Breeding area fidelity of the Pied Flycatcher *Ficedula hypoleuca* at Ammarnäs, Swedish Lapland

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The breeding area fidelity was studied in 840 males and 1260 females of the Pied Flycatcher in subalpine birch forest in Sweden.

As the catching efficiency differed between the years, a varying part of the population could not be accounted for. A sex- and year-specific correction factor was used to obtain the numbers of birds faithful to their breeding area. The influence of interruptions, polygyny and unmated males holding territories is discussed.

Altogether, 21—25 % of the males and 8 % of the females that spent their first breeding season in the study area returned in subsequent years; among the birds that had spent two or more seasons there, about 50 % of each sex returned. As regards the distances between breeding sites in consecutive years, the females settled further away from the previous year's site than did the males.

It is suggested that in comparison of breeding area fidelity in the same or different species, and geographical regions, the most relevant parameter is the "potential breeding area fidelity", because it takes the survival rate into account.

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Introduction

Much research has been focused on the biology of the Pied Flycatcher *Ficedula hypoleuca* in the southern and central parts of its range, e.g. in Germany, the Soviet Union, England, southern Sweden and Finland, and the breeding area fidelity ("Ortstreue") has received wide attention (Enemar 1948, v. Haartman 1949, Trettau 1952, Campbell 1955, Creutz 1955, Lichatshev 1955, Curio 1959, Berndt & Sternberg 1965, Winkel 1982). In central Europe and England the females and the males were found to return equally regularly to their breeding areas, while in Scandinavia there was a clear difference in this respect between sexes, the females being less faithful than the males.

The purpose of the present study, part of a long-term field project in the subalpine birch woodland at Ammarnäs, Swedish Lapland (the LUVRE project), was to assess the proportion of Pied Flycatchers returning to their breeding area in the margin of the species' range.

Material and methods

Study area. About 300 nestboxes were erected in mesotrophic and eutrophic subalpine birch forest, 500 to 600 m above sea level, on the south slopes of the mountains Gaissatj and Valle, near Ammarnäs (65°58'N), Swedish Lapland. Five sets of nestboxes were used (F, G, K, T and V).

Group F: 44 nestboxes, 25 to 150 m apart.
Group G: 23 nestboxes, 100 to 125 m apart.
Group K: 41 nestboxes, 100 to 125 m intervals along a line.
Group T: 63 nestboxes, about 30 m apart.
Group V: 130 nestboxes, about 30 m apart.

Numbers of breeding birds. The Pied Flycatcher was the most common hole-nester and only a few nestboxes were occupied by other species, viz. the Great Tit *Parus major*, Redstart *Phoenicurus phoenicurus*, and Wryneck *Jynx torquilla* (Table 1).

When estimating the numbers of breeding Pied Flycatchers of each sex, we excluded those which interrupted their breeding at such an early date that they could be expected to start breeding again in the same season. This was done in order to avoid double counts, and overestimation of the breeding rate. Interruptions were classified as "early" when the nest was abandoned during the first week of June, in the building and egg-laying phase. Gonadal regression starts about a fortnight later, at the end of the incubation period or soon after hatching, making renesting impossible (Silverin 1980). We could not verify rebreeding in most cases because the females were not ringed.

Catching and ringing. The females were caught when incubating, and the males while feeding the nestlings. Of the 840 breeding males and 1260 females, ringed (Table 2), 221 and 170, respectively, were recaptured as breeders in the following year(s).

Correction factor. It was impossible to catch the entire breeding population of Pied Flycatchers in any one year (75—99 % of the females and 29—85 % of the males were caught). This made it difficult to estimate the numbers breeding for the first time and the true rate of return of the birds to their breeding area. To solve the problems created by the year to year variation in the proportion of the birds caught, we used the ratio of

the number of breeding individuals to the number of individuals caught as a correction factor (Table 2).

The validity of this correction factor is discussed below.

