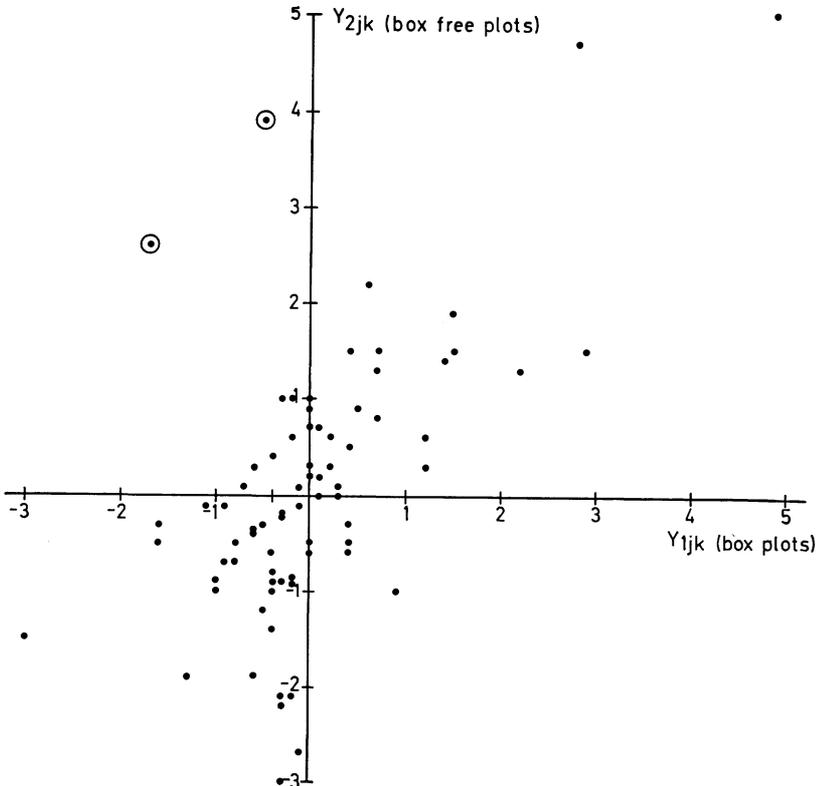


Fig. 3. Points denote (joint) distribution of residuals (see text for explanation) for each combination of year and species in box plots (y_{1jk}) versus box-free plots (y_{2jk}).

varying field experience. It is generally agreed that interspecific competition has been important for the adaptive radiation of the species (Lack 1971). This process leads to ecological isolation. Lack (op.cit.) has recently reviewed the isolating mechanisms in birds and analyzed the occurrence of direct or indirect evidence of ecological isolation between a large number of co-existing closely related species.

Opinions differ as to what extent interspecific competition is involved and affects the distribution of the birds when they occupy a common habitat for breeding. This problem is relevant because 1) it is going too far to presuppose that the ecological isolation between all species in a community is complete enough to make competition insignificant, and 2) most habitats available for study have recently been more or less modified by man, which means that the isolating adaptations evolved might be less suitable to-day.

In this context it is useful to adopt the view put forward by Miller (1967) and others that one can distinguish two component elements of the competition process, viz. 'interference' and 'exploitation'. Interference involves activities to gain access to a certain resource, e.g. space through territorial behaviour, whereas exploitation is the utilization of a resource once access to it has been achieved. Miller (op.cit.) suggests that 'competitive exclusion is achieved more frequently and more efficiently through interference than through exploitation'.

Interspecific territoriality belongs to the interference component of the competition process. It has been demonstrated to occur between closely related species in a few cases (Orians & Willson 1964 with references, Wiens 1965, Johnson 1966, Cody 1968, 1969, Miller 1968, Dyrce 1969). This type of interspecific competitive exclusion is comparatively easy to observe. A more controversial question is whether interspecific interactions could also be of importance for the distribution of the species in a common habitat in cases when the behaviour does not cause complete territorial exclusion and when the species involved are not closely related (congeneric). This possibility has been considered by many authors (cf.

Svårdson 1949, Morse 1967, Jablonski 1967, Jablonski et al. 1970, Frochot 1970) and has been extensively elaborated by Wasilewski (1967). Most signs of possible effects of such interactions between species are indirect because of the fact that they are extremely difficult to assess in the field, except in such special cases as struggles for nesting-holes, song-posts, and the like.

According to MacArthur (1958), it is very difficult to distinguish a mild repulsion of other species by territorialism from a preference for a slightly different habitat. It is certainly not going too far to say that the only way to receive reliable and conclusive information in these matters is to invent and perform adequate experiments in the field. The nest-box study presented in this paper partly serves as such an experiment. Obviously the information on competition given by this study will necessarily be restricted to the interference component.

