

# REPRODUCTION OF PIED FLYCATCHERS (*FICEDULA HYPOLEUCA*) IN GOOD AND BAD BREEDING SEASONS IN A NORTHERN MARGINAL AREA

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ABSTRACT.—We studied relationships between female size, date of egg laying, clutch size, egg size, and breeding success in Pied Flycatchers (*Ficedula hypoleuca*) in a marginal area in northwestern Finnish Lapland (69°N). Average June temperatures in 1975–1981 were used to classify years into “good” (warm) and “bad” (cold) breeding seasons. In general, early and warm springs were followed by “good” breeding seasons: females were heavier, laying was earlier, clutches were larger and contained larger eggs, and hatching and fledging success were better than in late and cold springs. Mainly due to low nesting success in “bad” breeding seasons, the local population could not maintain itself; immigration from the south was needed. We suggest that spring weather may provide information concerning the character of the coming breeding season, which may help birds to maximize their lifetime production of young. Received 20 April 1983, accepted 12 January 1984.

A BASIC principle of biology is that species are adapted to the environment they inhabit. For example, Järvinen (1983) showed that some of the adaptations the Pied Flycatcher (*Ficedula hypoleuca*) has evolved in the southern part of its range are not suitable for a northern marginal area, where this species was manipulated to breed in nest boxes in the 1950's. This northern marginal population has lived in an unstable state, with population parameters (e.g. mean breeding density, mean number of fledglings per nest) fluctuating strongly from year to year according to prevailing weather.

In an earlier paper, we demonstrated that the physiological state (“fatness”) of female Pied Flycatchers influenced successful breeding in the north (Järvinen and Väisänen 1983). Here, we address the following questions. (1) Does environmental variation over weeks and years affect the reproduction of a southern passerine in extreme northern conditions? (2) What are the responses of an individual to environmental variation, i.e. are some reproductive traits more sensitive than others to environmental changes? Our analysis will demonstrate the difficulties birds may have when attempting to colonize areas with climates colder than in the normal breeding grounds of the species.

## STUDY AREA, MATERIALS, AND METHODS

Our study area is situated in mountain birch (*Betula pubescens* ssp. *tortuosa*) woods (elevation 475–600 m) in northwestern Finnish Lapland near Lake Kilpisjärvi (about 69°03'N, 20°50'E). Kilpisjärvi is among the most “arctic” places in Fennoscandia, with a growing season of 100 days or less (Tuhkanen 1980). During the study period, mean monthly summer temperatures were as follows ( $n = 7$ ): May  $+1.7 \pm 0.8^\circ\text{C}$  (SD), June  $+6.8 \pm 2.3^\circ\text{C}$ , and July  $+9.9 \pm 2.0^\circ\text{C}$ . Snow melted in the beginning of June from the birch woods where nest boxes for Pied Flycatcher were placed. More details of the study area and history of the local Pied Flycatcher population are given by Järvinen (1980, 1983).

The data consist of 154 clutches from seven successive years (1975–1981). Järvinen conducted all fieldwork alone to avoid bias caused by individual differences in technical performance. Years were divided into “good” (1976 and 1978–1980) and “bad” (1975, 1977, and 1981) on the basis of weather conditions. In “good” years conditions during the main breeding season were more favorable than in “bad” years (Table 1).

Nests ( $n = 89$  in “good” and 65 in “bad” years) were visited regularly to determine the exact date of laying of the first egg, clutch size, and hatching and fledging success. The weight of Pied Flycatcher females drops markedly at the end of the incubation period but remains constant during the early incu-

bation phase (von Haartman 1954, Silverin 1981). Therefore, to make comparisons among years reliable, females were ringed, weighed, and measured 0–5 days after clutch completion. At that time eggs were weighed and measured. Females were not weighed during the early morning hours (0200–0900) in order to avoid effects of the night fast. We do not know the age structure of our population. Being a marginal population, however, it probably contains a relatively high proportion of yearlings (cf. Sternberg 1972).

