Do Pied Flycatchers *Ficedula hypoleuca* have a brood-survival or brood-reduction strategy?

Juha Ylimaunu & Antero Järvinen

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The study analyses some predictions of brood-survival and brood-reduction strategies in connection with material on the Pied Flycatcher obtained in 1982–1984. The egg size variation in clutches, the hatching synchrony, and the growth and survival of nestlings from different eggs are described. Egg volume is influenced by environmental and seasonal factors, and the relationship between laying order and egg size varied with the year. The hatching order was usually the same as the laying sequence, except in one year. The hatching order explained differences in the growth of siblings better than the laying order of the eggs. The last eggs in each clutch produced significantly fewer hatchlings than the other eggs, due to embryo deaths. The results support the view that the final eggs are of poorer quality than the others, but do not provide clear evidence of brood-survival or brood-reduction strategy.

Authors' addresses: Kilpisjärvi Biological Station, Arkadiankatu 7, SF-00100 Helsinki, Finland.

Introduction

Parent birds make an optimal investment in reproduction when all the eggs laid can be raised to fledglings and the parents survive the breeding season in good condition. The breeding success is always related to environmental conditions and to the birds' own condition during the reproductive period. In some birds of prey it is usual for the youngest nestling to die because of starvation, cannibalism or "fratricide" (e.g. Edwards & Colloby 1983). These birds have adopted a "brood-reduction strategy" as an adaptation to the lack of food (Lack 1954, Ricklefs 1965). In such a strategy the number of young is regulated by mortality; theoretically this means a stable clutch size in each season.

In many passerines, nestlings rarely starve (Nice 1957, Lack 1968). Birds with low nestling mortality are supposed to have a "clutch adjustment" or a "brood-survival" strategy (e.g. Clark & Wilson 1981, Richter 1982, Slagsvold et al. 1984), clutch size being adjusted to correspond to the optimal brood size.

A relatively small final egg and hatching asynchrony are considered to be typical of brood reduction (e.g. Slagsvold et al. 1984). Hatching asynchrony causes age and size hierarchy within the brood and in unfavourable environmental conditions sibling competition may lead to starvation of the chick(s) that hatched last. A relatively large final egg and hatching synchrony seem to be typical of the brood-survival strategy, the chicks all being equally well fitted for growth and sibling competition. In comparing the breeding strategies of birds, importance attaches to the last egg, because the theory assumes that the last egg is the last to hatch (e.g. Slagsvold et al. 1984).

Due to its relatively large final egg, the Pied Flycatcher *Ficedula hypoleuca* is classified, with many other passerines, as a brood-survival strategist (Ojanen 1983b, Slagsvold et al. 1984). Nestling Pied Flycatchers rarely starve (e.g. von Haartman 1954, Tompa 1967, Järvinen & Ylimaunu 1986a) and if they do the reason is the absence of parent birds or the low rate of feeding by polygamous males (Järvinen & Ylimaunu 1986a).

In this paper we discuss some predictions of the brood-reduction and brood-survival strategies in connection with the Pied Flycatcher. We analyse the size variation of final and other eggs in clutches, the hatching synchrony of the eggs, and the survival and growth of nestlings in relation to the orders of laying and hatching. Finally, we discuss the existence of reproductive strategies in the Pied Flycatcher.

Material and methods

The study was made in Kilpisjärvi, northern Finnish Lapland (69°03′ N, 20°50′ E) in 1982–1984 (for details of the area, see Järvinen 1983, 1984a). All the nests were in nest-boxes in mountain birch woods near the Kilpisjärvi Biological Station. The local population comprised 20 pairs in 1982, 22 pairs in 1983 and 24 pairs in 1984. In June 1982 the weather conditions were bad: compared with the long-term mean, the date of egg laying was delayed two weeks by cold weather. In 1983 and 1984, the egg laying times and weather were normal, but in 1984 the prelaying period (end of May) was unusually warm.

