Patterns and causes of long-term variation in reproductive traits of the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland

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Breeding performance of a marginal northern Pied Flycatcher population, known to have been founded in 1957, was studied during 22 years (1966–1987). The number of breeding pairs varied between 8 and 57. Of this annual variation, 44% was explained by the total number of fledglings produced in the preceding year and the mean temperature of June in the current year. The annual productivity of the population was usually either 'good' or 'bad'.

The mean temperature in May increased steadily during the study period, which resulted in an earlier date of egg-laying and larger clutches in the latter half of the study period (standardized selection differential of clutch size 1966–76 vs. 1977–87 0.40). However, the birds did not benefit from larger clutches, since there was no corresponding increase in the number of fledglings/nest. There were no clear trends in the size of the females (1974–87) or in the egg size (1975–87). The most important factor affecting hatching success was the mean temperature during the incubation period and the most important factor affecting fledging success was the female weight.

Population density, the mean date of egg-laying, the mean clutch size, and to a lesser degree nesting success varied in parallel in northern Finnish Lapland (69°N) and Swedish Lapland (66°N; Svensson 1987) in 1971–85. In Finnish Lapland the annual nesting success varied more than further south in Swedish Lapland.

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Introduction

Do reproductive traits of birds vary at random in time? Is there long-term stability or directional change in the trait means? To answer these and other questions, data on trait values over many generations are needed. If the traits are unselected, they will vary independently of environmental factors (Endler 1986).

Variation in the values of population parameters depends on the time scale used. Results obtained from short-term investigations are not necessarily comparable with those of long-term studies. However, "a long-term study" is a relative concept. As pointed out by Wiens (1984) and Calder (1984), the normal generation length may be a reasonable measure of the time scale needed for a long-term study of a particular species. For instance, ten years of study of a small 15-g passerine with a mean life expectancy of about 1.5 years (like the Pied Flycatcher *Ficedula hypoleuca*; v. Haartman 1951) is equivalent in terms of population dynamics to 24–245 years in gull species (Calder 1984).

A number of long-term population studies of the Pied Flycatcher have already been performed and a pioneer in this field is Lars von Haartman (1949, 1951, 1954). The Pied Flycatcher population of the Kilpisjärvi area, northern Finnish Lapland, has been studied since 1966. Thus, the 22-year (1966–1987) Pied Flycatcher study of the present paper is apparently long enough to span "the periodicity of the normal dynamics of the system" (Wiens 1984).

In addition to long-term dynamics and possible trends in the annual mean values of essential reproductive traits of the Pied Flycatcher, I shall evaluate the causes of variation in these traits in an area which lies near the northern distribution limit of the species. My aim is to examine whether the changes of one character cause simultaneous changes in other characters. I shall also discuss geographical similarities

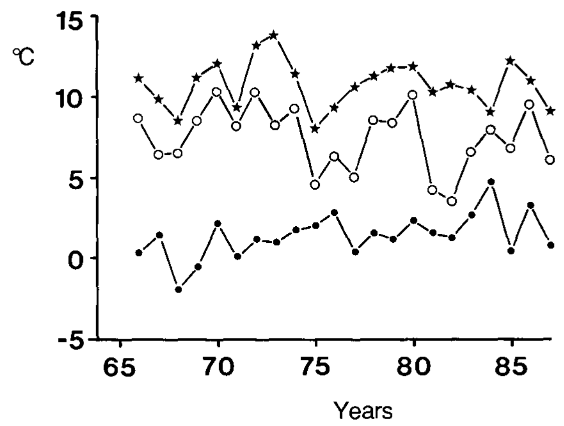

Fig. 1. Number of breeding Pied Flycatcher pairs in the permanent nest-box area (dots) and the total number of fledglings produced by these pairs (circles) at Kilpisjärvi in 1966–87. Pair = at least one egg laid.

and differences in the long-term population dynamics of the Pied Flycatcher in the light of my own data from Finnish Lapland and those published from Swedish Lapland (Svensson 1987) and southern Finland (Virolainen 1984).

