Timing of breeding and the clutch size in the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland

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Three Pied Flycatcher populations were studied during several years in Finnish Lapland (c. 67—69°N) with respect to timing of breeding and clutch size. The effects of latitude and climate were more pronounced in Lapland than in central Europe and southern Finland. The farther north breeding occurred, the later was the onset of laying and the colder the weather in which laying started. At Kilpisjärvi (69°N) the onset of laying coincided with the start of the growing season (+5—6°C; about 8 June), and the temperature sum on the mean date of laying was also very low.

The average clutch size was related to the date of the onset of laying. The size decreased during the season by about 0.08 eggs/day. The northward decline of the clutch size could be chiefly attributed to delay of the laying season caused by the rigorous climate.

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Introduction

In northern areas, compared to more southern latitudes, birds usually have a later and shorter nesting period. However, some late-nesting species seem to start reproduction at a lower temperature and under phenologically earlier conditions in the north, which is apparently an advantageous adaptation (v. Haartman 1963, Danilov 1967, Hussell 1972, Slagsvold 1975a, 1976). Of course, laying cannot begin until food has become sufficiently abundant for the females to form eggs, and this is a factor counteracting early breeding (e.g. Perrins 1970).

In this paper we compare the breeding seasons of the Pied Flycatcher with meteorological data in three study areas in Finnish Lapland, and discuss briefly the idea, put forward by v. Haartman (1967), that the average clutch size of the species is determined by the calendar.

Study areas and materials

From south to north the geographical location of the study areas was as follows (Fig. 1): Meltaus (66°54′N, 25°20′E), Värriö (67°44′N, 29°37′E) and Kilpisjärvi (69°03′N, 20°50′E). The material from Meltaus (363 nests; H. Lindén's unpubl. material) stems from 1969—79. The nest-boxes were situated in pine forests, pine swamps and spruce swamps at altitudes of 175—190 m. The mean temperature in June was +12.2°C. The data from Värriö (1973—76) were derived and re-analysed from Pulliainen's (1977) paper. His study area (alt. 320—472 m) was a mountain with an almost treeless summit and a typical mountain birch forest below, which was bounded by coniferous forests. Practically all 110 pairs nested in coniferous or mixed forests. The mean temperature in June

was +9.7°C. The data (377 nests) from Kilpisjärvi were collected in subalpine mountain birch forest at altitudes of 475—600 m during 1966—79. The snow in the forests melted in early June, and the mean temperature in June was +7.8°C. For details, see Järvinen (1980).

In all areas the nest-boxes were of the same type with a 30—40-mm entrance hole. Meteorological observations were made at near-by meteorological stations. At Kilpisjärvi and Värriö the Pied Flycatcher was very rare before the installation of nest-boxes.

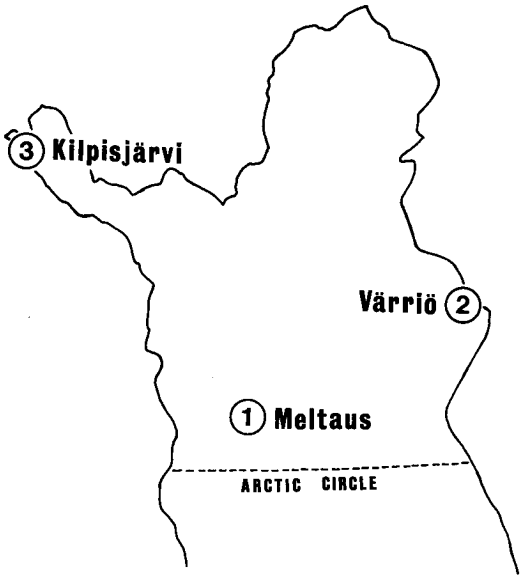

FIG. 1. The study areas in Finnish Lapland.

Results

Egg-laying. In 1966—79 the first egg was laid at Meltaus on 24 May — 4 June. The mean laying date varied yearly between 2 and 9 June, averaging 5 June ($N=309$, $SD=4.6$, $SE=0.3$) and correlated negatively with the mean daily temperature during 5 May —5 June ($r=-0.947$; $df=7$, $P<0.001$). The correlation between the first and mean dates was not statistically significant ($r=0.533$; $df=7$, $P>0.10$). The length of the laying season was 31 days (24 May — 23 June), averaging 15.5 ± 5.0 (*SD*) days annually. In Fig. 2 the laying season is presented together with the temperature diagrams. The thermic threshold value for egg-laying was about +9°C, and 5—6 days later over 50 % of all the pairs had started. By the mean date of laying, the temperature sum ($\Sigma\geq +5$°C) averaged +159.9±28.8 (*SD*; $N=9$).

Due to the smaller material, the results in Värriö are not as reliable as in Meltaus and Kilpisjärvi. In 1973—76 the first egg was laid on 25 May — 6 June. The mean laying date varied between 6 and 14 June, averaging 11 June ($N=110$, $SD=7.4$, $SE=0.7$). The length of the laying season was 40 days (25 May — 3 July), averaging 25.8 ± 4.1 days annually (we omitted the first clutch in 1975, because it was laid 13 days earlier than the next one, but we included several late clutches, which may have been replacement ones). The laying season started when the temperature rose to +7—8°C, and about 5—6 days later over 50 % of the pairs had started. By the mean date of laying the temperature sum averaged +137.5±6.6.

