Population dynamics in the Pied Flycatcher *Ficedula hypoleuca* at subarctic Kilpisjärvi, Finnish Lapland

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The Pied Flycatcher population nesting in boxes at subarctic Kilpisjärvi was studied during 14 successive years (1966—79) with respect to clutch size, nesting success and population density. The population dynamics was affected more by the physical environment than by intra- or interspecific relationships.

Egg-laying commenced, on average, about 14 June. The average clutch size was 5.42 ± 0.04 ($N=377$), the smallest known for the species. Both the annual variation and seasonal decline in clutch size were statistically significant. In early seasons females weighed more and laid larger clutches. It is argued that the small clutch size was due to the unfavourable climate and scarcity of food, which prevented Pied Flycatcher females from demonstrating their full clutch size potential.

Nesting success varied greatly from year to year, averaging 3.5 fledglings per nest. Most losses were due to hatching or fledging failures during cold and rainy spells. Predation was negligible. The modal clutch of five eggs tended to produce less fledglings than larger clutches. There was no difference in clutch size or nesting success between rich and meagre birch forests. It was estimated that the production of young was insufficient to maintain a stable population at Kilpisjärvi without immigration.

Breeding density fluctuated markedly and was not dependent on nesting success in the previous year. The maximum density was seven times the minimum. The densities corresponded fairly well with population changes elsewhere in the species' range and were highest after warm and early springs.

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Introduction

The breeding biology of the Pied Flycatcher is very well known. Most of the work has been done near the centre of the species' range, and the dynamics of marginal populations has received less attention, though treated by, for instance, Meidell (1961), Lind & Peiponen (1963), Hanson et al. (1966), Valanne et al. (1968), Pulliainen (1977), Järvinen (1978a) and Järvinen & Tast (1980). Long-term series covering at least 10 years are particularly needed.

Many theories concerning population regulation are based on studies in favourable regions, where the numbers may be density-dependent. In unpredictable marginal areas regulation is apparently achieved more by the physical environment. For a discussion of this point, see Krebs (1978: pp. 283—300).

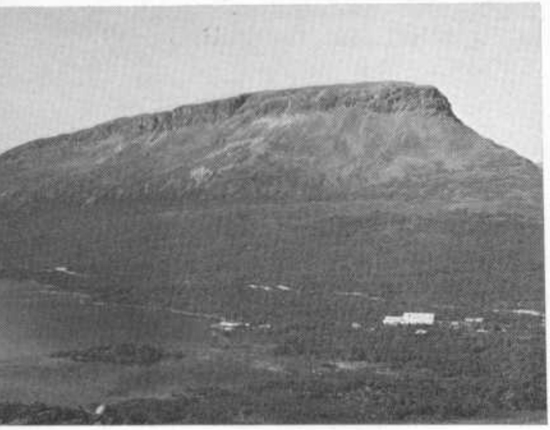

FIG. 1. The study area at the foot of the Saana mountain, alt. 1029 m, at the end of July.

The effect of nest-boxes on the numbers of hole-nesting passerines at Kilpisjärvi Biological Station has been investigated since 1957, and in 1966 a systematic study was started on the breeding biology of these species (see Valanne et al. 1968, Järvinen 1978a, b, c, d and Järvinen & Tast 1980). This paper discusses the clutch size, breeding success and population density of the Pied Flycatcher at the northern edge of its distribution, under harsh subarctic summer conditions. The timing of breeding will be treated in another paper.

Study area and material

The data were collected in subalpine mountain birch forest (69°03′N, 20°50′E) in Finnish Lapland during 1966—79 (Fig. 1). The birches are 4—6 m high and offer few cavities for hole-nesting birds. The area lies in a border zone between continental and maritime climates. The weather is unstable and the time available for breeding short. The snow in the birch forests melts in early June. The mean temperature in June is +8°C and in July +10.5°C. During the breeding season cold spells occur repeatedly, occasionally with falls of snow. For details, see Valanne et al. (1968) and Federley (1972).

At Kilpisjärvi the Pied Flycatcher breeds preferably in rich meadow birch forests, but meagre forests are also frequently chosen (Järvinen 1978a). The species was the commonest inhabitant of the nest-boxes (388 pairs or 72.0 % of all nestings), although it settled in the area only after the installation of boxes in the late 1950s. The other dominant species were the Redstart *Phoenicurus phoenicurus* (20.8 %) and the Siberian Tit *Parus cinctus* (4.5 %). The nest-boxes were situated 1—2 m above the ground at altitudes of 475—600 m (the upper boundary of the birch zone lies at c. 600 m). The distance between the boxes, placed along lines, was 20—50 m.

