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Breeding biology of the Pied Flycatcher Ficedula hypoleuca in relation to population density

Martti Virolainen

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The breeding biology of the Pied Flycatcher was studied in two nest-box areas with a fourfold difference in box density. Population size varied between 40 and 101 breeding pairs with a declining trend during 1971-83. Population density was on average 2.5 times higher in the high-density box area irrespective of population size in the low-density box area. The annual breeding success correlated to the temperature during the first two thirds of the nestling period, and the annual changes in population size to the breeding success in the preceding year. Probably due to the pronounced effect of density-independent weather factors, density-dependence of the annual fluctuations could not be demonstrated. However, keeping years apart, the breeding success was slightly better in the low-density area. Within any one year, male attendance during the nestling period was the most important factor influencing breeding success. Using the male absence as an indicator, the degree of polygyny correlated positively to the density of the population. Density-dependent regulation of the population size could thus act through the polygynous behaviour of the species.

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1. Introduction

Density-dependence is one of the most important concepts in population ecology. Much of the work concerning the regulation of bird populations has been done on hole-nesting birds, especially on the Great Tit *Parus major* (e.g. Lack 1966, Perrins 1979). The Pied Flycatcher is also suitable for studies of this kind. Breeding density of Pied Flycatchers is usually limited by the availability of nest-sites and, by providing nest-boxes, it is possible to increase the density far above the levels attained in managed forests (e.g. von Haartman 1971). It is of advantage that Pied Flycatchers are not sensitive to human interference, and that usually the sexes are easily distinguished at a distance. The polygynous behaviour of males adds an interesting aspect to the population ecology of the species (e.g. von Haartman 1951b, Alatalo et al. 1982b, Alatalo & Lundberg 1984). A drawback, however, is that the Pied Flycatcher is only a summer visitor to Europe, and therefore not possible to study during the non-breeding season. In view of the large body of data on the breeding biology of the Pied Flycatcher, relatively little attention has been paid to the regulation of its population size. The study by Tompa (1967) seems to be the only one directly concerned with density-dependence of population regulation in this species.

This paper reports the results of a thirteen-year study on the breeding biology of the Pied Flycatcher. The primary aim was to compare two experimental areas in which the density of flycatchers was different due to a difference in nest-box density. In addition, the annual changes of the population size in the whole study area were analyzed in order to find factors responsible for short-term fluctuations in numbers, and to test for density-dependent effects.

2. Study area and methods

The study was carried out in Siuntio commune, southern Finland (60° 15′ N, 24° 18′ E), about 30 km northwest of Helsinki during 1971-83. Two plots with different densities of nest-boxes were established west and east of Lake Kimpari, about 300 m apart. Plot A has 100 nest-boxes spaced over an area of 25 ha (4 boxes per ha), and plot B 58 boxes in an area of about 58 ha (1 box per ha). In 1971 the number of boxes was smaller, 82 and 44 respectively, and, therefore, this year was omitted from the results related to the annual changes in population size. In addition, both plots have included some nest-boxes for starlings and owls. Great Tits have frequently occupied these larger boxes. Pied Flycatchers have only twice accepted a box of starling size, and no cases of breeding in natural cavities have been observed. A standard box type made of board was used. The entrance was 32 mm, and the bottom area 8 1/2 × 10 cm. A total of about 60 boxes were in the study plots prior to the study, and about 10 % of the nest-boxes have been replaced annually by new ones.

The terrain is hilly with a total elevation of 75 m in plot A and 65 m in plot B. Both areas have some small bogs, and one side of both plots borders a field. Most of the area is covered by coniferous forest with mixture of deciduous trees, mainly birches *Betula* spp. Rocky elevations have open stands of pine *Pinus silvestris*, while spruce *Picea abies* dominates in moist areas. The immediate surroundings of a few nest-boxes at the edges of the study areas are dominated by deciduous trees and shrubs.

The boxes were regularly inspected to determine the start of laying, final clutch size, and numbers of hatched and fledged young. The numbers of hatched young are maximum figures, as missing young nestlings were counted as hatched eggs. Dead nestlings were removed. In 1972 the boxes were incompletely inspected during the nestling period, and the numbers of hatched and fledged young are based on an about 50 % sample of the population in both plots and of various periods of the breeding season.

Almost all females and nestlings were ringed. The percentage of males captured and marked individually with coloured rings varied annually between 5 and 93, with an average of 33 %. The presence and behaviour of males was always recorded, and since 1975 special attention was paid to the presence of males during the nestling period.

