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Variation in the laying intervals of the Pied Flycatcher and the Redstart

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The egg-laying pattern of two nest-box breeders, the Pied Flycatcher *Ficedula hypoleuca*, and the Redstart *Phoenicurus phoenicurus*, was studied in a forested region in Finnish Lapland during 1986–1993. Laying schedule and laying order were examined, and hatching and fledging success recorded. The coldness of the spring of 1993, caused laying gaps in the Pied Flycatcher of which the longest intervals between laying two eggs were 2×11, 2×10 and 1×9 days. Long lying of the first-laid eggs in the nest, because of laying gaps, resulted in a low hatching success for these eggs. Egg laying lasted for two or three days until the female could interrupt her egg-laying after a drastic drop in the temperature. The Redstart, unlike the Pied Flycatcher, did not respond to the exceptionally low temperatures during the time of egg-laying. The effect of the cold temperatures on the egg-laying of the Pied Flycatcher may be less than the impact due to the scarcity of food, especially flying insects.

1. Introduction

The short summer of the Arctic and Subarctic regions forces most of the birds breeding in these areas to commence egg-laying as early as possible in order to raise the young before the autumn migration. The prevailing weather conditions often disturb these breeding attempts very effectively; in late June the ground may still be covered by a 30-cm-deep new snow layer (Pulliainen 1978b). If a cold spell takes place during the egg-laying period, a bird may either continue egg-laying, interrupt it, or reject the whole clutch. The responses of a typical breeding bird of the Subarctic (e.g. the Redstart *Phoenicurus phoenicurus*) and a newcomer (e.g. the Pied Flycatcher *Ficedula hypoleuca*) differ in these situations. The latter species, which has colonized Europe from the southwest to the northeast during the past two centuries (Lundberg & Alatalo 1992), appeared in our study area in Salla, northeast Finland, in the 1910's (Finnilä 1914), but was still very sporadic there in the 1930's (Suomalainen 1952). Our systematic studies on the breeding biology of box-nesting birds in the Subarctic recorded the response and/or "pre-adaptation" phenomena, including possible laying gaps, and evaluated their biological significance. This paper is a record of these studies.

2. Material and methods

The present study was carried out in the surroundings of the Värriö Subarctic Research Station, a forested region in eastern Finnish Lapland (67°44′, 29°37′E, 218–472 m a.s.l.), during the summers of 1986–1993. Two hundred and ninety nest-boxes suitable for the Pied Flycatcher and the Redstart were available in eleven habitats. The nest-boxes were checked daily during the nest construction and egg-laying periods. Daily visits to the nests made it possible also to record any exceptional laying schemes (i.e. aberrations from one-egg per day schedule). During hatching the clutches were examined continuously in order to determine the hatching order of individual eggs. Meteorological observations were made from the Research Station's Meteorological Centre (355 m a.s.l.), in the middle of the study area.

3. Results

Table 1 shows the laying characteristics of the Pied Flycatcher during 1986–1993. The yearly number of nests and eggs laid, as well as the number of breeding pairs, fluctuated markedly. The mean time used for laying one egg, on average, was 1.18 days. The time used for laying one egg, on average, varied between 1.04–1.20 days during the years 1986–1992. The longest intervals between laying two eggs were 1×6 (1988), 1×5 (1988), 4×5 (1989), and 1×4 (1987) days (Table 2).

The egg-laying in the summer of 1993 differed from the pattern of the years 1986–1992. Egg-layings were started in two periods, on 4–6 June and on 12–18 June (Fig. 1). No clutches were initiated between 7 and 11 June. Twenty-two clutches were commenced on 4–6 June (Fig. 1). In these clutches a total of 122 eggs were laid in 245 days, i.e. one egg in 2.01 days on average. Temperatures during this first part of the egg-laying period in 1993 were low, as compared with that of the other years studied. Mean temperatures between 1 and 15 June changed in the years of 1986–1992 from +5.5°C (1990) to +14.9°C (1992), mean temperature was +8.8°C ± 3.7 (SD), and in 1993, the temperature was only +4.4°C. On 4 June in 1993, the day of the first layings, the temperature did fall markedly (the daily maxima was only +2.8°C), and the temperatures stayed quite low until 12 June (Fig. 1). It snowed during the night between 5 and 6 June and the snow depth was 5–10 cm in the morning of 6 June.