Study area, material and methods

The study area lies in the mountain birch forest zone (altitude 480–600 m) in northwestern Finnish Lapland (Kilpisjärvi, about 69°03′N, 20°50′E; Järvinen 1983). The nests were in nest-boxes (made of birch trunks, diameter of the nest cavity at least 10 cm). In the permanent nest-box area, the number of boxes suitable for the Pied Flycatchers was 51 in 1966 and about 100 from 1967 onwards. In addition, there were larger boxes for the Redstart *Phoenicurus phoenicurus* (Järvinen 1983) but these were rarely used by the Pied Flycatcher. To obtain more breeding data, I also checked nest-boxes elsewhere in Kilpisjärvi, near the permanent nest-box area and in a similar habitat. Therefore, in some years the sample size for the breeding data exceeds the number of breeding pairs given in Fig. 1.

The Pied Flycatcher population in Kilpisjärvi was probably founded in 1957, when the eight first nest-boxes were placed out in the local mountain birch forests, which have few natural nest cavities (Lind & Peiponen 1963, Järvinen 1983). The first observation of the species was made at Kilpisjärvi in 1954 and in 1957–62 a total of only three pairs nested in the boxes (Lind & Peiponen 1963). Thus, the population has had about 30 years to adapt to the harsh local breeding conditions.

The temperature data derive from an official climatological station of the Finnish Meteorological Institute situated within the study area at 480 m above sea level. The climate is cold (mean temperature in June 7.2°C, in July 11.6°C; Järvinen 1987a) and the growing season is short (about 100 days, threshold +5°C). The number of breeding pairs (a pair = at least one egg laid), mean date of laying of the first egg, clutch size, and number of hatchlings and fledglings per nest were determined by visiting the boxes regularly in 1966–87 (n=22). In addition, the mean weight and wing length of the females was measured in 1974–87 (n=14), and egg size in 1975–87 (n=13).

The female weight remains constant during the early incubation phase (v. Haartman 1954, Silverin 1981). Therefore, to make comparisons between years reliable, only females weighed 0–5 days after clutch completion were included (accuracy 0.1 g). Wing length was measured by the maximum chord method (accuracy 1 mm; Svensson 1975). The maximum length and breadth of each egg in a clutch were measured to the nearest 0.01 mm with sliding calipers, and from these values the mean egg volume per clutch was computed with the formula of Ojanen et al. (1978). The mean egg weight per clutch was determined by weighing eggs together with a 10-g Pesola spring balance to the nearest 0.1 g during the first five incubation days. The date of birch leafing was determined in 1973–87 and it was defined as the day when the petioles were visible on mountain birches growing at 480 m. In 1966–87 the field work was conducted by the staff of the Kilpisjärvi Biological Station (in 1973–87 mainly by the author). The statistical tests used are 2-tailed.

Results

Patterns of variation

The number of breeding pairs varied between 8 (1968) and 57 (1970) in the permanent nest-box area (Fig. 1). Fig. 1, which also shows the total number of flegdlings produced by the nest-box population, clearly reveals the "good" and "bad" breeding seasons. Thus, the pairs in the population either mainly failed or mainly succeeded in their breeding attempts.

There were no long-term trends in the numbers of breeding pairs or fledglings (Spearman's rank corre-

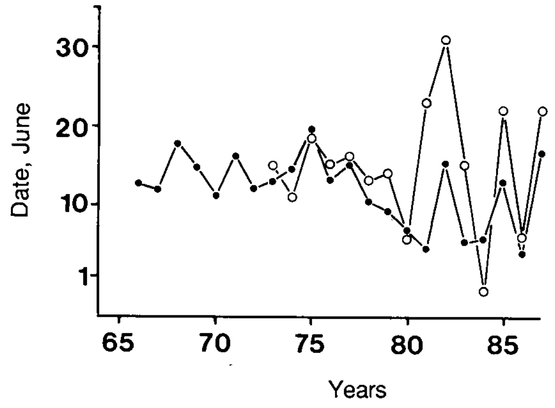

Fig. 2. Mean date of laying of the first egg in the Pied Flycatcher population (dots; 1966–87) and the date of birch leafing (circles; 1973–87) at Kilpisjärvi. Number of Pied Flycatcher nests in 1966–87: 9, 16, 8, 12, 43, 34, 33, 27, 52, 27, 16, 13, 11, 29, 37, 34, 21, 22, 34, 37, 45 and 65.