Nests which failed due to desertion, predation or accidents were omitted from the breeding data dealing with events after the failure. This procedure was justified as the failures seemed to be randomly distributed in time and space; the inclusion of failed nestings would have caused undue variation without biological significance. In 1979 predation was exceptionally high (see below) but due to lack of site-tenacity of the young (only 0.1 % of the ringed fledglings have been found breeding in the area), even high predation rates, if locally restricted, should have only minute effects on population changes.

During most of the years, a few females started laying substantially later than the main part of the population. Most of these clutches were genuine first broods, and they were included in the population size. Second broods were not encountered, and only one replacement nesting after accidental loss of the clutch was confirmed by ringing, but in this case the date of the replacement clutch fell within those of the main population. As some of the late clutches were probably replacements, and as these nestings differed greatly in clutch size and breeding success from the main population, clutches started later than 14 days after the annual median date of laying were not included in the breeding data. The number of these clutches varied annually between 0 and 5, the total being 22 (12 in plot A (2.6 %) and 10 in plot B (2.4 %).

Weather data are from Vihti, Maasoja, a meteorological station about 15 km north from the study area.

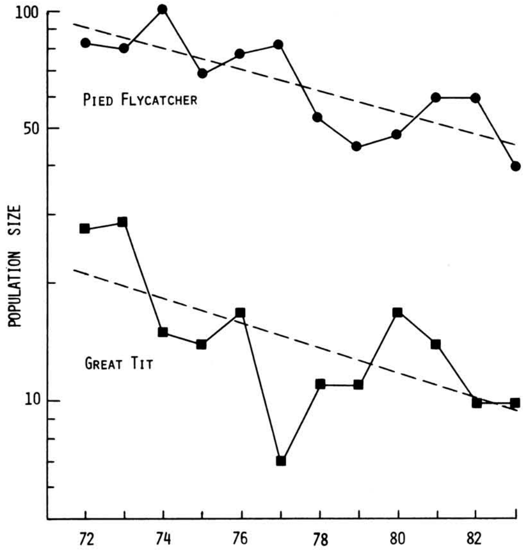

Fig. 1. Population size of Pied Flycatcher and Great Tit in 1972-83.

3. Results

3.1. Population fluctuations

Numbers of Pied Flycatchers and other birds nesting in the boxes in the study plots are given in Table 1.

In the whole study area, the number of Pied Flycatcher nests, where at least one egg was laid, varied between 40 and 101. The coefficient of variation (CV) was 28 %. Population size (y) was declining (Fig. 1). The regression equation for 1972-83 (1972=1) is $\log y = -0.0276x + 1.987$, $r = -0.799$, $P < 0.01$.

Populations size of the Great Tit also declined ($\log y = -0.0323 + 1.357$, $r = -0.643$, $P < 0.05$), but fluctuations were greater (CV 45 %). Annual changes did not correlate to those of the Pied Flycatchers, even when the declining trend in both species was removed using partial correlations.

3.2. Population density in relation to nest-box density

The density of Pied Flycatchers varied between 0.88 and 2.08 per hectare in plot A, and between 0.31 and 0.84 in plot B. On average,

Table 1. Numbers of nests in the study plots, and nest-box occupation percentages. Only first breedings are included. Nestings of other species comprise 23 nests of *Parus ater,* 12 of *Parus caeruleus,* 10 of *Phoenicurus phoenicurus,* and one each of *Jynx torquilla, Parus montanus* and *Certhia familiaris.* Means are calculated for 1972–83, since the number of boxes was smaller in 1971.

	F. hypoleuca			*Parus major*			Other spp.			Occupation%	
	A	B	A+B	A	B	A+B	A	B	A+B	A	B
1971	44	23	67	4	5	9	1	3	4	60	70
1972	49	34	83	11	17	28	3	1	4	66	87
1973	42	38	80	15	14	29	5	3	8	62	91
1974	52	41	101	8	7	15	2	3	5	62	91
1975	35	34	69	5	9	14	4	0	4	44	72
1976	39	39	78	7	10	17	2	0	2	48	79
1977	36	46	82	4	3	7	1	1	2	41	84
1978	28	25	53	5	6	11	0	1	1	33	54
1979	26	19	45	5	6	11	1	2	3	32	44
1980	23	25	48	8	9	17	3	1	4	34	60
1981	29	31	60	6	8	14	3	0	3	37	61
1982	30	30	60	4	6	10	1	1	2	35	58
1983	22	18	40	4	6	10	4	2	6	30	39
Total	455	411	866	86	106	192	30	18	48		
Mean	34.2	32.3	66.6	6.8	8.4	15.2	2.4	1.2	3.7	44	68
SD	9.8	9.7	18.6	3.3	3.8	6.9	1.5	1.2	2.0	13	18
CV%	28	30	28	49	46	45	62	84	54		