In 1966—79 the first egg was laid at Kilpisjärvi on 4—14 June. The mean date varied between 10 and 19 June, averaging 14 June ($N=334$, $SD=5.2$, $SE=0.3$), and it correlated negatively with the mean daily temperature during 15 May — 15 June ($r=-0.817$; $df=12$, $P<0.001$). The correlation between the first and mean dates was statistically significant ($r=0.964$; $df=12$, $P<0.001$). The length of the laying season was 26 days (4—29 June), averaging 16.3 ± 2.8 days annually. The laying season started when the temperature rose to +5—6°C, and 5—6 days later over 50 % of the pairs had

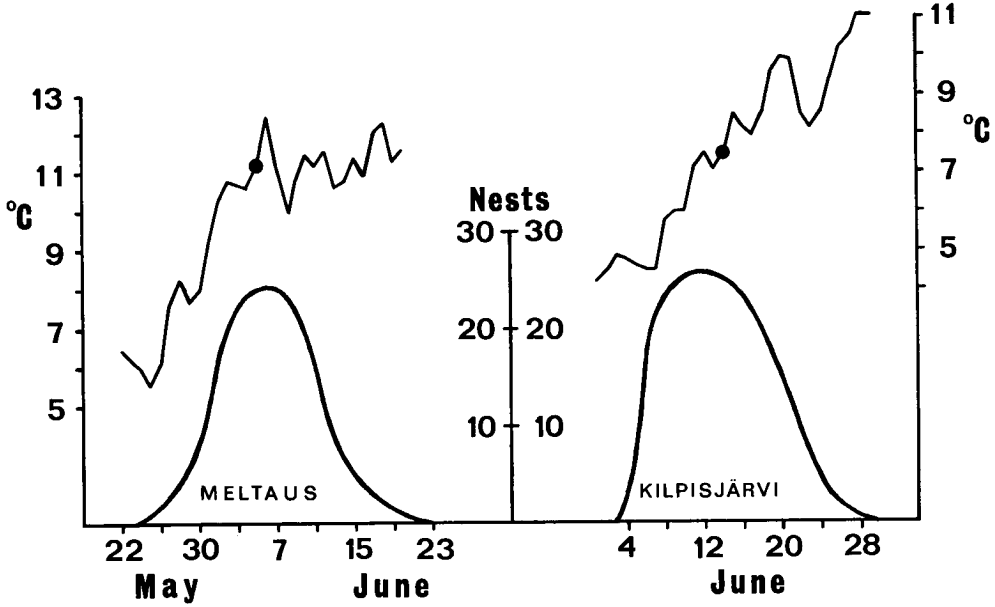

FIG. 2. The laying seasons of the Pied Flycatcher at Meltaus (1969—79, left) and Kilpisjärvi (1966—79, right) compared with the temperature diagrams. The zero days (●) are the average dates of egg-laying. From that day the average mean daily air temperatures have been calculated backwards and forwards for 1969—79 and 1966—79, respectively.

started (Fig. 2). By the mean date of laying the temperature sum averaged +86.2 ± 26.9.

Clutch size. The average clutch sizes in the three study areas were as follows: Meltaus 6.07 ± 0.04 (*SE*; N=363), Värriö 5.79 ± 0.09 (N=109), and Kilpisjärvi 5.42±0.04 (N=377). In all areas the range was 3—8 (we omitted a clutch of one egg from Värriö, because the clutch was not incubated and probably not completed; see Pulliainen 1977).

In Fig. 3 the relation between the average clutch size and the date of laying of the first egg is shown for Meltaus and Kilpisjärvi; the relation in Värriö was almost identical (see Pulliainen 1977). The decrease throughout the season was about 0.08 eggs/day.

Discussion

In several study areas in central Europe and southern Finland the average temperature on the determinant day (in the Pied Flycatcher about five days before the average date on which the population starts to lay) was +10—11°C (Slagsvold 1976). The temperature at the start of laying decreased progressively from Meltaus to Värriö to Kilpisjärvi, the onset of laying at Kilpisjärvi coinciding with the start of the growing season (about +5—6°C). Moreover, at Kilpisjärvi the temperature sum on the mean date of egg-laying was remarkably low. This conforms with v. Haartman's (1963) theory that late-nesting species (e.g. the Pied Flycatcher) start to breed at a lower temperature in the north (but see Slagsvold 1976:142).

Allowing for differences in altitude, the average retardation of breeding was 2—3 days per degree of latitude, about twice that found by Slagsvold (1975a). The average length of the laying season was nearly the same at Meltaus and Kilpisjärvi, but probably due to replacement clutches it was longer at Värriö. The weak correlation between the first and mean dates of laying at Meltaus may indicate a less strict laying season than at Kilpisjärvi.