The concept "breeding area fidelity". Since only the breeding part of the population could be studied, the concept "breeding area fidelity" is restricted to the birds that returned and bred at least twice in the study area nestboxes (cf. Berndt & Sternberg 1968). Part of the total male population held territories without breeding. v. Haartman (1951a) estimated the non-breeding fraction of the male population at 30 %, and a similar proportion of the males may have failed to mate in our area (Nyholm, unpubl.). According to v. Haartman (1951a), the vast majority of the non-breeding males are newcomers to the area.

Results

Return rate of birds that had bred once in the study area. The unringed part of the population that settled in the study area (except in 1965) presumably consisted of birds breeding for the first time in the area and birds that had escaped ringing when breeding earlier. When estimating the numbers of these birds we assumed that the birds caught formed a representative sample of the total population (Fig. 1).

The numbers of birds calculated to have been ringed when breeding for the first time (year x) in the study area in 1965—1975 were 731 males and 1155 females. On average 25 % of the males and 8.2 % of the females returned and bred the following year (x+1) (Table 3).

Return rate of birds breeding more than once in the study area. Tables 4 and 5 give the numbers of males and females returning in consecutive years. The return rates in the breeding populations were calculated from these tables. The numbers of males were calculated for the years 1965—1969, those for the females for 1965—1972, in order to be sure that none of the individuals taken into account returned more times.

The return rate of the males that had bred more than once before in the study area was 46 %. This did not differ statistically significantly from the return rate of the corresponding females.

Distances between breeding sites in different years. Most returning birds occupied a nestbox close to that of the previous year. Of the males, 20 %

Table 1. Numbers of nestboxes and breeding pairs, and occupation percentage.

Year	Number of nestboxes	*Ficedula hypoleuca*	Other species	Occupation %
1965	130	94	9	79
1966	130	76	6	63
1967	238[a]	85	8	39
1968	238	101	7	45
1969	300[b]	144	6	50
1970	300	175	5	60
1971	300	174	9	61
1972	300	151	3	51
1973	300	167	12	60
1974	300	203	11	71
1975	300	175	20	65
1976	300	120	5	42
Total		1664[c]	101	

a) The number of nestboxes was increased in June 1966.
b) The number of nestboxes was increased before the breeding season in 1969.
c) Excluding pairs abandoning nest at an early date (see text).

Table 2. The numbers of Pied Flycatchers caught and ringed, and the correction factor for the different years.

Year	Numbers caught		Numbers ringed		Correction factor[a)]	
	Males	Females	Males	Females	Males	Females
1965	80	92	80	92	94/80	94/92
1966	47	71	36	65	76/47	76/71
1967	25	76	21	63	85/25	85/76
1968	68	100	55	92	101/68	101/100
1969	96	132	82	115	144/96	144/132
1970	123	150	100	134	175/123	175/150
1971	106	139	83	122	174/106	174/139
1972	102	114	76	100	151/102	151/114
1973	106	137	80	116	167/106	167/137
1974	145	178	117	151	203/145	203/178
1975	79	136	56	115	175/79	175/136
1976	84	105	54	95	120/84	120/105
Total	1061	1430	840[b)]	1260[b)]		

a) For breeding numbers, see Table 1.
b) Includes individuals ringed when breeding for the first time in the study area (774 males, 1255 females) and birds not ringed during their first breeding season in the area (66 males, 5 females; calculated numbers).

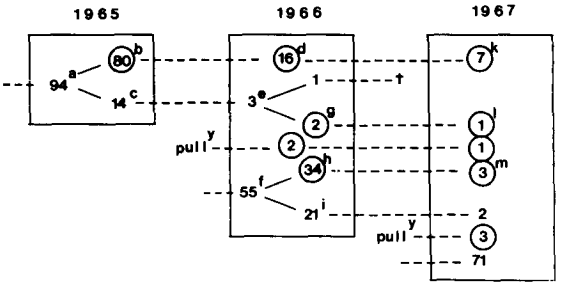

Fig. 1. Calculation of that part of the Pied Flycatcher population which return after having bred once in the study area. (The calculation for the males during the first three years is taken as an example.)

Explanations for Fig. 1.