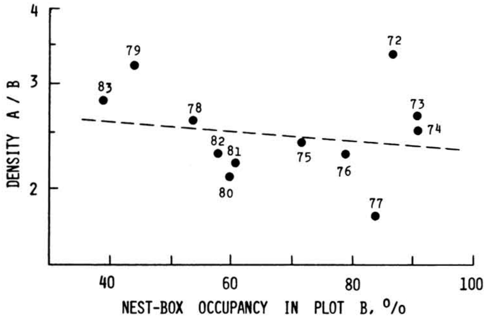

Fig. 2. Lack of relation between ratio of population density in plots A and B and nest-box occupancy (all species) in plot B.

density was 2.5 times higher in plot A than in plot B. The ratio of densities in plots A and B did not correlate to the occupancy of boxes in plot B (Fig. 2).

3.3. Interspecific competition

The Great Tit was the only common species to compete for nest-boxes with Pied Flycatchers. On average, Great Tits started laying 17 days (annual variation 10–25 days) before the flycatchers. In no case were flycatchers displaced from nest-boxes by Great Tits. In 7 cases Great Tits lost their nests to flycatchers, all during the egg-laying period. Six of these conflicts occurred in 1972–74, when populations of both species were high, and 4 of them took place in plot B.

Coal Tits *Parus ater* lost 4 of their 23 nests to flycatchers, all during the incubation period and in plot B.

One Pied Flycatcher nest was lost to the Wryneck *Jynx torquilla.*

3.4. Nesting failures

Of the 866 nesting attempts ("late nestings" included) 16% failed totally. Table 2 shows the causes of failures.

Predation rate was low, accounting only for 2.3% of nests and 15% of failures. The losses due to desertion and most of those due to predation were sporadic and randomly distributed over the study period and area. An exception was nesting failures in 1979, when probably Pine Marten *Martes martes* destroyed 8 broods totally; partial nestling losses in 4 other broods in this year were probably caused by the same predator.

Table 2. Causes of total nesting failures.

Cause of failure	Plot A	Plot B	Total	%
Desertion for unknown reason				
during the laying period	8	9	17	2.0
during the incubation period	6	10	16	1.8
Total	14	19	33	3.8
Nest site competition				
Jynx torquilla	0	1	1	0.1
Predation				
Martes martes (?)	4	4	8	
Dendrocopos major	1	5	6	
Vipera berus	1	0	1	
unknown predator	3	2	5	
Total	9	11	20	2.3
Accidents				
due to box inspections	2	2	4	
other	4	2	6	
Total	6	4	10	1.2
All eggs unfertilized	1	1	2	0.2
Death of the female in the nest-box	1	2	3	0.3
Death of whole brood for other reasons	41	26	67	7.7
Total	72	64	136	15.7

All three cases of female death in the nest-box occurred in 1982, when the breeding success was the lowest. One of the females died during the laying period and two during the nestling period.

One half of the nesting failures was due to the death of the whole brood. In most of these cases the nestlings apparently died of starvation. However, even in years with fairly good overall breeding success, some nestings failed due to death of young. In these cases, the nestlings had usually died simultaneously, and the failures were thus probably due to desertion or to death of the parent(s) rather than to starvation.

Failures due to predation by the Great Spotted Woodpecker *Dendrocopos major* were more frequent in plot B, explainable by the larger area of the plot. Failures due to the death of the whole brood were more common in the dense nest-box plot A. None of the differences was significant, however (χ^2-test).

3.5. Commencement of laying

Commencement of laying and other breeding data in the two study plots are summarized in Table 3.

Annual variation in the mean start of laying in the whole study area was 14 days. In the seasons of 1973 and 1974, laying started significantly ($P < 0.05$) earlier in plot B than in plot A. In these years, a high proportion of nest-boxes in plot B were occupied, and the difference is probably due to the scarcity of available boxes in plot B for later arriving birds. All years combined, laying was only 0.5 days earlier in plot B, this difference being not significant.

3.6. Clutch size

Both plots combined, the mean of the annual clutch sizes was 6.35 (*SD* 0.24). The mean varied annually from 5.94 to 6.77, and it correlated significantly to mean date of laying ($y = -0.050x + 7.804$, $r = -0.788$, $P < 0.01$, 1 May = 1). Keeping years apart, the daily decline in clutch size varied between 0.007 and 0.127 averaging 0.061. The annual values correlated negatively to the SD of the mean date of laying ($r = -0.660$, $P < 0.05$), *i.e.* the slope of the regression line was steeper in years when laying was more synchronous.