Females were weighed to the nearest 0.1 g with a 50-g Pesola spring balance and wing length was measured by the maximum method (Svensson 1975) to the nearest millimeter with a ruler. Maximum length (*EL*) and breadth (*EB*) of each egg were measured to the nearest 0.05 mm with sliding calipers, and from these values egg volume (*EV*) was computed with the formula:

$$EV = -0.042 + 0.4976 \times EL \times EB^2,$$

where *EV* is given in  $\text{cm}^3$  and *EL* and *EB* in cm. On average, this formula explains about 96% of the egg volume variance in the Pied Flycatcher (Ojanen et al. 1978). In addition, mean egg weight for each clutch was determined by weighing eggs together with a 10-g Pesola spring balance to the nearest 0.1 g. The median egg length, breadth, and volume of the clutch are used as basic variables for egg dimensions, because the median is less sensitive to rare events (very small or large eggs) with a strong effect (e.g. van Noordwijk et al. 1981a). Thus, if not otherwise noted, *n* refers to the number of clutches, not to the number of eggs.

## RESULTS

*Annual variations and correlation matrices.*—Mean values of several aspects of Pied Flycatcher breeding biology in our study area are given in Table 1. All traits varied significantly from year to year (ANOVA,  $P < 0.05$  or less). In general, if the summer was cold, laying was retarded, but 1981 was an exception to this rule (see Discussion). In “bad” years (1975, 1977, and 1981) females had lower weight, although they were by no means smaller than in “good” years (wing length as a measure of the body size; Table 1). Egg length and egg volume, and to a lesser extent egg breadth, were smallest in “bad” years. The general character of the breeding season (“good” or “bad”) largely determined the reproductive capacity of Pied Flycatcher.

In both “good” and “bad” years clutch size declined as the season progressed ( $R^2 = 27.0\%$

and 33.4%, respectively,  $P < 0.001$ ; Table 2). In “good” years laying date correlated significantly and negatively with the number of hatchlings and fledglings, and negatively, although not significantly, with egg dimensions (Table 2a). In “bad” years, however, these correlations were positive (Table 2b). These relationships are analyzed later in more detail.

Female body weight had positive effects on other reproductive parameters (Table 2). In general, heavy females were larger, they laid larger eggs, and their breeding success was better than that of light-weight females; the effect of female weight on egg size and breeding success seemed to be stronger in “bad” than in “good” years. In “good” years female weight also had a positive influence on clutch size ( $R^2 = 6.6\%$ ,  $P < 0.01$ ). In “bad” years female wing length did not correlate significantly with any other indices (Table 2b). In “good” years wing length correlated significantly with clutch size ( $R^2 = 11.0\%$ ,  $P < 0.01$ ) and egg volume ( $R^2 = 4.7\%$ ,  $P < 0.05$ ). In “good” years clutch size correlated significantly and positively with the number of hatchlings and fledglings and with egg parameters; in “bad” years these correlations were not significant (Table 2).

*Breeding performance in relation to date.*—In “good” years females tended to have an evenly high weight in each date class (= date of laying of the first egg), whereas in “bad” years individuals seemed to gain weight as the season advanced (Fig. 1a). In the latest date class (20–29 June), females had the same average weight in both “good” and “bad” years, but the total mean was higher in “good” than in “bad” years during the early incubation period [ $15.28 \pm 0.96$  (SD) g vs.  $14.32 \pm 1.09$  g, respectively;  $t = 5.03$ ,  $df = 130$ ,  $P < 0.001$ ].

In each date class, females had a somewhat longer wing in “bad” than in “good” years; yet this difference was statistically significant only in date class 2 (Fig. 1b). When all date classes were combined, mean wing length was not significantly longer in “bad” than in “good” years [ $78.1 \pm 1.4$  (SD) mm vs.  $77.7 \pm 1.3$  mm, respectively;  $t = 1.74$ ,  $df = 129$ ,  $P < 0.1$ ].

