Birth area fidelity and age at first breeding in a northern population of Pied Flycatcher Ficedula hypoleuca

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Out of 6459 ringed Pied Flycatcher nestlings that fledged, 68 (38 males and 30 females) were retrapped when breeding in the study area in later years. Thirteen of the males were retrapped as 1 yr old vs 20 of the females; most of the remaining birds were first retrapped when 2 yr old. A higher proportion of the males (3.3%) than the females (1.3%) were faithful to their natal area. The breeding sites of those birds (of both sexes) that returned were randomly distributed within the study area. The tendency of the offspring to return to their natal area seemed to be independent of the degree of site fidelity shown by their parents. Only about 25% of the returning males and 60% of the females seemed to breed when 1 yr old.

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Introduction

A large number of studies have treated the breeding biology of the Pied Flycatcher *Ficedula hypoleuca* throughout its European range, e.g. in Central Europe, the Soviet union, Great Britain, and southern and northern Scandinavia. One aspect that has received much attention is its fidelity to the breeding area (Trettau and Merkel 1952, Creutz 1955, Lichatshev 1955, Cambell 1959, von Haartman 1960, Berndt and Sternberg 1966, 1968). The comprehensive study of Berndt and Sternberg (1966), which included 25 study areas (totalling some 1000 ha) within a 2500 km² large area, and 544 recoveries of females ringed as nestlings, showed that these dispersed in random directions up to about 80 km from their birth site. In more moderately sized study areas thorough long-term studies are necessary to obtain enough data for a reliable estimate of the return rate to the natal area of birds ringed as nestlings.

The present study, which is part of a long-term project in subalpine birch forest in northen Sweden (the LUVRE project), aims at assessing the return rate of Pied Flycatchers to their breeding area in this northern part of the species' range. It also treats the age at which returning flycatchers first breed.

Material and methods

The study was carried out in a population of Pied Flycatchers breeding in nestboxes at an elevation of 500–600 m above sea level in meso- and eutrophic subalpine birch forest on the southern slopes of the mountains Gaissatjåkke and Valle, near Ammarnäs (65°58′ N), Swedish Lapland. The study was initiated in 1965 and the data used here were collected over 21 seasons, up to 1985. About 130–330 nestboxes were available, and 76–203 breeding attempts were made in each year.

The nestboxes were put up in groups. Within each group the boxes were placed about 30 to 120 m apart. The longest distance between any two boxes in the study area was about 5 km.

The nestlings were usually ringed and individually weighed when 7 d old. As a rule, breeding females were trapped during incubation and males when they were feeding nestlings. From 1966 to 1985 inclusive, on average about 78% of the breeding females and about 54% of the breeding males were caught.

The sample consists of 6459 ringed young that fledged in 1965–1982. Sixtyeight of these (38 males and 30 females) were retrapped between 1966 and 1985 when breeding in the area. The proportion of fledglings that

returned to their natal area in year B+1 was calculated using the following equations:

(1) $\quad P_R P_B P_F = \dfrac{X_1}{n}$

(2) $\quad P_R P_S P_F (1-P_B P_F) = \dfrac{X_2}{n}$

(3) $\quad P_R P_S^2 P_F (1-P_F)(1-P_B P_F) = \dfrac{X_3}{n}$

where P_R = Probability of returning to the study area in year B + 1
P_B = Probability of breeding in the study area in year B + 1
P_F = Probability of returning individuals being retrapped (trapping efficiency)
P_S = Probability of surviving from age i to i + 1; i = 1,2
X_i = Number of individuals found again for the first time in year B + i; i = 1,2,3
X_4 = Number of individuals not found again
n = Number of ringed young that fledged (6459/2 = 3230 of each sex).

Then the joint distribution of (X_1, X_2, X_3, X_4) is multinominal with the parameters 3230, $P_R P_S P_F$, $P_R P_S P_F$ (1-$P_B P_F$) and $P_R P_S^2 P_F$ (1-P_F)(1-$P_B P_F$). If the probabilities are estimated by the observed frequencies, the equations 1, 2, and 3 are obtained. From equations 2 and 3, P_S is

solved as $P_S = \dfrac{X_3}{X_2 (1-P_F)}$; P_R and P_B can then be solved from equations 1 and 2.

The calculations assume that the survival rate is similar for breeding and non-breeding flycatchers in the study area, and that non-breeding males and females are as faithful to the area as is the breeding part of the population. The latter assumption is supported, for males, by data in von Haartman (1949).