In the clutches commenced on 4–6 June the egg-laying became irregular, or even was interrupted after 6 June. The longest intervals between laying two eggs were 2×11, 2×10, 1×9, 1×8,

Table 1. Total numbers of nests and eggs laid, total time used for egg laying and average time used for laying one egg in the Pied Flycatcher nests at Värriö Nature Reserve in 1986–1993.

	Nests	Eggs	Time for egg laying total	one egg
1986	15	85	88	1.04
1987	31	183	204	1.14
1988	23	126	151	1.20
1989	43	240	274	1.14
1990	43	239	270	1.13
1991	31	170	189	1.11
1992	43	254	264	1.04
1993	39	213	343	1.61
1993[a]	22	122	245	2.01
1993[b]	17	91	98	1.08

[a] Clutches commenced on 4–6 May, [b] clutches commenced on 12–18 June.

Table 2. Numbers of laying gaps of different length in the Pied Flycatcher at Värriö Nature Reserve in 1986–1993 (for further details, see the Table 1).

	Length of laying gaps in days 1	2	3	4	5	6	7	8	9	10	11
1986	3										
1987	10	2	1	1							
1988	9	1	1		1	1					
1989	9	1	1		4						
1990	14	4	3								
1991	11	4									
1992	10										
1993	15	4	2		2	3	2	1	1	2	2
1993[a]	10	3	2		2	3	2	1	1	2	2
1993[b]	5	1									

[a] Clutches commenced on 4–6 May, [b] clutches commenced on 12–18 June.

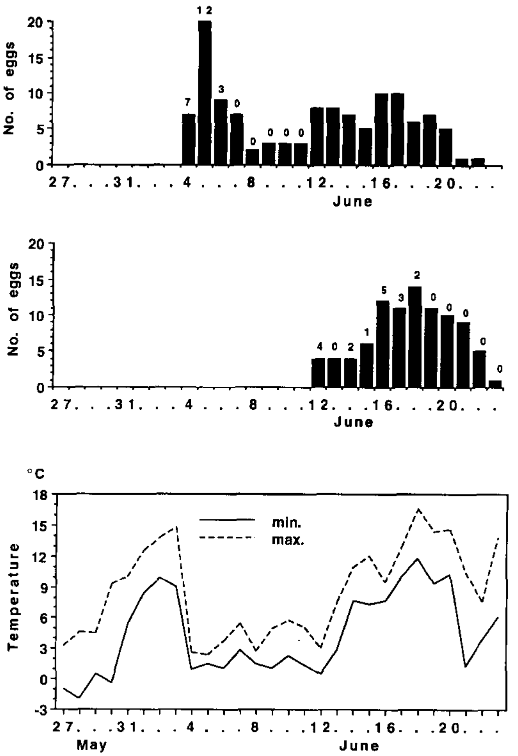

Fig. 1. Daily numbers of eggs laid in the clutches commenced on 4–6 June and on 12–18 June in 1993, and daily maximum and minimum temperatures (09.00–21.00 Finnish solar time). Figures above the columns show the numbers of clutches commenced on the day in question.

and 2×7 days (Table 2), with the longest times of egg-layings lasting 4×17, 1×16, 1×15, 3×13, and 2×11 days (Table 3). Most interruptions in the egg-laying began after the first egg in the clutch was laid, and after the cold spell had lasted for about two days (10 cases, see the Table 3). In cases where the egg-laying periods were extended, the first-laid eggs might lie in the nest up to 16 days before incubation commenced (incubation was assumed to begin from the moment of laying the last egg in the clutch). In two cases, two eggs were laid during a 24 hour period (numbers 4 and 14 in Table 3). The delay in the commencement of incubation seemed to have an effect on the hatching success of these eggs. If excluded total failure in the incubation period (the female of nest no. 1 was found dead in the nest-box, clutches no. 6 and 9 were robbed, and clutch no. 16 was abandoned) 64% (9 out of 14) from the eggs laying in the nest more than 10 days before incubation started and the eggs hatched, while the corresponding percentage of the eggs lying in the nest less than 10 days was 91 (80 out of 88 eggs, $\chi^2 = 7.70$, df = 1, $P < 0.01$).