The clutch size variation was parallel in plots A and B, and did not differ significantly in any single year (Table 3). However, for all years combined, the 0.13 eggs higher clutch size in plot B was significant ($P < 0.01$, paired *t*-test).

3.7. Hatching success

In the whole study area, annual variation in hatching success was 90.3-95.4 % with a mean of 93.4 %. No significant differences were observed between the plots.

3.8. Fledging success

Annual variation in fledging success was marked. Nestling mortality varied between 0.41 and 2.65, and the number of fledged young per brood between 3.22 and 5.61 (Table 3).

Table 3. Breeding data of Pied Flycatchers in p lots A and B and in the whole study area in 1971-83. Statistical tests applied: *t*-test for annual means in commencement of laying (1 May = 1) and clutch size; Mann-Whitney *U*-test for annual means in hatching failure, nestling mortality and number of fledglings; paired *t*-test for the means of the years. r = correlation between plots A and B. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Commencement of laying			Clutch size			Hatching failure			Nestling mortality			Number of fledglings		
	A	B	A+B	A	B	A+B	A	B	A+B	A	B	A+B	A	B	A+B
1971	25.9	24.9	25.6	6.70	6.65	6.68	0.40	0.48	0.42	2.19 *	0.88	1.78	4.11	5.24	4.46
1972	29.5	28.5	29.2	6.28	6.62	6.41	0.65	0.38	0.55	1.07	0.70	0.92	4.61	5.47	4.96
1973	26.0 *	23.8	25.0	6.46	6.41	6.45	0.36	0.16	0.28	1.38	0.83	1.14	4.78	5.34	5.01
1974	37.2 *	35.0	36.1	5.86	6.02	5.94	0.38	0.36	0.37	1.62	1.76	1.69	3.83	3.89	3.86
1975	27.6	28.7	28.1	6.82	6.71	6.77	0.27	0.48	0.38	1.70	1.45	1.58	4.85	4.77	4.81
1976	28.5	28.8	28.6	6.16	6.35	6.26	0.33	0.44	0.38	1.62	1.21	1.41	4.24	4.88	4.56
1977	31.5	30.5	30.9	6.26	6.41	6.35	0.18	0.39	0.29	2.56	2.74	2.65	3.53	3.29	3.40
1978	31.4	31.8	31.6	6.11	6.09	6.10	0.33	0.44	0.38	1.26	0.83	1.06	4.56	4.83	4.68
1979	30.4	28.2	29.5	6.00	6.47	6.20	0.48	0.58	0.52	1.67	0.50	1.16	3.72	5.07	4.31
1980	33.9	34.1	34.0	6.05	6.17	6.11	0.67	0.21	0.42	0.71	0.92	0.82	4.67	5.04	4.87
1981	26.1	26.7	26.3	6.34	6.48	6.41	0.25	0.43	0.34	1.71	1.43	1.57	4.36	4.61	4.48
1982	29.2	29.5	29.3	6.24	6.35	6.29	0.83	0.29	0.59	2.85	2.26	2.58	2.74	3.78	3.22
1983	22.3	22.6	22.4	6.50	6.67	6.58	0.67	0.44	0.56	0.39	0.44	0.42	5.44	5.78	5.61
Mean	29.2	28.7	29.0	6.29 **	6.42	6.35	0.44	0.39	0.42	1.59 **	1.23	1.44	4.26 **	4.77	4.48
SD	3.9	3.7	3.7	0.27	0.22	0.24	0.20	0.11	0.10	0.68	0.69	0.64	0.69	0.72	0.66
r	0.953***			0.810***			-0.223			0.759**			0.766**		

Fledging success in plots A and B was significantly correlated but, in most years, it was better in plot B. In the annual comparisons, a difference at 5 % level was found only in nestling mortality in the first study year but, all years combined, nestling mortality was significantly lower and the number of fledglings significantly higher in plot B than in plot A ($P < 0.01$, paired *t*-test).