Results

Out of 3230 ringed nestling Pied Flycatchers of each sex that fledged, 38 males and 30 females were retrapped when breeding in the study area for the first time at the age of 1, 2, or 3 yr (Tab. 1). Only about a third (13 out of 38) of the males were retrapped in year B + 1 against two thirds (20 out of 30) of the females. With the method used to calculate birth area fidelity, the proportion of fledglings that returned to their natal area in year B + 1 was estimated at 3.3% for the males and 1.3% for the females. With a survival rate of fledged Pied Flycatchers in their first year of 25–30% (von Haartman 1951, Curio 1959) about 10–13% of the surviving males were faithful to their natal area, and 4–5% of the females.

Tab. 1. Numbers of ringed male and female nestling Pied Flycatchers first retrapped in year B + 1, B + 2 etc. The total number of ringed young that fledged was 3230 of each sex.

	B+1	B+2	B+3	B+4	B+5	B+6	B+7
Males	13	2	1	0			
		21	4	3	1	1	1
			4	1	1	0	
Females ..	20	4	2	0			
		9	2	1	0		
			1	0			

Tab. 2. Distance between birth site and breeding site as 1 yr old of Pied Flycatchers expressed as the accumulated % of birds settling within each distance zone. The difference between the sexes was not significant (Mann-Whitney U-test). n = 9 for males, n = 27 for females.

Distance (m)	Males	Females
0	0	0
1–49	0	0
50–99	11	4
100–199	16	11
200–299	26	15
300–399	26	19
400–499	32	19
500–999	58	41
1000–1999	63	48
2000–2999	74	70
3000–3999	79	96
4000–4999	100	100

Tab. 3. Distance between breeding sites in successive years (year B + 1 and later) of Pied Flycatchers, expressed as accumulated % of birds settling within each distance zone. n = 11 for males, n = 8 for females. The difference between the sexes was statistically significant (p < 0.01, Mann-Whitney U-test, two-tailed.

Distance (m)	Males	Females
0	0	0
1–49	9	25
50–99	27	25
100–199	64	25
200–299	91	50
300–399	100	63
400–499		75
500–999		89
> 1000		100

The breeding sites of 1 yr old flycatchers that returned were fairly randomly distributed within the study area, and there was no difference between the sexes in the mean distance between birth site and breeding site in year B + 1 (Tab. 2). Apparently those flycatchers that returned to breed in the study area also in year B + 2 were often attracted to their former breeding area. Thus, all males in this category settled less than

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Tab. 4. Numbers and frequencies of ringed and fledged Pied Flycatcher nestlings, 1965–1982, which were retrapped as breeders in the study area in 1966–1985, in relation to parental status.

	Fledglings ringed	No. retrapped			Frequency (%)
		Males	Females	Males + Females	
Both parents faithful.....................	328	2	2	4	1.22
Male faithful, female not	1437	10	9	19	1.32
Male faithful, female not ringed..........	79	1	2	3	3.80
Female faithful, male not.................	563	6	4	10	1.78
Female faithful, male not ringed	195	1	1	2	1.03
Total...................................	2602	20	18	38	1.46
Neither of the parents faithful	2907	18	18	36	1.23

400 m from their former nest site while more than half the females did so (Tab. 3).

The fidelity of young Pied Flycatchers to their natal area seemed to be independent of whether their parents were faithful to their breeding area or not. Tab. 4 shows that 1.46% of the retrapped offspring originated from parents (one or both) that were faithful to the study area while 1.23% originated from parents (both ringed) that did not reappear in the study area after their first breeding.

Among those 1 yr old males that returned to the study area in year B + 1, the proportion breeding (P_B) was calculated to be about 25%, whereas about 60% of the females bred at that age. The majority of the 22 males and 9 females which were first retrapped in year B + 2 (Tab. 1) almost certainly belonged to the non-breeding stock of flycatchers in the study area in year B + 1.

The weight development as nestlings (until day 7) was similar for males that bred in year B + 1 and males that were first retrapped in year B + 2 (Tab. 5). The age at first breeding thus seems to be unrelated to nestling development in males. In females, the situation is less clear. Those few females that were first retrapped (breeding) when 2 yr old (B + 2) had slower weight development as nestlings than those breeding already as 1 yr old (Tab. 5).

Discussion

My ambition has been to present reliable data on the

Tab. 5. The weights (g ± s.e.) at the age of 7 d of Pied Flycatchers that first bred as 1 yr old (year B + 1) and 2 yr old, respectively.