The nest-box experiment at Ammarnäs

As mentioned above, a competitive effect of the rise in the population density of the Pied Flycatcher could in this experiment be manifested in two ways: 1) a decrease in the density of the open-nesting species during the whole of the nest-box period, and/or 2) a fluctuation pattern of the open-nesting species opposing that of the Pied Flycatcher. (Other effects, such as declining reproductive success of the open-nesting species, could have occurred, but as mentioned above it is not possible to consider them in this study.) We were, however, by means of the statistical treatment not able to show that any of these manifestations were at hand in the material from the nest-box experiment at Ammarnäs. Thus it is justifiable to conclude that the experimentally induced immigration of the Pied Flycatcher did not involve a disturbance strong enough to cause, by interference, a demonstrable change in the population numbers of the other species.

It is not possible to explain conclusively the results of this experiment because too much information is lacking. The following problems or aspects may be worth studying further to reach a better understanding of the fact that

a very dense population of Pied Flycatchers could be established without affecting the abundance of the other species. Presumably the Pied Flycatcher is fairly efficiently isolated ecologically in relation to the other species. Two facts speak in favour of this view. There are no closely related species in the community which could be expected to be ecologically adapted in the same way as the Pied Flycatcher. The investigated habitat is only slightly or not at all modified by man, which means that the adaptations gained by the different species may be effective to-day. In this context, the special type of territorial behaviour displayed by the Pied Flycatcher should also be remembered. According to von Haartman (1956) this species does not establish territories with clear-cut defended boundaries. The territories are defended in a 'centripetal' way, i.e. most of this activity concerns the defense of the nesting-hole. Finally, it could be possible that the habitat in question, the rich subalpine birch forest, is not populated by breeding birds near the limits of its capacity.

Comparison with nest-box experiments in Fågelsångsdalen, Southern Sweden

A similar experiment with nest-boxes has been carried out in mixed deciduous wood in Fågelsångsdalen, southernmost Sweden (55°42'N, 13°20'E) (Enemar et al. 1972). In this case, a four-year period with 70 to 80 nest-boxes within the study plot (13 hectares) was compared with the four-year periods (with only 10 to 20 boxes in part of the plot) immediately before and after the nest-box period with regard to the density of the different species. The introduction of a large number of nest-boxes was followed by increased numbers of breeding Pied Flycatchers and Great Tits, but this did not cause a demonstrable change in the totals of the other birds. The results from the experiment in Fågelsångsdalen were difficult to interpret because no box-free control plots were established and, moreover, habitat changes of unknown significance might have occurred during the 12-year period.

A comparison between the density and composition of the bird populations in the nest-box

plots in Fågelsångsdalen and at Ammarnäs is shown in Fig. 4. In the mixed deciduous forest of Fågelsångsdalen the density of the Pied Flycatcher is only half that of the subalpine birch forest. The natural density of the species is about the same in both habitats, i.e. a few