Male attendance during the nestling period was the most important factor influencing fledging success. In the broods which were not known to be secondary nestings of polygynous males, and in which the male was seen feeding or warning near the nest-box, the average final brood size was 4.98 (1973-83, $N = 454$). Broods in which only the female seemed to take care of the young produced, on average, only 3.18 fledglings ($N = 121$). The difference was greater in years with an overall poor breeding success (Fig. 3). In secondary broods with at least some male assistance, the mean number of fledglings was 4.2 ($N = 10$). Fledging success was poorer later in the season irrespective of male attendance, and a higher proportion of the late broods were without males, but the date of the

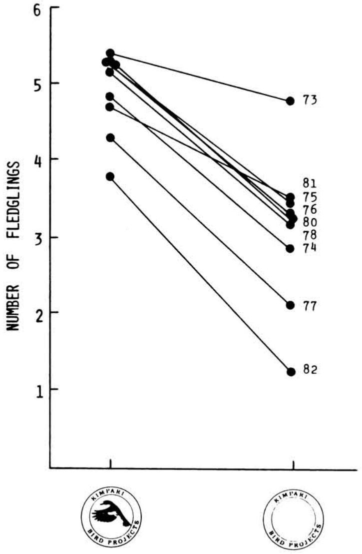

Fig. 3. Mean annual fledging success in broods with and without male attendance during the nestling period. Years (1979 and 1983) with less than five broods without male attendance are omitted.

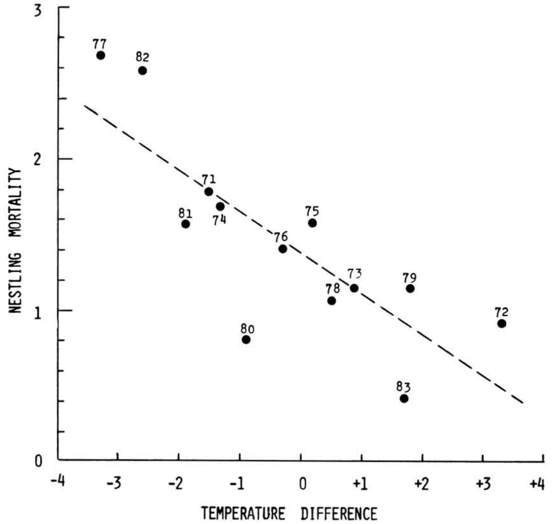

Fig. 4. Correlation of nestling mortality with mean temperature on the first 10 days after the mean hatching date of the population. Temperature is expressed as difference of observed and long-term mean temperatures. Regression equation: $y = -0.273x + 1.37$, $r = -0.806$, $P < 0.01$.

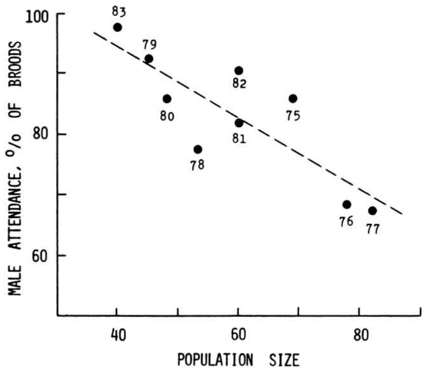

Fig. 5. Correlation of the percentage of broods with male attendance to population size. Regression equation: $y = -0.588x + 118.0$, $r = -0.830$, $P < 0.01$.

nesting explained only a fraction of the difference accounted for by the male attendance.

Correlations were searched for between annual fledging success and various climatic factors. Nestling mortality correlated positively with total precipitation and with numbers of rainy days during the nestling period, but these were not significant. In comparing nestling mortality with temperature, various periods were tried: the whole of June, the latter half of June, and the days 1-5, 1-10, 1-15 and 6-10 after the mean hatching date of the population. The best fit was obtained when the difference between the mean temperature for the 10-day period after hatching and of long-term mean temperature for that period, was applied ($r = -0.806$, $P < 0.01$, Fig. 4).

3.9. Polygyny

Eleven cases of polygyny were confirmed by ringing. The time interval of the two layings varied between one and 16 days (mean 7 days) and the distance of the nests between 100 and 430 m (mean 230 m). Four of the cases occurred in plot A, six in plot B, and in one case the nests were in different plots.

Since polygynous males do not usually participate in feeding secondary broods, or feed only infrequently or after the primary brood has fledged, the proportion of broods without male attendance can be used as an estimate of the frequency of polygyny. Fig. 5 shows the correlation between the percentage of broods with male attendance confirmed and population size. Broods without male attendance were significantly more frequent in years with high population density ($r = -0.830$, $P < 0.01$). However, the means of the annual percentages (1975-83) of broods with male attendance in plots A and B were almost the same, 85 and 82 %, respectively.