In each year eggs of the Pied Flycatcher were marked individually according to the laying sequence in about 20 nests (291 eggs in total). The eggs were measured with sliding calipers and the volumes were calculated from the maximum egg length and breadth, using the regression model of Ojanen et al. (1978). The hatching order of the eggs and the egg from which a particular chick hatched were determined by visiting nests once every 30 min during the time of hatching. The hatchlings were also marked individually.

The nestlings were weighed and their wing length measured daily between 09.00 and 14.00 h. Nestlings 0–5 days old were weighed with a 10-g Pesola spring balance (accurate to 0.05 g) and older nestlings with a 50-g Pesola spring balance (accurate to 0.1 g). The wing length was measured by the maximum chord method (Svensson 1975) to the nearest 0.5 mm. The hatchling weight was determined only on hatchlings that were still damp (less than 2 h old). Eggs which did not hatch were collected and the embryo development was checked.

Results

Egg size and hatching order

We present the results separately for each year, since egg size is affected by the yearly weather variation.

In the cold year 1982, the mean egg volume decreased as the ordinal number in the laying sequence increased, but in the other years it increased (Fig. 1). These trends were significant in large clutches in 1983 (r=0.81, P<0.001) and 1984 (r=0.58, P<0.01). In 1982, the second and third eggs were usually the largest. In that year the egg volume was smaller in large than in small clutches, this difference being significant for the first-laid egg (Fig. 1); the mean size deviation of the final egg from the clutch mean was –2.9% (n=17 clutches).

In 1983, the final eggs were as large as the other eggs in the clutch (deviation 0.0%, n=17). In large clutches the first and second eggs were the smallest, but in small clutches they were the largest and the three last eggs in these clutches were of equal size (Fig. 1).

In 1984, when warm weather prevailed before the egg laying, the first and second eggs were the smallest and the last ones the largest (Fig. 1). The last egg was, on average, 2.6% larger than the other eggs in the clutch (n=26, see Fig. 1). In that year the mean egg volume was larger in large than in small clutches (Fig. 1).

The young of the Pied Flycatcher usually hatch within a single day. In general, the hatching order seems to follow the laying sequence (Table 1), but the variation in a single brood can be considerable. An interesting and unexpected result was the early hatching of many final eggs in 1982 (Table 1): the final egg hatched, on average, 5 h before the median chick of the brood in that year. In the other years, the final egg hatched about 14 or 19 h (means) after the median chick (Table 1). This delay in hatching time in 1983 and 1984 was probably caused by the earlier start of incubation: almost all the females started to incubate one day before laying the final egg. The early hatching of final eggs in 1982 might be related to the small size of these eggs. In 1982 we found a negative, though not significant, correlation between the relative egg size and hatching order in the brood.