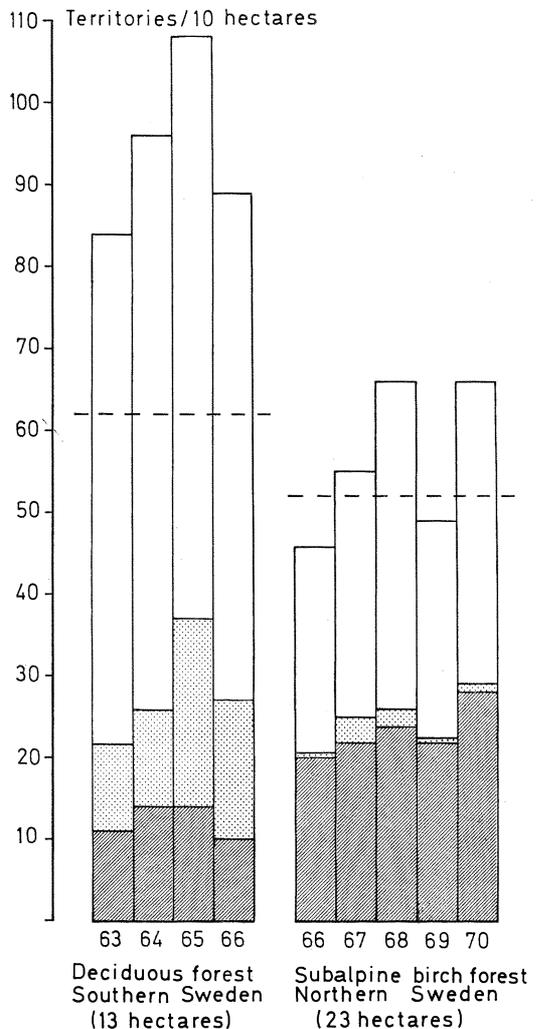


Fig. 4. Density fluctuations during a four-year nest-box period in Fågelsångsdalen, Southern Sweden (left diagram) and during a five-year nest-box period in two study plots at Ammarnäs, Northern Sweden. The Pied Flycatcher is represented by the hatched parts of the columns, other hole-nesting species by the stippled parts, and the open-nesting species by the white upper parts. The broken horizontal lines show the densities of nest-boxes.

pairs per 10 hectares. The problem is how to understand this difference in the density of the flycatcher populations in the southern and northern nest-box plots. The following viewpoints may deserve consideration.

1. In box-free areas, access to suitable nesting-holes strongly limits the population density of the Pied Flycatcher (von Haartman 1956). This limiting factor is eliminated in the experiments because there is a large surplus of empty boxes in both cases. This means that other limiting factors are operating in the nest-box plots.

2. The 'carrying capacity' with respect to the Pied Flycatcher might be different as concerns the essential resources in the southern and northern habitats, i.e. the southern deciduous forest of Fågelsångsdalen could be inferior to the birch forests at Ammarnäs. Moreover, the northern and southern nest-box plots are different as regards the size and the density of the trees, the size of open areas and so on.

3. A large number of nest-boxes are occupied by tits, mostly the Great Tit, in Fågelsångsdalen. This is not the case at Ammarnäs where tits are sparsely occurring (Fig. 1). It is not very likely that the lower density of the Pied Flycatcher in the southern habitat is due to competition with tits for the boxes because there is always a large surplus of empty boxes. Moreover, Tompa (1967) found that competition with the Great Tit for the nest-boxes is significant only when the nest-box density is very low, i.e. when almost all boxes are occupied (distance between nest-boxes about 200 metres). The nest-box density in Fågelsångsdalen and at Ammarnäs is high (distance between boxes mostly less than 50 metres).

4. The density of the passerine bird community in Fågelsångsdalen is about 850 stationary males per square kilometre belonging to 18 species on average (Enemar 1966b), whereas in the study plots at Ammarnäs only slightly more than 300, belonging to about 12 species (Enemar & Sjöstrand 1970). Does this mean that the denser community with more species displays a more effective resistance to the immigrating flycatchers? If so, the low density of the flycatcher population in the southern

habitat is a manifestation of interspecific repulsion.

Further experimentation is needed to explain the different results of the nest-box studies in Fågelsångsdalen and at Ammarnäs and to evaluate the speculations under points 2, 3, and 4 above. One adequate experiment is to remove the tits from the nest-box plot in Fågelsångsdalen; another is to remove the tits together with part of the open-nesting population in order to lower the density to the same level as that of the nest-box plots at Ammarnäs. The ensuing response of the Pied Flycatcher as regards its population density would help at least partly to sort out the above-mentioned points.

Other investigations

To our knowledge there are only a few nest-box investigations which have considered the abundance of the open-nesting species in the nest-box areas (Pfeifer 1955, Weinzierl 1958, Wellenstein 1968). These papers do not contribute conclusive results as to the relations between the fluctuations of the hole-nesting and open-nesting populations. Wellenstein found that the experimental increase of the hole-nesting populations was also accompanied by a considerable increase in the density of the open-nesting species. He could not explain this, but supposed that it might have been caused by a 'social effect' created by the accumulation of the hole-nesting species.

According to Udvardy (1969, p. 52) 'among the best means of studying niche requirements and competitive phenomena is to concentrate our research on the ecology of introduced animals.' By this he means the introduction of species which are new to the habitat or the area. He also points to the fact that in known cases, e.g. the introduction of passerine birds into New Zealand, it is difficult to assess whether competitive replacements have occurred because the introduction is often preceded and aided by habitat alteration by man. Such cases differ from the nest-box experiments, since the latter contrive to introduce increased numbers of a species native in the habitat. But Udvardy's statement is valid in

this case as well, and the nest-box experiments no doubt deserve a follow-up of detailed ecological investigations involving comparisons between the nest-box plots and the other plots with regard to different interactions between the flycatcher and the other species, changing reproductive rates, and so on. In fact, the nest-box experiments cannot be fully understood unless the results of such studies are available. The results on the density fluctuations as presented in this paper only represent a first step.

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