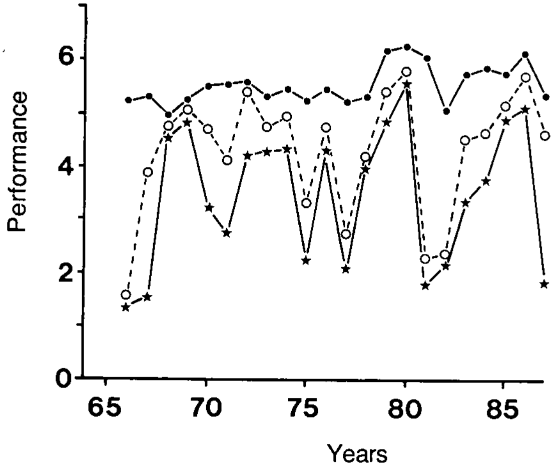

Fig. 3. Mean number of eggs (dots), hatchlings (circles) and fledglings (stars) per Pied Flycatcher nest at Kilpisjärvi in 1966–87. Number of Pied Flycatcher clutches in 1966–87: 17, 28, 8, 16, 55, 42, 32, 27, 52, 27, 17, 15, 11, 30, 37, 30, 22, 23, 36, 43 and 62.

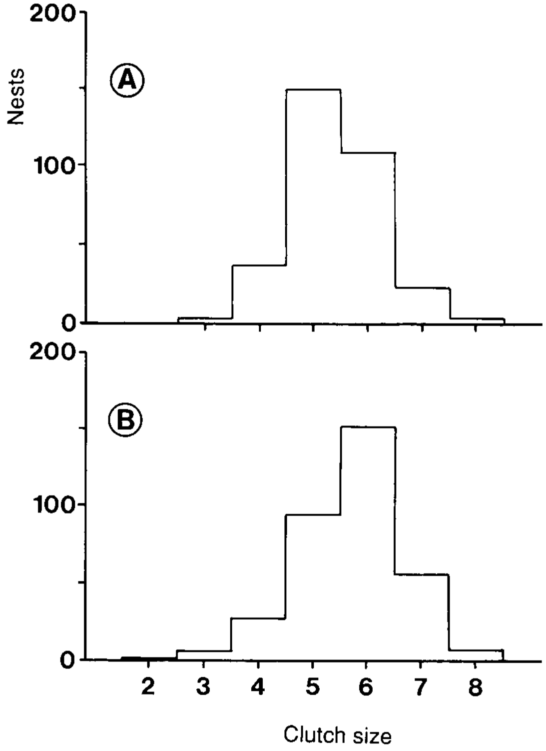

Fig. 4. Long-term directional change in the clutch size frequency distribution of the Pied Flycatcher at Kilpisjärvi. A=1966–1976: mean=5.37, SD=0.84, n=321. B=1977–1987: mean=5.71, SD=0.98, n=342.

lation coefficient $r_s=0.023$, P=0.916 and $r_s=0.130$, P=0.567, respectively), but there was an indication of serial non-randomness in the "goodness" of the breeding season, measured by the total number of fledglings produced per year (runs test, P=0.045). The coefficient of variation in the mean annual number of breeding pairs was 43% and in the mean annual number of fledglings 61% (these figures do not differ significantly from each other; t=1.199, df=42, P=0.237; test according to Sokal & Braumann 1980).

Egg-laying tended to become earlier in the population in 1966–87 (Fig. 2; $r_s=-0.391$, P=0.072), and the laying date correlated with the birch leafing in 1973–87 (Fig. 2; r=0.525, P=0.044).