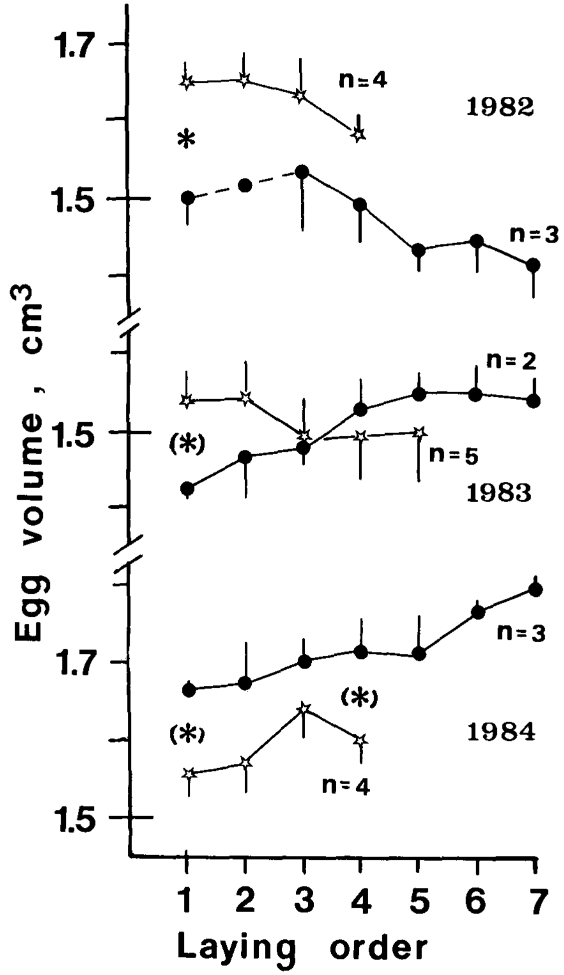

Fig. 1. Relation of egg volume to laying sequence in small (stars) and large (dots) clutches in 1982–84. The large clutches had seven eggs and the small four (except in 1983, when five-egg clutches were the smallest). Large clutches are common early in the breeding season and in this material were laid before or on the median day of the egg-laying period (calculated for the whole Kilpisjärvi population); small clutches were laid on or after the median day of the egg-laying period. t-tests were made between small and large clutches (*)= P<0.1, *= p<0.05, n= number of clutches.

Table 1. Differences in hatching times of eggs in a clutch from time of median-hatched egg (± 0.0 h). + = hatched before median egg, – = hatched after median egg. t-test made between means of final and other eggs in each year.

Laying order	1982			1983			1984		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
First	+0.8	2.4	11	+0.0	1.9	5	+1.4	2.1	5
Second	–0.9	4.0	18	+2.0	2.5	5	+2.2	1.0	4
Third	–0.7	2.0	13	+2.0	2.0	6	+1.7	1.0	6
Fourth	–0.3	2.1	11	–3.3	4.5	6	–1.7	3.2	3
Fifth	–3.2	6.1	4	–4.8	4.1	5	–3.0	3.7	4
Sixth	–3.0	–	1	–4.0	–	1	–5.0	–	1
Final egg	+5.1	9.0	16	–13.9	6.6	10	–19.3	11.6	6
	3.67***			5.08***			5.82***		

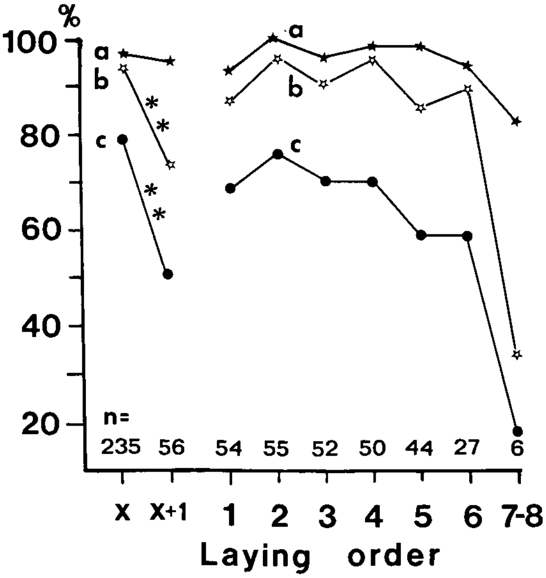

Fig. 2. Relation of egg productivity to laying sequence. Black stars: embryo development observed in eggs, white stars: hatched eggs, and dots: fledged young per egg. x= eggs excluding final eggs, x+1= final eggs, n= number of eggs. G-tests were made between classes x and x+1, ** = P<0.01.

Survival of embryos and nestlings

The productivity of the eggs depended on the laying order: the final egg produced significantly fewer hatchlings than the other eggs (Fig. 2). Failure to hatch was caused by the death of embryos during incubation, because the proportion of undeveloped eggs (no embryo development in the egg) was almost the same in the final eggs (5.0%, n=56) as in the others (3.0%, n=235), but the hatchability of the final eggs was significantly inferior (Fig. 2). Most embryo deaths seemed to happen during the last days of incubation. The survival of nestlings from different eggs did not differ significantly after hatching (Fig. 2).