The Pied Flycatcher nested almost exclusively in boxes with a 30-mm entrance hole, although boxes with a 45-mm entrance were available (Järvinen 1978c). No nests were found in natural cavities. In 1966 there were 51 boxes with the smaller entrance, but the next year the number was doubled. Since 1970 there have been about 170 nest-boxes in total, but even in the most favourable seasons more than half have remained unoccupied. In spite of this, competition for nest sites sometimes occurred between the Pied Flycatcher and the Siberian Tit, the former being the more successful competitor (Järvinen 1978b).

The nest-boxes used at Kilpisjärvi were relatively large, the diameter of the nest cavity being $\geq$ 10 cm. Hence, the size of the boxes can hardly have affected the clutch size or nesting success, particularly as the Pied Flycatcher does not respond to the nest-box area as strongly as, for instance, *Parus* species (Karlsson & Nilsson 1977).

Results

Clutch size. Laying started, on average, on 14 June and coincided with the leafing of the birches. About 95 % of the clutches were commenced between 6 and 23 June. The size of the complete clutch was recorded for 377 nests (Table 1). The range was 3—8, the modal size five and the mean 5.42 ±0.04 eggs per clutch. The yearly variation of the means was 4.88—6.13, being statistically significant ($F=2.71$, $P<0.001$). Clutches commenced on 4

TABLE 1. Clutch size of the Pied Flycatcher at Kilpisjärvi in 1966—79.

Year	3	4	5	6	7	8	*N*	$\bar{x}$	*SE*
1966	—	5	5	6	1	—	17	5.18	0.23
1967	—	4	14	8	2	—	28	5.29	0.15
1968	—	2	5	1	—	—	8	4.88	0.23
1969	—	1	11	4	—	—	16	5.19	0.14
1970	1	4	26	17	6	1	55	5.47	0.12
1971	—	3	20	16	1	2	42	5.50	0.13
1972	—	4	10	14	4	—	32	5.56	0.16
1973	1	2	14	9	1	—	27	5.26	0.16
1974	1	3	25	19	4	—	52	5.42	0.11
1975	—	6	11	9	1	—	27	5.19	0.16
1976	—	2	8	5	2	—	17	5.41	0.21
1977	—	2	8	5	—	—	15	5.20	0.17
1978	—	2	4	5	—	—	11	5.27	0.24
1979	—	—	6	15	8	1	30	6.13	0.14
Total	3	40	167	133	30	4	377	5.42	0.04
%	0.8	10.6	44.3	35.3	8.0	1.1	100.1		

—14 June ($N=180$) averaged 5.77 and those commenced on 15—29 June ($N=152$) 5.11 eggs ($t=7.43$, $P<0.001$). There were no second clutches and only one clutch is known to have been repeated.

Nesting success and population density. The nesting success is summarized in Table 2. It varied greatly from year to year, averaging 1.4—4.9 fledglings per nest. Especially poor years were 1966, 1967, 1975 and 1977. The mean for the 14 study years was 3.5, or 64 fledglings per 100 eggs laid. The breeding density (expressed as the percentage of 30-mm nest-boxes occupied) fluctuated markedly, but was not dependent on nesting success in the previous summer (Table 2).

The suitability of a habitat can be estimated from nesting success. At Kilpisjärvi the mean clutch size in rich birch forests (GDrM and TrG type, see e.g. Järvinen 1978a, b) was 5.41 and the mean number of fledglings 3.37 ($N=196$). The corresponding values for meagre birch forests (EM and ELi type) were 5.34 and 3.35 ($N=104$). Thus there was no difference between the two habitats. Habitat selection did not seem to differ between periods of high and low density (Järvinen 1978d).

The modal clutch of five eggs produced, on average, 2.85 fledglings per nest, significantly less than clutches of 6—8 (Table 3).

Discussion

Clutch size. The northward decrease in climatic predictability causes instability in the biological communities, the effect of the weather extremes being aggravated by the shortness of the growing season (Kalela 1962, O. Järvinen 1979). According to my observations, birds frequently suffer from lack of insect food during cold spells at Kilpisjärvi. Hence, the weather is obviously one of the prime factors affecting reproduction and survival in many species inhabiting arctic and subarctic regions. This is especially true of the Pied Flycatcher when it is

TABLE 2. Breeding success of the Pied Flycatcher at Kilpisjärvi in 1966—79. In nine (2.4 %) of the 377 completed clutches data on breeding success were not available.