The mean clutch size varied annually between 4.88 (1968) and 6.22 (1980; Fig. 3), the mean number of hatchlings per nest between 1.47 (1966) and 5.77 (1980), and the mean number of fledglings per nest between 1.35 (1966) and 5.60 (1980). The coefficients of variation were as follows: clutch size 7%, hatchlings 27% and fledglings 38%, the CV of clutch size being significantly smaller than the other two CVs (P<0.001). The mean annual clutch size seemed to increase during the study period ($r_s=0.525$, P=0.011), but there were no corresponding trends in the number of hatchlings or fledglings per nest.

In 1966–76 the mean clutch size was 5.37, but in 1977–87 5.71 (Fig. 4). The standardized selection

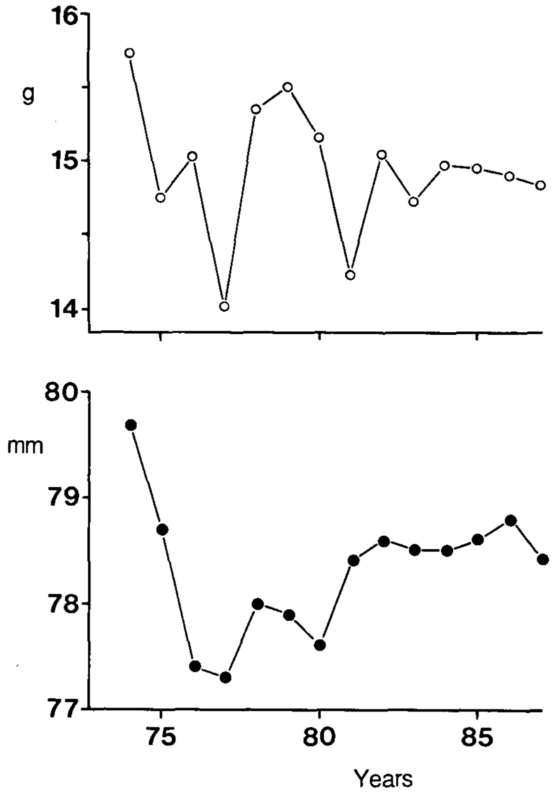

Fig. 5. Mean weight (g; circles) and wing length (mm; dots) of the Pied Flycatcher females in the early incubation phase at Kilpisjärvi in 1974–87. Number of females measured in 1974–87: 37, 15, 14, 15, 10, 30, 32, 16, 21, 22, 31, 27, 37 and 40.

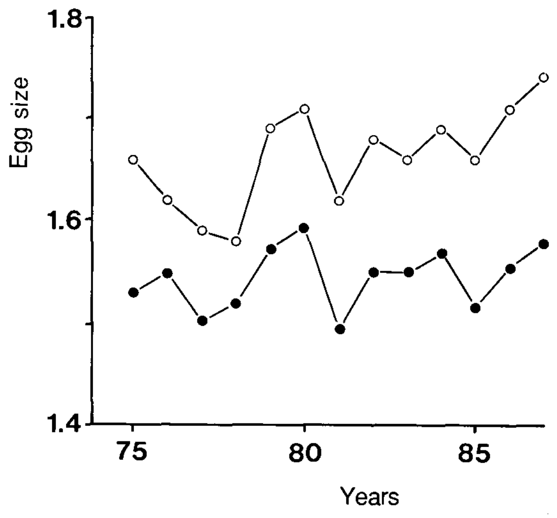

Fig. 6. Mean egg volume per clutch (cm³; dots) and mean egg weight per clutch (g; circles) in the Pied Flycatcher at Kilpisjärvi in 1975–87. Number of clutches measured in 1975–87: 26, 16, 15, 10, 30, 33, 24, 21, 22, 33, 27, 36 and 39.