3.10. Key factor analysis

To estimate the contribution of separate mortalities within the annual cycle to fluctuations in population size, and to test for their density-dependence, key factor analysis of Varley & Gradwell (1960; see also Krebs 1970, Podoler & Rogers 1975, Southwood 1978) was applied. This method consists of expressing mortalities (k-values) as the logarithm of the ratio of the populations before and after the particular mortality in question has acted. Mortality rates calculated for each stage of the annual cycle are summed to obtain the total annual mortality ($k_1 + k_2 + k_n = \mathrm{K}$). Separate k-values were calculated for clutch size variation (k_1; potential maximum average clutch size taken as 7),

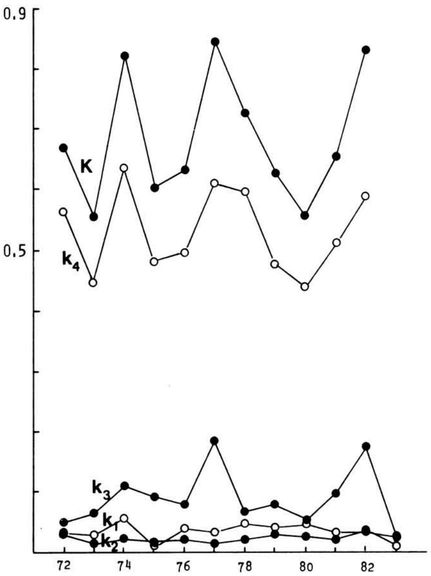

Fig. 6. Key factor analysis of population data 1972-83. k_1 = clutch size variation, k_2 = hatching failure, k_3 = nestling mortality, k_4 = "mortality outside the breeding season", K = total mortality. k_4 and K for 1983 not yet available.

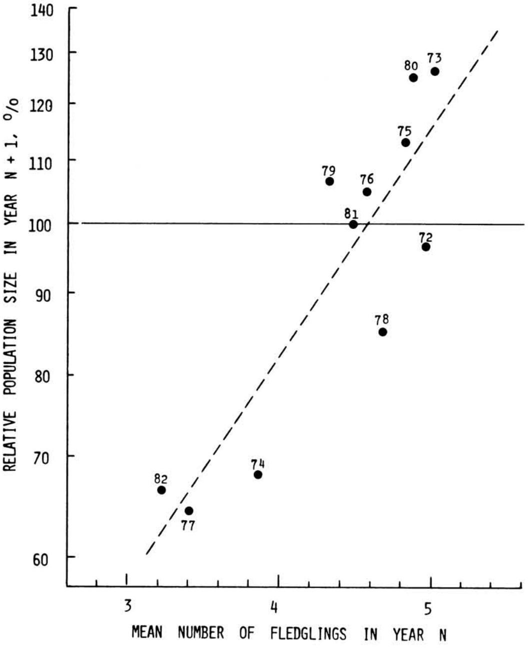

Fig. 7. Correlation of annual changes in population size with breeding success in the preceding year. Regression equation: $\log y = 0.150x + 1.31$, $r = 0.874$, $P < 0.001$.

hatching failure (k_2), nestling mortality (k_3) and "mortality outside the breeding season" (k_4). The last factor includes emigration from and immigration to the study area, and it should, strictly, be referred to as e.g. "loss of young and adults between fledging and next breeding season".

In Fig. 6 k-values are plotted against generations. By visual correlation, "mortality outside the breeding season" is clearly the key factor; it constitutes the largest section of the annual mortality and it fluctuates in parallel with the total K. For a quantitative evaluation of the relative importance of each submortality on annual fluctuations, correlation and regression coefficients were calculated between the k-values and the total K (Podoler & Rogers 1975):

k_1: $r = 0.346$, NS	$b = 0.037$
k_2: $r = 0.142$, NS	$b = 0.008$
k_3: $r = 0.799$, $P < 0.01$	$b = 0.317$
k_4: $r = 0.953$, $P < 0.001$	$b = 0.638$

Correlation of nestling mortality to total K is significant, and the regression coeffient suggests that about one-third of the total mortality, *i.e.* of the annual fluctuation, is due to this factor. Correlations of clutch size variation and of hatching failure were positive, although not significant, and thus the correlation of combined breeding success ($k_1 + k_2 + k_3$) to the total K was more significant than that of nestling mortality. This correlation is shown graphically in Fig. 7 but, for better visualization, average final brood sizes and relative changes in population size rather than the k-values have been employed.

"Mortality outside the breeding season" correlated positively to nestling mortality ($k_4 = 1.03k_3 + 0.426$, $r = 0.604$, $P<0.05$).

Density-dependence is tested by plotting the k-values against the logarithm of the initial populations size. A significant positive slope indicates density-dependence. The correlation coefficients were:

k_1: $r = 0.116$, NS
k_2: $r = -0.438$, NS
k_3: $r = 0.378$, NS
k_4: $r = 0.147$, NS

The correlation of nestling mortality to population size was highest, but none was significant, and density-dependent relationships could thus not be verified.