Year	Nests	Eggs	Hatched	Hatched/ 100 laid	Fledg- lings	Fledg- lings/ 100 eggs	Fledg- lings/ nest	Nest- boxes occupied (%)
1966	17	88	25	28.4	23	26.1	1.35	33.3
1967	26	138	101	73.2	39	28.3	1.50	27.7
1968	8	39	37	94.9	37	94.9	4.62	7.9
1969	16	83	80	96.4	78	94.0	4.87	17.8
1970	54	294	253	86.1	174	59.2	3.22	56.4
1971	42	231	172	74.5	114	49.4	2.71	44.6
1972	30	168	162	96.4	125	74.4	4.17	35.0
1973	27	142	128	90.1	115	81.0	4.26	27.3
1974	52	282	257	91.1	224	79.4	4.31	53.1
1975	26	136	86	63.2	58	42.7	2.23	30.2
1976	15	81	71	87.7	64	79.0	4.27	17.9
1977	15	78	41	52.6	31	39.7	2.07	15.6
1978	11	58	45	77.6	45	77.6	4.09	11.5
1979	30	184	162	88.0	145	78.8	4.83	31.2
Total	368	2002	1620	80.9	1272	63.5	3.46	(29.3)

living at the northern and altitudinal limit of its range.

In contrast to the trend in many other passerines, the mean clutch size of the Pied Flycatcher seems to decrease through southern and central Finland to subarctic Kilpisjärvi; the value from Kilpisjärvi is the smallest known for the species, being about one egg smaller than, for instance, in S Finland (Ojanen et al. 1978). The same trend is evident from records made in different parts of the Scandinavian mountain chain (Järvinen 1978a). In the Redstart the clutch size decreases comparatively little along the same geographical gradient. This migrant species is a natural inhabitant of boreal and subarctic zones and consequently better adapted to northern environments (Järvinen 1978c). The decline in the clutch size of the Pied Flycatcher during the season seems to be less pronounced at Kilpisjärvi than in southern Finland (v. Haartman 1967).

Exact data on avian clutch sizes in arctic and subarctic areas are still scanty. Salomonsen (1972) considers that arctic species may be expected to lay smaller clutches, as it is well known that birds sometimes do not breed at all during very inclement years. Laying a small clutch would be a compromise between breeding and not breeding. In uncertain environments, however, the species should be *r* selected (e.g. Cody 1971). At Kilpisjärvi the Pied Flycatcher should maximize the number of offspring produced, but apparently there is a limit to the capacity of the females; they cannot afford to spend more than a limited amount of energy on reproduction when conditions are as unfavourable as in N Lapland (cf. Wagner 1957).

Thus, the small clutch size of the Pied Flycatcher in high latitudes seems to be explained by the adverse climate and scarcity of food (Valanne et al. 1968, Pulliainen 1977, Järvinen 1978a). On the Falkland Islands, Pet-

TABLE 3. Survival in relation to clutch size in the Pied Flycatcher at Kilpisjärvi in 1966—79.

Clutch size	Nests	Fledglings/ nest	Fledglings/ 100 eggs
3	3	1.00	33.3
4	39	2.26	56.4
5	159	2.85	57.0
6	133	3.91	65.2
7	28	4.36	62.2
8	4	4.00	50.0

tingill (1960) attributed small clutches in several species to the adverse climate, but they may be partly due to the 'island effect' (Cody 1971).

The average clutch size of 1979 is remarkably large. This was probably due to the exceptionally favourable summer: the onset of breeding was earlier than ever before (only one clutch commenced after 15 June) and the weather was warm and sunny throughout the season, making it possible to lay extra eggs. It was the first year when there were no clutches of four eggs.

In 1974—79 I weighed females to discover whether there were any differences in the physical condition of the birds between early and late seasons. On average, the birds were weighed seven days after they had laid their first egg. In early seasons (1974, 1976, 1978 and 1979; average onset of breeding before 15 June) the females weighed 15.55 ± 0.11 *(SE)* g, but in late seasons (1975 and 1977; average onset of breeding after 15 June) only 14.43 ± 0.19 g ($t = 4.93$, $P < 0.001$; $N_1 = 90$, $N_2 = 29$). As seen in Table 1, parallel variation occurred in clutch size. Thus the well-known tendency to lay larger clutches in early springs seems to be related, at least at Kilpisjärvi, to the better condition of the females. The exceptionally large clutches in 1979, connected with the body weight differences described above, indicate that Pied Flycatcher females have the potential to lay larger clutches than are produced in most years.