	Bred in year B + 1	First bred in year B + 2
Males	11.2±0.30 n=15	11.7±0.67 n=7
Females..........	12.0±0.46 n=10	9.1±1.19 n=3

proportion of fledgling Pied Flycatchers that returned to their natal area when 1 yr old (i.e. in year B + 1). To attain this, however, one must consider methodological problems such as incomplete trapping of the breeding population and lack of individual idenfication of the non-breeders. Several males and females were first identified when retrapped at two or three years of age (in years B + 2 or B + 3); at that time their numbers have become reduced by mortality acting during one or two years after year B + 1. One also has to guess the future faithfulness to the study area of those non-breeders that occur there in year B + 1 (and sometimes also in year B + 2), and their mortality in relation to that of the breeding ones. Here it was assumed that the non-breeding birds were as faithful as the breeding ones, which, for males, is supported by data in von Haartman (1949). It was also assumed that the mortality of the breeding Pied Flycatchers was not substantially different from that of the non-breeders.

The proportion of 1 yr old flycatchers that returned in year B + 1 was estimated at 3.3% for the males and 1.3% for the females. These values agree closely with those for Pied Flycatchers in southern Finland, 2.5% and 1.1%, respectively (von Haartman 1960). They thus support the existence of a difference in faithfulness to the natal area of Pied Flycatchers of North and Central Europe (pointed out by von Haartman 1960). The return ratios reported from Central Europe are generally higher, especially for the females, than further north (males: 4.4%, females: 6.7%, Trettau and Merkel 1952; males: 2.5%, females: 2.7%, Creutz 1955; males: 3.3%, females: 4.4%, Campbell 1959; males: 12.4%, females: 8.4%, Curio 1959; males: 2.9%, females 2.4%, Winkel 1982). In this study, and in southern Finland (von Haartman 1960), between two and three times as many 1 yr old males as females returned to the natal area, whereas in Central and Western Europe, return ratios were close to unity (1:1.3, Trettau and Merkel 1952; 1:1.1, Creutz 1955; 1:1.3, Campbell 1959; 1:0.7, Curio 1959; 1:0.8, Winkel 1982). While the return ratios of northerly breeding males were rather similar to those found in Central Europe (except for the higher values

reported by Curio 1959), those of the females were lower (cf. von Haartman 1960, Nyholm and Myhrberg 1983).

The breeding sites occupied by birds that had been ringed as nestlings were rather randomly distributed within the study area. This was true for both males and females. Similar results have been obtained in Germany (Berndt and Sternberg 1966, 1968, 1969) and in England (Campbell 1959). Thus, those birds that return do not seem to be guided by any attachment to their birth site when choosing their subsequent breeding site in the study area. Site tenacity has been suggested to develop during the first months of life in different migratory (*Phylloscopus trochilus, Hippolais icterina, Sylvia nisoria, Fringilla coelebs, Sturnus vulgaris,* Sokolov 1976) and non-migratory (*Parus atricapillus,* Weise and Meyer 1975) species. In my study area, young flycatchers may stay up to 40 d after fledging. During that period they may disperse several kilometres in random directions (Å. Lindström, unpubl.).

Having bred once in the study area, returning birds of both sexes showed a distinct attachment to the previous breeding site, the males significantly more so than the females. This attachment was similar in flycatchers which had not been born in the study area (Nyholm and Myhrberg 1983).

The present study cannot add much to the discussion on genotypic versus phenotypic control of site fidelity in the Pied Flycatcher. The similar return ratios of nestlings whose parents were faithful and whose parents were found breeding only once in the study area, respectively, indicate parental influence on area tenacity of the offspring only in a very wide sense. This is in accordance with Curio's (1958) statement that environmental quality alone determines the faithfulness of young Pied Flycatchers to their birth place.

Data from several studies support the conclusion that part of the returning 1 yr old Pied Flycatchers do not breed. In most studies where both sexes were considered, the proportion of non-breeding males exceeded that of the females (> 50% among males, c. 30% among females: Trettau and Merkel 1943, von Haartman 1949, Creutz 1955, Curio 1959). Harvey et al. (1985) found that at least 40% of both sexes did not breed when 1 yr old. In the present study about 75% of the males, and 40% of the females that returned after the first winter did not breed. A large proportion, about 30%, of the Pied Flycatcher territories in the study area may be held by males that fail to attract a female (Nyholm 1984). It seems resonable to assume that most of these males are 1 yr old.

Even though the material was small, there was an interesting indication that those females that were first retrapped when breeding as 2 yr old, on average showed a slower weight development as nestlings than those that bred as 1 yr old. In the males, there was no indication that age at first breeding was influenced by poor weight development during the nestling period. Lichatshev

(1955) found that more female young from late than from early broods did not breed until 2 yr old. Löhrl (1954) found the same thing, for borth sexes, in the Collared Flycatcher *F. albicollis,* the tendency being stronger in females than in males. In female flycatchers delayed sexual maturity may be a main reason for not starting breeding as 1 yr old; in males, lack of unmated, sexually mature females may be a common reason for not breeding at this age (cf. Nyholm 1984).

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