4. Discussion

The primary aim of the study was to investigate the effect of population density on breeding success. Based on experiences from nest-box studies in 1958–60 in the same area, the box densities in the plots were designed so that in the low-density plot B density of boxes would set an upper limit to population density, whereas plot A would have a surplus of boxes. During the first years of the study, when the population size was high (normal?) and nearly all of the boxes in plot B were occupied, the 2.5 times higher population density in plot A was expected and explicable by the availability of boxes. However, during the latter part of the study the density in plot A remained 2.5 times higher, although in some years only less than half of the boxes in plot B were occupied.

Since the habitats of the plots seem to be fairly similar, apparently the higher nest-box density *per se* makes plot A more favourable for flycatchers. This is probably related to the polygynous behaviour of the species. Males are attracted by the high number of nest-boxes because a single male can more easily control several available nest-sites. This probably increases the fitness of the male and its chances to get a mate and possibly a secondary female as well. On the other hand, although the number of males which have settled in the low-density nest-box area was lower than the number of boxes, their polyterritorial behaviour would make it difficult for new intruders to establish themselves in the area. Attraction of males by the song of other males and the use of song as a clue in locating nest-sites, as suggested by Alatalo et al. (1982a), may also contribute to the higher density in plot A.

The pronounced effects of climatic conditions on breeding success of the Pied Flycatcher have been pointed out by several authors (e.g. Tompa 1967, Järvinen 1983, Borgström 1983). In the present study, the marked annual differences in breeding success correlated with temperature during the nestling period. The first two thirds of this period seemed to be decisive as far as fledging is concerned. If the mean temperature of the whole nestling period was used in the regression analysis instead of the first two thirds, the r-value dropped from 0.806 to 0.403. Evidently, poor weather conditions during the last third of the nestling period did not interfere with fledging, but they may well have influenced the immediate postfledging survival. The positive correlation of mortality outside the breeding season to nestling mortality is probably due to an increase in the immediate postfledging mortality in years with poor breeding success rather than to mortality later in the non-breeding season. In the subarctic Kilpisjärvi area, significant correlations between climatic factors and fledging success were not found, but the best fit was obtained for the same period; the ten first days after the mean hatching date (Järvinen 1983). Under these northern conditions, hatching success was very variable, and it correlated with temperature during the incubation time. In the present study, the effect of adverse weather on hatching success could be noticed in 1982. Both hatching and fledging success were the poorest that year and half of the unhatched eggs had large embryos, whereas during the other years hatching failure seemed to be mainly due to infertility. The diversified effect of climatic factors was present in adult mortality as well. This same year was the only one when death of the female on the nest was recorded. In the Kilpisjärvi study, adult death was also restricted to a single year (Järvinen 1983). In this year, 1981, the effects of cool and rainy weather were pronounced over large areas of Fennoscandia (Hildén et al. 1982, Borgström 1983), but the present study area was not as badly affected.

Annual changes in population size correlated with breeding success in the preceding year. This effect was mainly due to the poor breeding success in three years (Fig. 7). In 1977 and 1982 the poor success was mainly due to high nestling mortality, and in 1974 the late breeding season and the consequently low clutch size contributed to the low number of fledglings.

The correlation of population change with breeding success seems to be quite expected. However, in analysing Campbell's data of a 16-year study of Pied Flycatchers in England, Lack (1966) states: "... as in other species discussed in this book, the annual variations in the output of young had no obvious influence on the subsequent changes in the number of breeding pairs". In the subarctic Kilpisjärvi population, no significant correlation of population change to breeding success was found, but the addition of the spring temperature to a multiple regression analysis resulted in a significant correlation (Järvinen 1983).

Climatic factors could affect breeding success through availability of food in a density-dependent way. However, as pointed out by Järvinen (1983), a single day of inclement weather can be disastrous, and this seems to hold true for more southerly populations as well. Under these conditions it is hard to believe that the number of foraging birds would have any substantial effect on the availability of food. Concerning the Pied Flycatcher, the effect of weather should thus be largely density-independent.

Density dependence of the separate mortalities during the annual cycle could not be demonstrated in the key factor analysis. This may have been due to a masking effect of density-independent factors, mainly climatic. In addition to nestling mortality, clutch size variation is highly dependent on climatic factors, as a warm spring is followed by early laying which in turn causes high clutch size due to the "calendar effect" (e.g. von Haartman 1967).