In the north the proportion of females breeding for the first time is presumably great (v. Haartman 1949). Although I do not know the age structure of the Kilpisjärvi population, it includes old females, too. For example, in 1977 three of the 15 females had been ringed earlier: two as breeding birds at Kilpisjärvi in 1974 and 1975, one 1-year-old as a nestling in Swedish Lapland 100 km to the SW. If the first-breeders tend to lay somewhat smaller clutches at Kilpisjärvi, as they do in more southern areas (Berndt & Winkel 1967, v. Haartman 1967), then the low average clutch size could partly result from the age structure.

Production of young. The average nesting success of the Pied Flycatcher at Kilpisjärvi was relatively low and, compared with that in southern areas (e.g. Källander 1975), varied greatly from year to year. Valanne et al. (1968) attributed the heavy losses to the adverse climate: the eggs failed to hatch during cold spells or the nestlings starved when rain reduced the amount of insect food available. Of the three regularly breeding hole-nesters, the Redstart did best (Järvinen 1978b, c, d).

Although covering a fairly long period, my data do not show a clear correlation between the average values of climatic variables (temperature and precipitation) and nesting success. However, the average values are not good indicators, for a single night of frost can be disastrous (cf. Jehl & Hussell 1966, Formozov 1970, Pulliainen 1977, 1978a). In the Canadian tundra, Jehl & Hussell (1966) attributed the substantial nestling mortality in passerines to exposure, not to starvation, and Pulliainen (1978a) observed heavy losses in the broods of many passerines, including box-nesting species, during a fall of snow in NE Finnish Lapland. In western Finland, the Starling *Sturnus vulgaris,* a southern species, was likewise sensitive to changes in temperature (Korpimäki 1978).

Ricklefs (e.g. 1973) suggests that, broadly speaking, the intensity of predation on passerines may be negligible in the Arctic. His view is consistent with my observations from Kilpisjärvi, where predators did not cause appreciable nesting losses in the Pied Flycatcher. Only two nests with eggs and two with nestlings were plundered by weasels *(Mustela erminea* and/or *M. rixosa).* This is 1 % of the nests containing at least one egg. The plundering took place in 1971 (included in Tables 2 and 3), after the small rodent populations had crashed. There was no predation in 1975 or 1979, although these were crash years, too. Similarly, in the Redstart at Kilpisjärvi predation on the nests was slight, about 5 % (Järvinen 1978c). In open-nesting species, however, especially in years when small rodents are scarce, the impact of predation may be strong (e.g. Custer & Pitelka 1977).

In an area in Russia, fewer nestling Pied Flycatchers died in deciduous than in coniferous forests (cited according to v. Haartman 1971), and habitat-linked differences in clutch size have been observed in central Europe and southern Sweden (Berndt & Winkel 1967, Källander 1975), though not in Finland (v. Haartman 1954, 1971; see also the present paper). At Kilpisjärvi, where the populations are relatively small, density did not seem to be related to the suitability of the habitat.

In the Pied Flycatcher the annual adult mortality is approximately 50 % (v. Haartman 1951). In a stable population the proportion of first-breeders should equal the adult mortality, but at Kilpisjärvi they compose only about 39 % of the population (calculation based on Soikkeli's (1970) formula and v. Haartman's (1951) estimates). Hence the production of young seems to be insufficient to maintain a stable population without constant immigration.

According to Lack's theory (e.g. Lack 1966), the clutch size of nidicolous birds has evolved to correspond with that brood size from which, on average, most young are raised. The information available on survival in relation to clutch size in the Pied Flycatcher is somewhat conflicting (see e.g. Lack 1966:97, Tompa 1967, Askenmo 1977), and the use of averages has also been criticized (Mountford 1973).

My results do not confirm the theory: the modal clutch of five eggs gave rise to fewer fledglings than larger clutches. Moreover, in four seasons (1966, 1972, 1978 and 1979) a clutch of six was the most frequent. v. Haartman (1954) and Askenmo (1977) observed that the young in large broods were lighter, and in the Great Tit *Parus major,* though not in the Pied Flycatcher, the recovery rate of birds from unusually large broods was reduced (Lack 1966:48, but see v. Haartman 1971). At Kilpisjärvi neither the weight of the young nor their fate after leaving the nest was studied, which makes it impossible to decide which clutch size was most successful.