Seventeen egg-layings of the Pied Flycatcher commenced on 12–18 June (Fig. 1). In these clutches 91 eggs were laid in 98 days, i.e. one egg/1.08 days. The egg-laying scheme was thus normalized. The interesting point is that 12 June, the day of the first layings, was a very cold day (four commencements of egg-laying probably occurred on the morning of 12 June), the daily maxima being +3.0°C, and the temperatures did not start to rise until 13 June.

The hatching success of the clutches commenced on 4–6 June was equal to those commenced on 12–18 June (87.5% and 89.2%, respectively, total failures excluded). The hatching success of the eggs laid regularly one egg per day, in clutches commenced on 4–6 June, seemed to be high despite the low air temperatures (see, e.g. the nests no. 10 and 14 in Table 3). In the clutches commenced on 4–6 June, 84.6% of the hatched young fledged, whereas the corresponding value for the clutches commenced on 12–18 June was 76.5%. The primary cause of this difference was predation by a mustelid (a stoat *Mustela erminea* or a least weasel *Mustela nivalis*) on some clutches commenced in the latter period.

In the Redstart, the egg-laying schedule of 43 clutches was recorded during 1986–1993. Only six laying gaps of one day were observed in total (278 eggs were laid in 284 days, the average time for laying one egg was 1.02 days). The Redstart commenced four egg-layings on 2–5 June in 1993, at the beginning of a cold spell. In these clutches 25 eggs in 26 days were laid (one egg/1.04 days). Low temperatures and the snow during the egg-laying period did not have any effect on the egg-laying scheme by the Redstarts. These clutches were also very successful (hatching success 96.0%, fledging success 100.0%).

The breeding success of the Redstart was higher than that of the Pied Flycatcher during 1986–1993. In the Redstart, 82.8% of the eggs laid fledged (n = 49 clutches, total failures included), while in the Pied Flycatcher fledged only 66.3% (270 clutches). These figures also include the clutches where the laying schedule and/or the laying order were not successfully recorded. There were, however, great annual variations in the breeding success of both species. In the Redstart, the range of the breeding success was 65.0% (1988, n = 7) to 90.3% (1993, n = 6), and in the Pied Flycatcher 56.1% (1992, n = 43) to 87.2% (1991, n = 31).

4. Discussion

The present study revealed a clear difference between the Redstart and the Pied Flycatcher in the egg-laying response to a cold spell: the females of the latter species had a gap of up to 11 days between laying (Tables 1 and 2), whereas the individuals of the former species had no such gaps. The main point is: Does this response pattern of the Pied Flycatcher indicate a real adaptive capability or uncapability? The former might be a kind of "preadaptation" to nesting in the Subarctic.

Some earlier observations support the theory of low capability: in our study area the yearly number of breeding pairs of the Pied Flycatcher fluctuates extensively (Pulliainen 1977, 1978a), the breeding success also varies widely (Pulliainen 1977), and the annual variation in the date of egg-laying seems to increase (Järvinen 1983) and the clutch size to decrease (Valanne et al. 1968, Pulliainen 1977, Järvinen 1986) from south to north. The two latter observations are connected to the group in which the Pied Flycatcher belongs, where the clutch size decreases as the season progresses (Klomp 1970).

Other observations supporting the theory of low capablity have been reported. von Haartman (1956) noted that the temperatures on the seventh to fifth days preceding the start of egg laying by the Pied Flycatcher were clearly higher than on average during that time of the year. Pulliainen (1977) stated that at least during five days earlier than the first egg of the species was laid the daily mean temperature had exceeded 10°C in our study area, while in Kilpisjärvi (69°03′N, 20°50′E) the start of egg-laying was preceded by 0-5 days of higher temperature than on average (Järvinen 1983).