Encircled figures are numbers of ringed birds.

a) Number of males breeding in the nestboxes in the first year. The number breeding in natural holes in the study area was insignificant.
b) Number of males ringed in 1965.
c) Number of breeding unringed males in 1965; a–b.
d) Calculated number of males ringed in 1965 that bred in the study area in 1966 also; correction factor × number of controlled ringed males (cf. Table 2).
e) Calculated number of unringed males that bred in the study area in 1965 also; d/b × c.
f) Male immigrants in 1966; breeding number – (d+e+x).
g) With the catching efficiency reached in 1966, two out of three birds breeding for the second time in the study area were ringed; e/corr. factor.
h) 34 out of 55 immigrants in 1966 were caught; number ringed (cf. Table 1) – g.
i) Number of unringed immigrants in 1966; f–h.
k) Calculated number of birds breeding for third time and ringed in 1965; correction factor 1967 × number of controlled ringed males.
l) Calculated number of birds breeding for third time but not ringed until 1966; g × k/d.
m) Calculated number of birds breeding for second time and ringed in 1966; number of ringed controls × correction factor.
y) Males born in the study area and breeding for the first time; number of ringed controls × correction factor.
†) Probably dead before next breeding season.

Table 3. Percentages of birds breeding in the study area for the first time that returned in subsequent years.

Year	Males %	Females %
1966	20.0	6.5
1967	8.8	10.8
1968	30.0	7.9
1969	29.1	12.2
1970	22.4	7.0
1971	27.1	7.5
1972	23.7	4.1
1973	25.0	16.0
1974	26.3	8.9
1975	30.3	9.2
1976	26.5	2.7
1966—1976	25.0	8.2

returned to the same nestbox and about 50 % to a box within 100 m (Table 6). The females moved significantly further than the males (χ^2 = 21.20, P<0.01); only about 25 % nested within 100 m of the site of the previous year.

Discussion

The validity of the correction factor. The size of the correction factor depends on the number of birds caught and the true number of breeding birds. Assumptions made in calculating the size of the breeding population were that all the birds that abandoned their nests early in the season started breeding again, and that polygyny was infrequent.

As pointed out above, it was not usually possible to verify that the birds that abandoned their nest actually renested later in the season. In every year some birds started breeding late in the season, and the number of such observations corresponded approximately to that of the nests abandoned early. In some cases rebreeding females were actually identified. In other cases the birds may have arrived late in the study area. But even if none of the birds that abandoned their nests early started breeding again, this would mean in addition of less than 1 % to the frequencies of returning breeders given in Table 3.

In the Ammarnäs population the frequency of polygynous males was certainly lower than in any other population studied so far (Germany 12 %, Creutz 1955; Finland 7 %, v. Haartman 1951b; southern Sweden 20—25 %, Askenmo 1977, Silverin 1980). Preliminary calculations for 1965—1976 indicate that the proportion of polygynous males did not exceed 3 %. In 1980, not a single polygynous male could be identified in about 120 breeding pairs (Nyholm, unpubl.). Thus, any overestimation of the number of breeding males because of polygyny should be negligible.

Other factors influencing the calculated return rate to the breeding area. We cannot exclude the possibility that some of the Pied Flycatchers that had bred in the nestboxes returned and bred in natural holes outside the study area in the following years. However, this source of error is certainly negligible as the density of the Pied Flycatcher population outside the nestbox area was small. In the years 1963—1970 the number of territories/km^2 was less than 15 (Enemar & Sjöstrand 1972). Every year many of the nestboxes in the study area remained unoccupied, and there is no reason to assume that a significant number of birds had to move outside because of overcrowding.

The unmated individuals in the population were not considered in this study, as they could not

Table 4. Numbers of males returning to the breeding area. The year of ringing is denoted by x. The numbers for x+1, etc. are calculated.