The production of fledglings seemed to decrease as the ordinal number of the egg increased: the second egg had the best mean fledgling productivity (76%), and only 17% of the seventh and eighth eggs produced a fledgling (Fig. 2). The relatively low productivity estimate of the first eggs was caused by a large proportion (28%) of undeveloped first eggs in the cold season of 1982; in the other years the development and productivity of the first eggs were almost the same as those of the second eggs.

Table 2. Differences in wing length and weight of first and last chick to hatch from those of median-hatched chick. The nestlings fledged, on average, at the age of 15 days. –1d = young that hatched one day (> 20 hours) after the median-hatched young. The last and the –1d young were compared with the first hatched young with t-tests. Statistical significance: * = P<0.05, ** = P<0.01, *** = P<0.001.

		Age of nestlings								
		0 day			8 days			13 days		
Year		First	Last	–1d	First	Last	–1d	First	Last	–1d
1982										
Wing:	Mean	0.2	–0.2**	–1.3***	0.5	–1.0	–5.5***	0.4	–0.9	–4.6**
(mm)	SD	0.2	0.2	0.4	2.3	0.7	0.5	2.0	0.8	1.2
Weight:	Mean	0.1	–0.1*	–0.7**	0.1	–0.1	–2.0***	0.3	0.0	–0.4
(g)	SD	0.2	0.0	0.4	0.7	0.5	0.5	0.6	0.5	0.6
	n	8	8	4	8	8	4	8	8	4
1983–84										
Wing:	Mean	0.0	–0.1	–0.7**	1.0	–0.9*	–4.9***	0.8	–1.0**	–3.9***
(mm)	SD	0.2	0.2	0.5	1.4	1.2	1.7	1.3	1.1	2.2
Weight:	Mean	0.0	–0.1	–0.7***	0.4	–0.1	–1.3***	0.2	0.1	–0.2*
(g)	SD	0.1	0.2	0.3	0.8	0.7	0.5	0.4	0.3	0.5
	n	12	8	14	11	7	14	10	7	12

Effect of laying and hatching orders on nestling growth

The hatching order of the eggs had a conspicuous influence on the growth of nestlings within the brood: the first chick to hatch was, on average, heavier and larger than the median hatchling and the last chick to hatch was lighter and smaller than the median chick (Table 2). If the chick hatched one day after its siblings, the differences were highly significant, and the wing length still differed significantly just before fledging (Table 2).

The effect of the laying order in the clutch was tested as shown in Table 2: the growth of the chicks from the first and final egg (hatching during the same day) were compared with the means for each brood. These comparisons did not reveal any significant differences. In 1982, the chicks from the first eggs were significantly larger than the chicks from the final eggs during the whole nestling period (t-tests on wing length measurements). However, these differences in growth seem to be related to egg size rather than to laying order, because in that year chicks from large (first) eggs grew significantly better than chicks from small (and final) eggs (details in Järvinen & Ylimaunu 1984).

Discussion

The results on egg volumes in the clutch and on the hatching order did not provide clear evidence of brood-survival or brood-reduction strategy. The trends in egg sizes and the hatching order within clutches differed between years (Fig. 1 and Table 1). In the warm season of 1984 the relation of egg volume to laying sequence indicated brood-survival strategy, but in that year and also in 1983, the final egg hatched much later than the others (Table 1). The start of incubation before the final egg in 1983 and 1984 indicates a brood-reduction strategy.

In the cold and late breeding season of 1982, egg size decreased as the ordinal egg number increased. In that year, the first 1–3 eggs in the clutch were large and the nestlings from these eggs grew significantly better than nestlings from small eggs (see also Järvinen & Ylimaunu 1984). In other words, the females invested more in the first 1–3 eggs than in the later eggs in 1982. This suggests a brood-reduction strategy in that year, or, as we believe, physiological difficulties in egg laying) though the earlier hatching of the small final eggs (Table 1) could enhance the growth of hatchlings from those eggs.