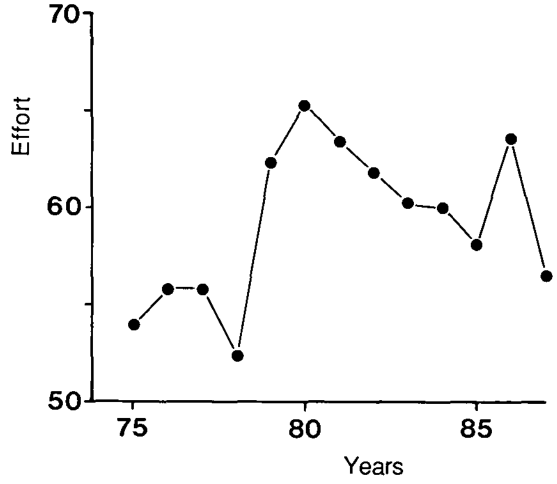

Fig. 7. Mean reproductive effort of the Pied Flycatcher females at Kilpisjärvi in 1975–87. Reproductive effort = (100 x clutch volume)/(female weight). Females weighed 0–5 days after clutch completion. For sample sizes, see Figs 3, 5 and 6.

differential (Endler 1986) was 0.40 (t=4.738, df=661, P<0.001), i.e. the mean clutch size was 0.40 SD units greater in the second than in the first 11-year period. Thus, there has apparently been directional selection for larger clutches in the population. The mean number of fledglings per nest was slightly greater in 1977–87 (3.52, n=338) than in 1966–76 (3.33, n=315), but this difference was not significant (Mann-Whitney test, z=1.269, P=0.204).

There was no clear trend in the annual mean weight or wing length of the Pied Flycatcher females (Fig. 5). As expected, the mean egg weight and the mean egg volume per clutch correlated with each other (r=0.802, P<0.001; Fig. 6), and there was some indication of an increase in egg size (egg weight: r_s=0.627, P=0.020; egg volume: r_s=0.363, P=0.229). However, the egg size variables were conservative: the CV of the mean annual egg volume was 2% and that of egg weight 3%. It should be noted that egg weight is affected by the incubation stage (the eggs were weighed 0–5 days after clutch completion), whereas egg volume is not.

The reproductive effort of Pied Flycatcher females varied relatively little annually (CV 7%; Fig. 7), and due to the relatively large clutches and eggs in

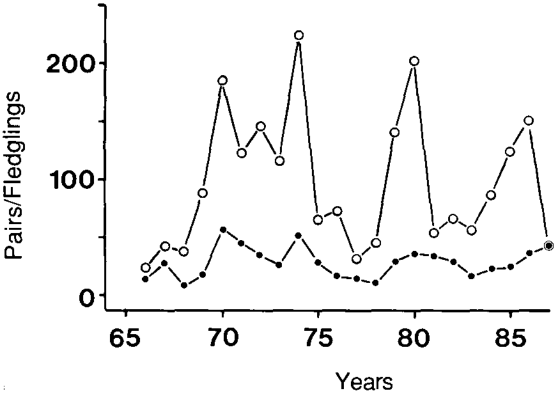

Fig. 8. Mean air temperature (Celsius degrees) in May (dots), June (circles) and July (stars) at Kilpisjärvi in 1966–87.

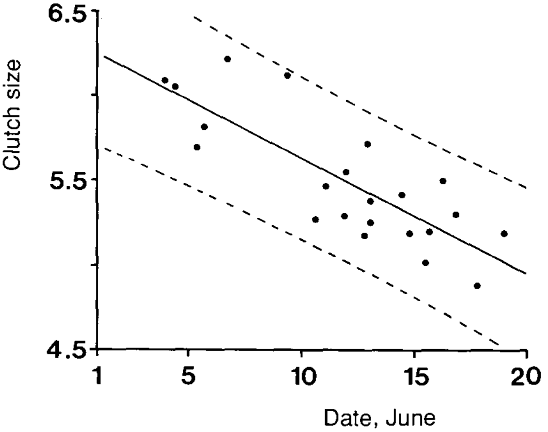

Fig. 9. The relationship between the annual mean date of laying of the first egg (June) and the mean clutch size of the Pied Flycatcher at Kilpisjärvi in 1966–87. The regression line ($y=6.313 - 0.068x$, $r^2=65.3\%$, $P<0.001$) and its 95% confidence interval are shown.

the latter half of the study period (Figs 3 and 6), the reproductive effort was higher in 1979–87 than in 1975–78.