Although the weather differed greatly from one spring to another, there was relatively little variation in the onset of laying. At Kilpisjärvi the first egg was laid, on average, on 8 June ± 3.0 days (*SD*), and at Meltaus on 30 May ± 2.8 days. Although the start was probably equally synchronous in both areas, laying seemed to advance more rapidly at Kilpisjärvi (cf. the curves in Fig. 2).

The date of laying affected the clutch size similarly in the three study areas. In SW Finland the average clutch size declined from about 7.0 on 15—25 May to about 4.5 on 24—29 June (v. Haartman 1967). If absolute values are used, the decline is less pronounced in Lapland, but if we consider the slopes of the regression lines, the decline seems to be as great as in SW Finland.

In both southern and northern Finland the average clutch size decreases by 0.07—0.08 eggs/day. For instance, at Kilpisjärvi the laying commences in the pentad 4—8 June, the average clutch size then being 6.1, about the same as on the same date in SW Finland, Meltaus and Värriö (v. Haartman 1967, Pulliainen 1977, present paper). The clutch sizes correspond well with each other in other pentads as well. v. Haartman (1967) observed that the clutch size seems to remain stable until about 25 May, and at Meltaus (though not at Kilpisjärvi) it was apparently even smaller in the first than in the second pentad (Fig. 3).

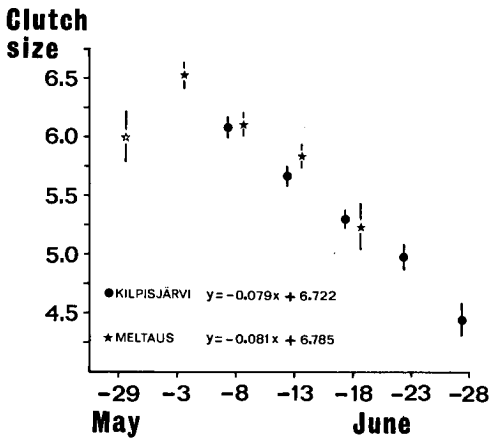

FIG. 3. The seasonal decline of the clutch size in the Pied Flycatcher at Kilpisjärvi (circles) and Meltaus (stars). Average clutch size (± *SE*) in five-day periods in May-June.

Broadly speaking, the variation in the clutch size of the Pied Flycatcher in Finland seems to be chiefly explained by the date of the start of laying (it may be noted that in early springs, when larger clutches are laid, the females are in better physical condition at Kilpisjärvi, see Järvinen 1980), but minor annual differences are probably due to prevailing weather conditions and other factors (e.g. the age structure of the population). At Kilpisjärvi, for instance, the average clutch size varied somewhat (0.1—0.2 eggs) in several years, although the laying seasons were almost identical. Population density did not show an inverse relationship with clutch size (Järvinen & Tast 1980).

According to v. Haartman (1967), in years when the spring is late the Pied Flycatcher has a smaller average clutch size than in years when it is early, and Pulliainen (1977) argued that in the north birds never have the

opportunity to demonstrate their full clutch size potential. It seems that in this connection "lateness" and "northernness" are almost equivalent.

The similarity of the dependence of clutch size on the calendar in the whole of Finland indicates that the Finnish Pied Flycatcher population is genetically fairly uniform. As the species started to inhabit Lapland quite recently (in the 1950s) and its population is still small there, differentiation has not occurred.

Our results do not support the idea proposed by Slagsvold (1975b) that the geographical variation in the clutch size is explainable by the earlier phenology of the environment in which breeding occurs in the north. The environmental phenology is in fact earlier for the Pied Flycatcher in Finnish Lapland, but this seems to have little influence on clutch size. The fact that the clutch size is not larger in the north, but smaller (e.g. Järvinen 1980, present paper) may be explained by the delay of the laying season caused by the adverse climate. Of course, other species may behave in a different way.

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Selostus: **Kirjosiepon pesinnän ajoittuminen ja munamäärä Lapissa**

Meltauksen (kuva 1; 363 pesää), Värriön (Pulliainen 1977; 110 pesää) ja Kilpisjärven (377 pesää) kirjosieppopopulaatioiden muninta-aikoja ja munamääriä verrattiin toisiinsa sekä Etelä-Suomen ja Keski-Euroopan populaatioihin. Vuosina 1969—79 ensimmäinen muna munittiin Meltauksessa keskimäärin 5.6. Viisi päivää aikaisemmin lämpötila oli kohonnut n.+9°C:een (kuva 2). Värriössä (1973—76) ja Kilpisjärvellä (1966—79) vastaavat arvot olivat 11.6./+7—8°C ja 14.6./+5—6°C. Lapissa linnut aloittivat muninnan myöhemmin ja kylmemmässä säässä kuin E-Suomessa ja Keski-Euroopassa.

Kaikilla alueilla munamäärä (keskiarvot: Meltaus 6.07, Värriö 5.79 ja Kilpisjärvi 5.42) oli tiettynä kalenteripäivänä käytännöllisesti katsoen yhtä suuri (kuva 3). Tämä yleistys näytti pätevän myös E-Suomessa. Munamäärä väheni 0.08 munaa/vrk. Ankaran ympäristön aiheuttama myöhäinen pesintä näyttää pääasiassa selittävän kirjosiepon pienet munapesyeet pohjoisessa.

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