Year	x	x+1	x+2	x+3	x+4	x+5	x+6
1965	80	16	7	4	5	3	0
1966	36	3	3	0	1	0	0
1967	21	6	0	0	0	0	0
1968	55	14	9	2	1	0	0
1969	82	20	8	4	2	1	0
1970	100	25	9	5	1	2	1
1971	83	19	11	1	2	1	—
1972	76	16	7	4	1	—	
1973	80	20	7	9	—		
1974	117	33	9	—			
1975	56	13	—				

Return rate (weighted mean, %) in the breeding populations in 1965—1969 (as calculated from year x+1 onwards):

$$\frac{27+10+9+4}{59+27+10+9+4} = 46\ \%$$

Table 5. Numbers of females returning to the breeding area. The year of ringing is denoted by x. The numbers for x+1, etc. are calculated.

Year	x	x+1	x+2	x+3	x+4
1965	92	7	6	1	0
1966	65	7	3	1	1
1967	63	5	4	0	0
1968	92	11	6	1	0
1969	115	8	8	5	1
1970	134	10	5	2	1
1971	122	5	4	0	0
1972	100	16	14	5	0
1973	116	11	6	2	—
1974	151	15	3	—	
1975	115	3	—		

Return rate (weighted mean, %) in the breeding populations in 1965—1972 (as calculated from year x+1 and onwards):

$$\frac{50+15+3}{69+50+15+3} = 50\ \%$$

be caught by methods used. v. Haartman (1951a) and Curio (1959) reported that the frequency of unmated males holding territories in Finland and Germany was about 30 %. Most of the unmated males were newcomers to the study area (mainly 1 year old); very few older males remained unmated (v. Haartman 1951a:43). The frequency of unpaired females was low, about 3 % (Curio 1959). In the Ammarnäs area, the frequency of territory-holding unmated males may likewise be about 30 %, as judged from a one-year study (Nyholm, unpubl.).

According to v. Haartman (1949:40), the unmated males were as faithful to the area as were the breeding "year (x) males". If this is also true in the Ammarnäs area, the return rate of the males breeding for the first time (25 %, Table 3) could relate to a heterogeneous group consisting of males that bred and others that were unmated during their first year in the study area. The presence of the latter category will give an overestimation of the return rate of the males that bred during their first year. Assuming that 30 % of the males were unmated each year, and that these were as faithful to the study area as were the breeding year (x) males, the return rate of the latter would be about 21 %.

Return rate of birds breeding for the first time.

Males. The return rate of the birds spending their first breeding season in the study area was thus lower than 25 %. This is also suggested by the return rate (20 %) of the males that bred in the first year the study, in 1965, when the calculation was not disturbed by returning unmated males.

In 1967 the return rate, 8.8 %, was markedly lower than in any other year. This was possibly due to the low breeding success that year, which made it difficult to catch the males.

Male Pied Flycatchers in the Ammarnäs area return to the breeding area less often than in more central parts of the species' range, where the corresponding rates are reported to be: in Germany 35.1 % (Trettau 1952), 27.5 % (Creutz 1955), 44.7 % (Curio 1959) and 38.2 % (Winkel 1982); in England 39 % (Campbell 1955); in southern Finland 35.6 % (v. Haartman 1960); in southern Sweden 38 % (Askenmo 1979).

Table 6. Distances between breeding sites in consecutive years.

Metres	Year x to x+1 Accumulated percentage	Year x+1 to x+2 Accumulated percentage
Males		
0	20	25
1— 49	33	31
50— 99	47	56
100—199	71	75
200—299	85	88
300—399	90	94
400—499	92	94
500—999	98	100
1000—	100	
	n=88	n=16
Females		
0	13	0
1— 49	17	9
50— 99	23	35
100—199	47	48
200—299	61	66
300—399	67	75
400—499	74	84
500—999	80	89
1000—	100	100
	n=69	n=23

Females. The return rate of the female Pied Flycatchers after their first breeding season in the Ammarnäs area averaged 8.2 %. This rate is lower than those reported in other Scandinavian studies: 13.6 % (Enemar 1948) and 13.9 % (v. Haartman 1960). Much higher rates are reported for the European continent and England: 21.7 % (Trettau & Merckel 1943), 37.5 % (Trettau 1952), 27.1 % (Creutz 1955), 30 % (Curio 1959, Lichatshev 1955), 24 % (Winkel 1982) and 40 % (Campbell 1955).