Causes of variation

The mean temperature during the breeding season varied considerably (Fig. 8). During the study period, the mean temperature in May steadily increased ($r_s=0.425$, $P=0.048$), but there were no corresponding trends in the June or July temperatures ($r_s=-0.265$, $P=0.237$ and $r_s=-0.070$, $P=0.760$, respectively). The May temperature fluctuated according to its own rhythm, but the June and July temperatures fluctuated in parallel ($r=0.558$, $P=0.006$).

Simple and partial correlation analyses were performed to reveal possible causal links between the variables and the relative importance of the different factors affecting the breeding parameters of the Pied Flycatcher in the north.

Temperature seemed to be the factor behind most relationships between the variables. Although the date of egg-laying correlated with birch leafing (Fig. 2), the annual variation in egg-laying was more strongly correlated with the mean temperature during the period 15 May to 15 June ($r=-0.700$, $P<0.001$); clutch size was accordingly reduced in late seasons (Fig. 9). Thus the larger clutches in the latter half of the study period were probably due to the increased spring temperatures and earlier date of egg-laying.

There seemed to be two factors which determined the mean number of hatchlings per nest: mean temperature during the incubation period (partial correlation coefficient, $r_p=0.767$, $P<0.001$) and clutch size ($r_p=0.554$, $P=0.009$). Together, these variables explained 67% ($P<0.001$) of the variation in the mean annual number of hatchlings per nest. Female weight and egg volume did not have significant effects on the number of hatchlings per nest when the effects of temperature and clutch size were controlled for, although their simple correlations with the number hatchlings per nest were significant ($r=0.600$, $P=0.022$ and $r=0.653$, $P=0.014$, respectively).

The relative number of hatchlings/nest (hatching %) was most strongly correlated with the mean temperature during the incubation period ($r=0.777$, $P<0.001$). The significant positive correlation between clutch size and the number of hatchlings implies that clutch size was not related to hatching % ($r=0.183$, $P=0.414$). Also, egg volume and female weight were not significantly related to the hatching % when the effects of temperature were controlled for.

The number of fledglings per nest was directly related to the number of hatchlings per nest, but the relative fledging success (fledglings/eggs hatched) was most strongly related to two factors, viz. female weight ($r_p=0.570$, $P=0.042$) and breeding density ($r_p=-0.498$, $P=0.084$); temperature was not related to the relative fledging success. The mean annual wing length of females was not related to breeding performance.

The number of breeding pairs in year t was significantly dependent on two factors, mean temperature in June in year t (r_p=0.487, P=0.029) and the total number of fledglings produced in year t-1 (r_p=0.588, P=0.006). Together, these variables explained 44% (P=0.006) of the annual variation in the number of breeding pairs.

Discussion

Local patterns

During the study period the mean temperature in May increased by nearly two degrees (Fig. 8). With the amelioration of spring conditions, the egg-laying of the Pied Flycatcher became earlier (Fig. 2) and its clutch size increased (Fig. 3). Despite the larger clutches in the latter half of the study period (1979–87), there were no accompanying increases in the numbers of hatchlings or fledglings per nest (Fig. 3).

The mean temperature in June and July did not increase (Fig. 8), and because the nesting success of the Pied Flycatcher is so dependent on external temperature conditions, it is understandable that the earlier date of egg-laying and larger clutches in the latter half of the study period have not resulted in an increased number of offspring per female, and that an early date of egg-laying is apparently not strongly selected for. However, some females apparently automatically respond to warm spring weather by laying early and large clutches, although this does not seem to increase their fitness.