From the standpoint of the insectivorous Pied Flycatcher the daily maxima temperatures can be decisive. Thus, on 30 May to 3 June 1993, i.e. 1–5 days before the first layings, the daily maxima

Table 3. Laying dates of individual eggs in 22 Pied Flycatcher nests commenced on 4–6 June 1993 (x = hatched egg, o = unhatched egg).

Nest	Laying date 4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1		o							o	o		o	o	o					
2		x	x	x															
3		o											x	x	x	x	x		
4		x									x	x	xx	x					
5			x	x		x		x	x	x	x								
6	x	x	x						x	x	x								
7		x						x	x	x	o	x	x						
8	o	o	o																
9		o												o	o	o	o	o	
10			x	x	x	x	x	x											
11		o											x	x	x	x			
12			o												x	x	x		o
13	o	o								x	x			x	x	x	x		
14	x	xx		x	x	x													
15	x	x	x										o	x	x	x	x		
16	o	o		o															
17		x								x	x	x	x	o					
18		x	o	x															
19		x							o	x	o	x	x	x					
20		x							x				x	o		x			
21	x	x	x				x		x										
22		x		x			x		x	x									

were +9° to +14°C, whereas the daily maxima during the five days before this period were +2° to +5°C. The two or three days delay before most females interrupted their egg-laying after the coldness had started (Fig. 1) suggests that it is not the coldness itself, but the scarcity of nutritious food that results in the interruption of egg-laying. The difference between the two species appears also when the weather is warming again; the Redstart needs less time for starting egg-laying than does the Pied Flycatcher.

The Pied Flycatcher usually lays once a day (von Haartman 1956, Järvinen 1993), which is commonly used as a basic figure in the breeding studies on this species. Already in 1950, Campbell reported that in Great Britain laying had been interrupted by low temperatures after the earliest pairs started. A similar finding was mentioned by Lundberg & Alatalo (1992) in Central Finland. Pulliainen (1977) reported three cases in the present study area in 1976, where the layings lasting 2 × 21 days (seven eggs in both) and 1 × 12 days (6 eggs), and the longest intervals between two layings were 1 × 14 and 1 × 13 days. The longest interruptions during the egg-laying period in that year took place between 28 May and 9 June, the mean daily temperatures varying between 0°C and +6°C. This cold spell also resulted in poor breeding success, especially for the Pied Flycatcher: of all eggs laid only 29.5% produced fledglings by the Pied Flycatcher and 68.2% produced fledglings by the Redstart.

Laying gaps are one possible response to a cold spell. This response is supported by the cold tolerance of the eggs; they may stay alive up to a couple of weeks or more at temperatures close to zero, before the start of incubation. Another, probably a less successful alternative, would be the rejection of the whole clutch produced so far and replacement breeding. According to our observations in the present study area this response is rare.

The Redstart commenced egg-laying a little earlier than did the Pied Flycatcher in 1993. These Redstarts laid more or less regularly one egg per day and their breeding success was also very good. In addition to obviously better tolerance to cold by the Redstarts, also their energy storage may have been better than that of the Pied Flycatchers (for adaptation of the Redstart to northern conditions, see, e.g. Pulliainen et al. 1982). In addition, it is noteworthy that the Redstart feeds mainly on the ground (see also Alatalo & Alatalo 1979, Järvinen 1983), whereas the Pied Flycatcher depends more on flying insects (name "flycatcher") and, thus is also dependent on the effect of prevailing weather conditions on its feeding habits. The habit of feeding on the ground is especially helpful when the ground is covered by snow and snowless spots are available along the shores of waterways (see Pulliainen 1978b).