Regulation of density. Some authors (see Lack 1966) have presented strong evidence that clutch size is negatively correlated to population density. At Kilpisjärvi the correlation seems to be positive rather than negative (Järvinen & Tast 1980). In my study area density was high in favourable summers, and in these conditions the clutch size also tended to be higher. Compared with that in more southern areas, the density of Pied Flycatchers is low at Kilpisjärvi. Thus, the simultaneous increase of both density and clutch size does not cause too heavy a burden for the population. This conforms with Krebs' (1978:293) view that in unpredictable environments the numbers will change because of density-independent processes.

In subarctic regions the Pied Flycatcher is a 'stranger', a migratory species that has taken advantage of nest-boxes. In consequence, its density fluctuations there may be influenced by the population level elsewhere (cf. Kalela 1944). It is interesting to note that the fluctuations in the numbers at Lammi, S Finland, in 1971—77 closely parallelled those at Kilpisjärvi (Tiainen & Solonen 1979).

The lowest densities were found in 1968 and 1978. As Valanne et al. (1968) have remarked, in the former year the weather in the whole of northern Europe was exceptionally bad and probably stopped migration earlier than normal. In 1976—78 a strong decline in the numbers of the Pied Flycatcher was recorded in many localities in Finland, including Kilpisjärvi (Pulliainen 1978b, Järvinen & Tast 1980), so that the reserves must have been greatly depleted.

Warm and early springs apparently induce prolonged migration, since the densities were highest in those years at Kilpisjärvi (Järvinen 1978a). That the output of fledglings in one season had no influence on the numbers of breeding pairs in subsequent seasons is a common phenomenon in many other species (see e.g. Lack 1966). Mortality outside the breeding season is presumably more important.

According to v. Haartman (1971), the Pied Flycatcher populations in southern Finland and central Europe are "remarkably stable", the maximum densities being twofold the minimum at most. In his study area in SW Finland, the mean rate of fluctuation from year to year (expressed as the coefficient of variation) was about 15 % (calculated for 1953—68 from his Fig. 9). At Kilpisjärvi in 1967—79 — when the number of nest-boxes remained constant — the minimum was 8 (1968) and the maximum 57 (1970) pairs. The difference is sevenfold and the coefficient of variation 54 %.

The present study provides substantial evidence that population fluctuations may be more pronounced in northern and/or marginal areas, reflecting the more pronounced environmental variation. It supports Siivonen's (1948) conclusion, based on quantitative bird surveys, that the average abundance varies about twofold in southern and central Finland and about tenfold or even more in the most northern parts of Lapland. The numbers of the 'native' Redstart at Kilpisjärvi fluctuated about as much as those of the Pied Flycatcher and in fair synchrony with small rodents (Järvinen & Tast 1980).

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Selostus: Kirjosiepon populaatiodynamiikasta Kilpisjärvellä

Kirjosiepon populaatiodynamiikkaa tutkittiin 1966—79 Kilpisjärvellä tunturikoivuvyöhykkeessä, joka on lajin kannalta äärialuetta. Kaikki pesät sijaitsivat linnunpöntöissä.

Ensimmäinen muna munittiin keskimäärin n. 14.6. Munamäärä oli keskimäärin 5.4/pesä, mutta keskiarvon vuosivaihtelu oli suuri (taul. 1). 4—14.6. aloitetuissa pesissä oli 5.77 ja 15—29.6. 5.11 munaa. Aikaisina keväinä naaraat painoivat merkitsevästi enemmän ja munivat suurempia pesyeitä kuin myöhäisinä keväinä. Alhainen munamäärä — keskiarvo pienempi kuin missään muussa tutkimuksessa — selitetään ankaran ilmaston ja ravinnon puutteen avulla.

Pesintätulos vaihteli suuresti vuosittain keskiarvon ollessa 3.5 lentopoikasta/pesä (taul. 2). Epäedullinen sää oli tärkein pesätappioiden aiheuttaja, petojen vaikutus oli sen sijaan vähäinen. Poikastuoton arvioidaan olevan riittämätön itsenäisen kannan ylläpitämiseen Kilpisjärvellä ilman jatkuvaa immigraatiota. 5-munainen tyyppipesye tuotti keskimäärin vähemmän lentopoikasia kuin suuremmat munapesyeet (taul. 3). Munamäärässä ja poikastuotossa ei havaittu eroja tuoreiden ja kuivien tunturikoivikoiden välillä.

Pesivän kannan tiheys vaihteli tutkimusjakson aikana lähinnä kevätlämpötilojen mukaan eikä se ollut riippuvainen edellisen vuoden poikastuotosta. Tihein kanta oli 7-kertainen harvimpaan verrattuna.

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