The tendency for breeding area fidelity to decline towards the north is accentuated by the rates observed in the Ammarnäs area, for both female and male Pied Flycatchers.

In the Ammarnäs area, as in other Scandinavian studies (v. Haartman 1960), but in contrast to those of the European continent and England (ref. op. cit.), the return rate of the female Pied Flycatchers was markedly below that of the males.

Return rate of Pied Flycatchers that had bred at least once in the study area, and their survival rate. The return rate of the Pied Flycatchers that had bred twice or more in the study area was about 50 %, which was significantly higher than the rate for the birds that had bred once. Like v. Haartman (1951a:17, 18), we found that the males and females which had bred more than once in the study area were equally faithful to their breeding sites, and we assume that they return regularly and that their *return rate is equal to their survival rate,* about 50 %. Similar survival rates (female 40 % and male 45 %) were obtained when they were calculated by Haldane's (1954) method.

Frequency of birds potentially faithful to their breeding area. When the breeding area fidelity is compared between different geographical regions, the possibility of variation in the survival rate should be taken into account. This can be done by basing the comparison on the frequency of potentially faithful birds, i.e. those individuals in the breeding population which would return if they survived till the next breeding season.

Both this and earlier studies (e.g. v. Haartman 1949) indicate that all male and female Pied Flycatchers that have returned to their breeding area once are potentially faithful to it. Among those males and females which breed for the first time, on the average 50 % and 16 %, respectively, are likely to return to the Ammarnäs area, if they survive. The corresponding figures in southern Finland, where the survival rate was the same as at Ammarnäs (about 50 %), would be about 70 % and 28 % for the males and females, respectively (based on v. Haartman 1949, 1960).

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Selostus: **Kirjosiepon pesimäalueuskollisuudesta Ammarnäsissä, Ruotsin Lapissa.**

Kirjosiepon palaamisuskollisuutta pesimäalueelleen tutkittiin subalpiinisessa tunturikoivikossa Ammarnäsissä (65°58'N), lajin esiintymisen reuna-alueella. Aineistoa on 12 vuodelta (1965—76). Tutkimusalueella on vuodesta 1969 lähtien ollut 300 pönttöä (taul. 1), joista vuosittain oli asuttuja 39—79 %. Kirjosiepon osuus pönttöpesijöistä oli keskimäärin 94 %. Kaikkiaan rengastettiin 840 pesivää koirasta ja 1260 naarasta, joista 221 koirasta ja 170 naarasta pyydystettiin pesivinä seuraavina vuosina.

Pyydystystehokkuus vaihteli melkoisesti vuosien välillä, mikä vaikeutti ensipesijöiden määrän ja pesimäalueuskollisuuden arviointia. Molemmille sukupuolille käytettiin arvioiden korjaamiseksi vuosikohtaista korjauskerrointa (pesivien määrä/pyydystettyjen määrä) (taul. 2). Pesien hylkäämisten, moniavioisuuden ja pesimättömyyden vaikutuksia tuloksiin tarkastellaan.

Ensimmäisen pesimäkautensa jälkeen 21—25 % koiraista ja 8 % naaraista palasi tutkimusalueelle seuraavana keväänä. Vähintään kahdesti alueella pesineistä yksilöistä n. 50 % palasi alueelle (taul. 3—5). Pesimäalueuskollisuuden selvittämisessä käytettyä menetelmää on esitetty kuvassa 1. Koiraat pesivät merkitsevästi lähempänä edellisvuotista pesäänsä kuin naaraat (taul. 6).

Vertailtaessa pesimäalueuskollisuuden alueellisia eroja lajinsisäisesti tai eri lajien välillä, on mielekkäintä käyttää tunnuslukua "potentiaalinen pesimäalueuskollisuus", mikä ottaa huomioon myös eloonjäävyyden.

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