The quality and quantity of food seem to be more important in causing laying gaps, by the Pied Flycatcher, than the coldness of the air itself. This may be connected to the protein obtained by the birds. In the case of the Red-billed Quelea (*Quelea quelea*), breeding colonies can form only when sufficient protein-rich food is available. The females need to accumulate reserves in order to initiate egg production and sustain the rapid decline in body protein during egg formation (Jones & Ward 1976). It is easy to understand that cold spells, especially during the first part of the breeding season, may drastically reduce the amount of protein-rich food available for the Pied Flycatcher in the present study area.

Redstarts seem to breed on an average more successfully than Pied Flycatchers in the present study area and also in other Subarctic areas (see Järvinen 1983, 1989). This difference is especially evident during the summers of unfavourable weather conditions (see also Pulliainen 1977). Pied Flycatchers are not able to compensate for the problems arising due to the scarcity of protein-rich food. This, however, does not necessarily reflect the size of the breeding population the next summer. This is due to the low site-tenacity of the Pied Flycatcher (e.g. Järvinen 1993, Nyholm & Myhrberg 1983, our observations in the present study area); the low breeding result during one summer is compensated by newcomers from the south during the next summer. Adaptive selection operates via few individuals which return to nest in the Subarctic.

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Selostus: **Kylmyyden vaikutus kirjosiepon ja leppälinnun munintaan Itä-Lapissa**

Värriön tutkimusaseman maastossa Pohjois-Sallassa tutkittiin pönttölintujen pesintää vuosina 1986–1993. Alueella oli tarjolla yhteensä 290 pönttöä sijoitettuna erilaisiin elinympäristöihin. Pesintää seurattiin tarkoin muninta- ja kuoriutumisjärjestyksen määrittämiseksi ja pesimämenestyksen selvittämiseksi.

Kirjosiepolla toisin kuin leppälinnulla todettiin yleisesti poikkeamia tavanomaisesta munintarytmistä yksi muna vuorokaudessa. Erityisen runsaasti munintakatkoksia havaittiin poikkeuksellisen kylmänä keväänä 1993. Tällöin 4.–6. kesäkuuta aloitetuissa 22 kirjosiepon pesyeessä 122 munan munintaan käytettiin aikaa yhteensä 245 vuorokautta eli keskimäärin yli 2 vrk yhtä munittua munaa kohti. Pisimmät munintakatkokset kahden peräkkäisen munan välillä olivat 2 × 11, 2 × 10 ja 1 × 9 vrk. Jo ensimmäisten munien munintapäivä 4. kesäkuuta oli varsin kylmä (vuorokauden ylin lämpötila +2.8 °C), ja lämpötilat pysyivät alhaisina aina 12. kesäkuuta asti. Useimpien emojen muninta muuttui epäsäännölliseksi tai keskeytyi kokonaan 1–3 päivän kuluttua muninnan alkamisesta. Useimmat munintakatkokset alkoivat heti ensimmäisen munan munimisen jälkeen. Pitkään pesässä ilman haudontaa olleiden munien kuoritumismenestys näytti laskevan. Sensijaan kylmän jakson alussa aloitetuissa leppälinnun pesyeissä todettiin vain yksi yhden vuorokauden munintakatkos. Ilman lämmettyä 12–18 kesäkuuta 1993 vielä 15 kirjosieppoemoa aloitti muninnan. Näissä pesyeissä munintarytmi lähestyi tavanomaista yksi muna vuorokaudessa.

Monet piirteet kirjosiepon pesinnässä osoittavat, että laji on alueen verrattain uutena pesimälajina vielä huonosti sopeutunut Lapin usein vaikeisiin pesintäolosuhteisiin. Esimerkiksi pesivien parien määrä ja pesimämenestys vaihtelevat vuosittain voimakkaasti. Kirjosiepon munintakatkokset saattavat johtua valkuaispitoisen ravinnon, lähinnä hyönteisten puutteesta kylminä munintajaksoina. Lisäksi esim. ravinnon varastointikyky ja -hankinta voivat eteläisellä kirjosiepolla soveltua esim. leppälintua huonommin Lapin yllättäviin pesimäoloihin.

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