The ambient temperature and weather conditions have clear effects on egg volume and egg composition in the Pied Flycatcher (Ojanen et al. 1981, Ojanen 1983b). The mean air temperature 1–3 days before laying of the final egg correlated significantly with the volume of the final egg in 1982–84 in the Kilpisjärvi population (Järvinen & Ylimaunu 1986b). It seems likely that the physiological condition of the female during egg-laying mainly determines the mean egg size in a clutch (Järvinen & Väisänen 1984), and the trend in intra-clutch egg volumes (see also Järvinen & Ylimaunu 1986b). A decrease in egg size from the first egg to the last may be a consequence of deteriorating conditions during the breeding season. In Rydén's (1978) study of the Blackbird *Turdus merula*, the food supply in early spring was better than later on and egg volume increased as laying progressed in the early clutches, but not in the late clutches.

The hypothesis of brood-survival strategy predicts equal survival of embryos and nestlings in a clutch, whereas according to the hypothesis of brood-reduction survival should depend on the order in which the eggs are laid (Slagsvold et al. 1984). Our results support the view that the final egg is of poorer quality than the others. The final egg produced fewer hatchlings and fledglings than the other eggs, because many of the embryos died (Fig. 2). The final eggs of the Pied Flycatcher are usually lighter in colour than the other eggs in the brood and their shell seems to be thinner (Ylimaunu, unpubl.). These features may be related with egg quality (e.g. a thin egg shell increases evaporation, Ojanen 1983a).

The decreasing trend in egg yolk weight from the first to the last egg (Ojanen 1983b) also indicates that the last eggs are inferior to the others, although the last eggs were larger in a population in central Finland (Ojanen 1983b). The egg yolk is the most important energy reserve for the embryo (Ojanen 1983a). In 1982 the young from small and later eggs grew significantly less well than the young from larger and earlier eggs, probably due to poorer energy reserves (Järvinen & Ylimaunu 1984). It seems likely that the egg yolk was also smaller in the later eggs in 1982.

In a Pied Flycatcher population in Germany, the proportion of the first and final eggs producing fledglings was at most 50%, whereas the value for the other eggs was 62–88% (n=8 broods, Creutz 1955). In our study, the first eggs had a lower productivity (72% hatched, n=18) than the second eggs only in 1982, but the results for the final egg were the same as in the German study.

The theory of the brood-survival strategy predicts that the nestlings will not differ greatly in their growth; in the brood-reduction strategy, the nestling from the final (and last hatched) egg should grow more slowly than the others (e.g. Slagsvold et al. 1984). In the Kilpisjärvi population, the hatching order explained the differences in the growth of siblings better than the laying order. The hatching order favoured the young from the first 1–3 eggs in the clutch, because they usually hatched earlier than the others (except in 1982, Table 1). If the smaller eggs in the clutch hatch earlier than the others (as in 1982), the nestlings from small eggs start to grow earlier and benefit in sibling competition. However, the sizes of the eggs and hatchlings generally correlate positively in our population (Järvinen & Ylimaunu 1984, 1986a), which may balance the differences in growth.

The hatching order is undoubtedly important for growth and survival: e.g. in the Fieldfare, *Turdus pilaris*, asynchrony in hatching increases differences in growth between nestlings and, finally, differences in nestling mortality (Slagsvold 1982, our unpubl. data from Kilpisjärvi). The Pied Flycatcher eggs hatched within some hours (as in typical brood-survival strategy), but the late hatching of the final egg in 1983 and 1984 caused a typical brood-reduction situation.