Due to northern stress, the birds have not benefited from the earlier laying date and larger clutches. On the contrary, the increased reproductive effort (Fig. 7) may have lowered their fitness, if a high reproductive effort decreases the survival of females. Had a similar increasing trend in clutch size occurred in the south, it might be expected to result in improved productivity of young, and the Pied Flycatcher might evolve a new reproductive strategy of laying early and large clutches. In the north this has not been possible because the birds are at the mercy of physical factors.

At Kilpisjärvi, the Achilles heel of the breeding success of the Pied Flycatcher seems to be hatching success. Although fat females and large eggs tended to enhance hatching, hatching success was largely dependent on the temperature during the incubation period. However, fat females were apparently more efficient in feeding their young than lean females, which resulted in better relative fledging success. There was also some indication of negative effects of intraspecific competition on fledging success (r_p=–0.498, P=0.084). Predation (chiefly by mustelids) caused relatively few losses, and these mainly occurred in years when small rodent populations were low (Järvinen 1985 and unpubl.; 2% of nests robbed in 1970, 18% in 1971, 6% in 1972, 17% in 1984, 4% in 1985 and 2% in 1987).

Although mortality during the nesting period is considerable in the Pied Flycatcher at Kilpisjärvi (Fig. 3), mortality outside the nesting season seems to be a density-dependent factor regulating the local population (Järvinen 1987b).

Comparisons between Kilpisjärvi and other areas

Virolainen (1984) published basic breeding data on the Pied Flycatcher in southern Finland (60°N) in 1971–83 (n=13) and Svensson (1987) presented similar data for Ammarnäs in Swedish Lapland (66°N) in 1971–85 (n=15). Virolainen's (1984) study area comprised coniferous and mixed forest. Svensson (1987) gives some data for coniferous forests as well, but for comparisons with Kilpisjärvi, I shall use only his data on the mountain birch forest zone (Fig. 2 in Svensson 1987).

In southern Finland (Virolainen 1984), the laying date of the first egg correlated negatively with the mean temperature in May (r=–0.713, P=0.005), and clutch size correlated with the laying date (r=–0.719, P=0.004). In Ammarnäs, the correlation between clutch size and the mean annual laying date was –0.90 (P<0.001). The linear regression line has the slope of –0.07 eggs per day in both Ammarnäs and Kilpisjärvi.

Despite the considerable distance between the two areas in Lapland (340 km), the mean annual date of egg-laying was about the same in the birch zone in Ammarnäs (11 June) and Kilpisjärvi (12 June) in 1971–85, and there was a close correlation between the mean laying dates between in the two areas (Table 1), and between the mean annual clutch size values (Table 1). In both areas the annual variation in the mean clutch size was small in 1971–85 (CV 8% in Ammarnäs and 7% in Kilpisjärvi; t=0.820, df=28, P=0.42).

At Kilpisjärvi hatching success (%) correlated with the mean temperature in June (r=0.613, P=0.002), whereas in southern Finland (Virolainen 1984) the corresponding correlation was 0.015 (P=0.962) and 0.120 (P=0.703) for the mean temperature in May and June, respectively. In southern

Table 1. Spearman's rank correlation coefficients between the mean breeding variables of the Pied Flycatcher in Ammarnäs (Swedish Lapland; Svensson 1987) and Kilpisjärvi (Finnish Lapland; present study) in 1971–85. Nesting success = percentage ratio of fledged young to eggs laid in completed clutches.

Variable	r_s	2-tailed P	n
Population density	0.760	0.001	15
Date of egg-laying	0.854	<0.001	14
Clutch size	0.749	0.001	15
Nesting success (%)	0.492	0.089	13

Finland, nestling mortality was high if the mean temperature was low during the early part of the nestling period, but within any one year the most important factor influencing nesting success was male absence during the nestling period (Virolainen 1984).