In the present study the reduction of clutch size during the breeding season averaged 0.06 eggs per day, which agrees fairly well with the findings in other areas. A daily reduction of 0.07–0.08 eggs has been reported in Germany (Berndt & Winkel 1967), southern and central Sweden (Källander 1975, Lundberg et al. 1981) and southern and northern Finland (von Haartman 1967, Järvinen & Lindén 1980). One-year-old females lay, on average, smaller clutches but they also start laying later in the season than older ones (Berndt & Winkel 1967, von Haartman 1967). The effect of laying date on clutch size is thus partially due to the age of the females. The steeper decline in clutch size in years with more synchronous laying is consistent with this view.

Keeping years apart and comparing plots with different breeding densities, effects of density-independent factors could be largely overcome. Both clutch size and final brood size were slightly higher in the low-density area, suggesting that density-dependent regulation of population size could operate during the breeding season. The design of the study by Tompa (1967) was comparable to the present one. He had areas with five different nest-box densities, but the most dense plots were very small which makes edge effects important. The results were in the same direction as the present ones but, presumably because of the short study period of only two breeding seasons, significant correlations of clutch size and of fledging success to breeding density could not be established.

The reduction of clutch size during the season explains about one-fifth of the 0.13 eggs higher clutch size in the low-density plot, but the difference between the plots is still significant. This difference may be due to the density *per se*, but the mechanism behind the small difference may be connected with other factors modifying clutch size. Difference in the female age composition between the high- and low-density plots would be a good candidate.

Polygyny could be confirmed only in a few cases. Except in the last two study years, males were captured only during the nestling period and so polygyny could not be acertained in the secondary broods which were not attended by the males. Probably the majority of the broods where the male was not observed were secondary, and so male absence could be used as an indicator for the degree of polygyny. The correlation of the non-attendance of the males with the annual population size (Fig. 5) strongly suggests that polygyny is more frequent in dense populations. Some correlation between male absence and population density was also observed by Tompa (1967).

The explanation of this correlation may be associated with the sex-ratio of the population. In the last two study years the relative number of non-mated males and the age composition of breeding and non-breeding males and of breeding females were estimated (Virolainen, unpubl.). The results suggest a highly skewed sex-ratio in favour of males especially in 1983 when the population was at its lowest level, but comparable results for years with high population density are lacking. If population density and sex-ratio are associated, a new question arises: What is the reason for male preponderance at low levels of population density?

The correlation of the degree of polygyny with population density would imply that the frequency of polygyny were higher in plot A in which the population was denser. However, significant differences were not observed in male absence between the plots. If the lack of difference is real, the mechanism behind the correlation of polygyny to population density would act regarding annual fluctuations in density, but not in regard to local within-year differences in density. Sex-ratio could easily be thought to act in this way. However, the inability to detect a difference in male attendance between the plots may be due to sources of error connected with the methods. Erroneous interpretations due to males from nearby nests warning at "wrong" nest-boxes are more likely in a dense population. The distance of the nests of polygynous males may be shorter in an area of high nest-box density, making it easier for the male to notice a disturbance in the secondary brood and to cause warning behaviour by the male.

Within any one year, male absence during the nestling period was the most important factor influencing breeding success. In broods which were not attended by males, the majority of which were probably secondary broods of polygynous males, the average production of young was 64% of that in broods with male attendance. Closely similar figures have been reported by other authors (Askenmo 1977, Alatalo et al. 1982b).

A higher degree of polygyny in a dense population would result in a lower reproductive rate. Thus, density-dependent regulation of population size could act through the polygynous behaviour of the species.

According to the regression equation of population change with breeding success (Fig. 7), self maintenance of the population would require a mean production of 4.6 fledglings per brood. However, in the data on which the equation is based, total failures, except those due to the death of the whole brood, were excluded. If the failed nestings are included, and a small allowance for probable replacement nestings is made, the reproduction rate necessary for a steady state population would be 4.3. This agrees well with the theoretical estimate of 4.4 (Järvinen 1983), which is based on estimated annual mortalities of 50% for adults (von Haartman 1951) and 70% for juveniles (von Haartman 1951, Curio 1959, Lack 1966), and on a 50% breeding frequency of one-year-old birds (von Haartman 1951). The regression between population change and breeding success is probably curvilinear, as the regression in Fig. 7 would result in a 50% reduction in population size with a production of 2.6 fledglings per brood. This seems to be incompatible with the estimate of 50% adult mortality, even if the increased adult mortality during the breeding season in the years of very poor breeding success is taken into consideration. However, a curvilinear regression would hardly have an effect on the intercept of the regression line and the steady state level.

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