To conclude, this study shows that the Pied Flycatcher cannot be classified as a brood-survival strategist if only the trends in egg volume are considered. The egg volume pattern within clutches seems to be affected by environmental and seasonal factors (see also Ojanen et al. 1981). The survival of embryos and the growth measurements showed that the nestling from the final egg grew more slowly and had poorer chances in sibling competition. Studies of breeding strategy should take account not only of egg volumes, but also of the quality of the eggs and the patterns of hatching and growth.

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Selostus: **Mikä on kirjosiepon lisääntymistapa munien koon, muninta- ja kuoriutumisjärjestyksen perusteella?**

Tutkimuksessa selvitettiin, mitä vallitsevaan teoriaan perustuvaa "lisääntymisstrategiaa" kirjosiepot noudattavat. Tutkimus tehtiin Enontekiön Kilpisjärvellä 1982–84 otoksen perusteella (n. 20 pesää vuosittain, yht. 291 munaa).

Teorian mukaan brood-survival -lisääntymistavassa emot panostavat saadakseen kaikki poikasensa aikuisiksi huolimatta vaihtelevista ravinto- ym. oloista (tyypillistä esim. pienille varpuslinnuille). Brood-reduction — lisääntymistavassa puolestaan on tavallista, että vain suotuisissa oloissa kaikki poikaset saadaan lentoikään: tavallista on nuorimpien poikasten menehtyminen sisarusten välisessä kilpailussa (esim. petolinnut).

Perinnölliseksi oletetun lisääntymistavan ilmentäjinä pidetään trendiä pesyeen munan koossa, munintajärjestyksessä, munien kuoriutumisjärjestyksessä sekä poikasten kasvua (menestymistä) suhteessa munintajärjestykseen.

Munan koko pesyeessä pieneni munintajärjestyksessä 1982, mutta suureni muina vuosina (kuva 1), todennäköisesti sääoloista ja ravintotilanteesta johtuen. Munien kuoriutumisjärjestys noudatti keskimäärin munintajärjestystä, mutta poikkeamia esiintyi: v. 1982 pienet viimeiset munat kuoriutuivat odottamattomasti ennen muita (taulukko 1). Vuosina 1983–84 viimeinen muna kuoriutui sen sijaan lähes vrk:n muita myöhemmin (taulukko 1).

Kuoriutumisjärjestys näytti vaikuttavan poikasten kasvuun: ensimmäisenä kuoriutuneet olivat pesäpoikasajan muita suurempia (paino, siivenpituus) ja viimeisenä kuoriutuneet muuta poikuetta pienempiä. Kuitenkaan erot eivät olleet merkitseviä poikasajan lopulla kuin tapauksissa, joissa viimeinen muna (poikanen) oli kuoriutunut n. vrk:n muita myöhemmin (taulukko 2).

Munien poikastuotto laski suhteessa munintajärjestykseen: toinen muna tuotti keskimäärin eniten lentopoikasia ja tuotto laski jyrkästi siten, että munintajärjestyksessä 7. ja 8. munan tuotto oli enää keskim. 17% (kuva 2). Syynä ilmiöön oli pesyeen viimeisten munien heikko kuoriutuvuus, mikä johtui alkion kuolemisesta haudontavaiheessa.

Tulokset eivät tue yksiselitteisesti kumpaakaan teorian ennustamaa lisääntymistapaa ainakaan tutkittujen indikaattorien osalta. Sen sijaan ulkoiset ympäristötekijät vaikuttavat pesyeen sisäiseen munan koon vaihteluun ainakin Lapin äärevissä oloissa. Viimeisen munan heikko laatu ja myöhäinen kuoriutuminen asettaa kyseenalaiseksi tehdyn lisääntymistapaluokittelun kirjosiepon osalta. Mikäli varpuslintujen lisääntymistavan luokittelu on tarkoituksenmukaista, tulisi tulevaisuudessa kiinnittää huomiota nimenomaan munien laatuun ja poikastuottoon erilaisissa ympäristöissä.

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