Svensson (1987) observed a correlation in the Pied Flycatcher densities between Ammarnäs and Kilpisjärvi in 1971–79 (r=0.84, P=0.003). In 1971–85 the population densities fluctuated in parallel in these areas (Table 1). Earlier, I have shown that parallel fluctuations also occurred in the Redstart populations in Ammarnäs and Kilpisjärvi (1969–78; Järvinen 1981). A common climatic factor is apparently responsible for the similarities between these areas. It is noteworthy that the mean temperature of the 15-day periods in April and June in 1966–87 correlates significantly between southern Finland and Kilpisjärvi even though these regions are about 1000 km apart (A. Järvinen, unpubl.).

The weather conditions experienced by birds during the spring migration are probably similar over a large geographical area, either prolonging or shortening migration (Järvinen 1978). As, moreover, the nesting success (number of fledglings/eggs laid) also correlates between Ammarnäs and Kilpisjärvi (Table 1), it is not surprising that the population densities correlate between the areas. However, in Kilpisjärvi the annual variation in nesting success (mean 65%) was more pronounced (CV=30%) than in Ammarnäs (mean 84%, CV=10%; t=3.023, df=26, P=0.005) in 1971–85. Thus, the more northern and apparently harsher breeding conditions at Kilpisjärvi did not manifest themselves in the early phases of the breeding cycle, when clutch size was determined. It was not until the later phases of the cycle, when nesting success was determined, that there was more annual variation in northern than southern Lapland.

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Selostus: **Kirjosiepon pesimäbiologisten tunnuslukujen pitkäaikaisvaihteluista Kilpisjärvellä 1966–1987**

Kilpisjärven kirjosieppopopulaatio syntyi 1950-luvun lopulla pöntötyksen ansiosta. Pesiviä pareja oli 1966–87 8–57 (kuva 1) ja parimäärä riippui edellisen pesimäkauden poikastuotosta (kuva 1) ja kuluvan pesimäkauden kesäkuun keskilämpötilasta (kuva 8). Populaation poikastuotto oli yleensä joko 'hyvä' tai 'huono', mutta harvoin keskinkertainen.

Tutkimusjakson aikana toukokuun keskilämpötila kohosi lähes kaksi astetta (kuva 8), minkä vuoksi muninta-aika tuli varhaisemmaksi (kuva 2) ja munapesyeet suuremmiksi (kuvat 3 ja 4). Suurista munapesyeistä ei kuitenkaan ollut linnuille hyötyä, sillä lentopoikastuotto/pesä ei vastaavasti kohonnut (kuva 3). Haudonta-ajan lämpötila vaikutti eniten kouriutumisen onnistumiseen ja naaraan paino (kuva 5) kuoriutuneiden poikasten hengissä säilymiseen.

Kilpisjärven (69°N) ja Ammarnäsin (Ruotsin Lappi, 66°N; Svensson 1987) kirjosieppokannat, keskimääräinen munintaaika ja munamäärä sekä vähäisemmässä määrin pesinnän onnistuminen (%) vaihtelivat samansuuntaisesti 1971–85 (taulukko 1). Kilpisjärvellä pesimämenestyksen vuotuinen vaihtelu (vaihtelukertoimella mitattuna) oli suurempi kuin Ammarnäsissä.

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20th International Ornithological Congress 1990

Final Notice

The 20th International Ornithological Congress will take place in Christchurch, New Zealand, on 2–9 December 1990. The Congress programme will include 7 plenary lectures, 48 symposia, contributed papers (spoken and poster), workshops, round-table discussions and films. There will be a mid-Congress excursion day. Longer tours are planned to interesting ornithological sites in New Zealand before and after the Congress, including the post Congress cruises to sub-antarctic islands.

The Second and Final Circular of the Congress will be available from 1 October 1989 and will include the registration papers and forms for submitting papers. In late 1990 New Zealand will also host the 20th World Conference on the International Council for Bird preservation in Hamilton on 21–27 November 1990 and a Pacific Festival of Nature Films in Dunedin on 27 November – 1 December 1990. Requests for this Final Circular, which includes information on the above events, should be sent to:

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