In “good” years the average clutch size was  $5.93 \pm 0.89$  eggs (SD;  $n = 89$ ), and in “bad” years the corresponding figure was  $5.55 \pm 0.88$  eggs ( $n = 65$ ;  $t = 2.62$ ,  $P < 0.01$ ). In “good” years  $5.12 \pm 1.62$  ( $n = 89$ ) eggs hatched per nest (hatching success 86%), and  $4.78 \pm 1.79$  young fledged per nest (fledging success 93%). In “bad”

TABLE 1. Mean daily air temperature ( $^{\circ}\text{C} \pm \text{SD}$ ) at Kilpisjärvi in June 1975-1981, the number of days in June with mean temperature  $\leq 4^{\circ}\text{C}$  and  $\geq 8^{\circ}\text{C}$ , and reproductive traits [mean  $\pm \text{SD}$  (*n*)] of the Pied Flycatcher in 1975-1981. The temperature values were derived from a meteorological station situated within the study area (alt. 480 m) and were used to divide the years into "good" and "bad" breeding seasons. The significance of *F*-tests is shown with asterisks (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ , and \*\*\* =  $P < 0.001$ ; asterisks in parentheses denote a particular significance level almost reached).

Years	1975 (bad)	1976 (good)	1977 (bad)	1978 (good)	1979 (good)	1980 (good)	1981 (bad)	<i>F</i> - tests
Mean June $^{\circ}\text{C}$	4.6 $\pm$ 2.6	6.5 $\pm$ 3.5	5.0 $\pm$ 2.5	8.6 $\pm$ 4.4	8.4 $\pm$ 3.6	10.1 $\pm$ 3.9	4.3 $\pm$ 2.3	—
Days $\leq 4^{\circ}\text{C}$	14	8	12	3	2	3	15	—
Days $\geq 8^{\circ}\text{C}$	3	13	3	14	13	22	2	—
Laying date (first egg in June)	18.7 $\pm$ 3.3 (26)	13.2 $\pm$ 4.4 (15)	16.8 $\pm$ 5.3 (14)	11.0 $\pm$ 4.4 (10)	9.7 $\pm$ 3.6 (30)	6.1 $\pm$ 3.6 (33)	1.7 $\pm$ 5.0 (24)	***
Female weight (g)	14.74 $\pm$ 1.13 (15)	15.02 $\pm$ 0.85 (14)	14.01 $\pm$ 0.91 (15)	15.34 $\pm$ 0.72 (10)	15.50 $\pm$ 1.08 (30)	15.15 $\pm$ 0.94 (32)	14.22 $\pm$ 1.15 (16)	***
Female wing (mm)	78.7 $\pm$ 1.9 (15)	77.4 $\pm$ 1.2 (14)	77.3 $\pm$ 0.7 (15)	78.0 $\pm$ 1.5 (10)	77.9 $\pm$ 1.2 (30)	77.6 $\pm$ 1.3 (32)	78.4 $\pm$ 0.7 (15)	*
Egg length (mm)	17.69 $\pm$ 0.76 (26)	17.83 $\pm$ 0.76 (16)	17.51 $\pm$ 0.63 (15)	17.87 $\pm$ 0.46 (10)	17.77 $\pm$ 0.58 (30)	18.11 $\pm$ 0.60 (33)	17.55 $\pm$ 0.52 (24)	*(*)
Egg breadth (mm)	13.35 $\pm$ 0.41 (26)	13.40 $\pm$ 0.31 (16)	13.35 $\pm$ 0.31 (15)	13.27 $\pm$ 0.32 (10)	13.51 $\pm$ 0.30 (30)	13.48 $\pm$ 0.24 (33)	13.26 $\pm$ 0.36 (24)	*
Egg volume ( $\text{cm}^3$ )	1.53 $\pm$ 0.14 (26)	1.55 $\pm$ 0.13 (16)	1.51 $\pm$ 0.09 (15)	1.53 $\pm$ 0.09 (10)	1.58 $\pm$ 0.10 (30)	1.60 $\pm$ 0.09 (33)	1.50 $\pm$ 0.11 (24)	*(*)
Egg weight (g)	1.66 $\pm$ 0.16 (26)	1.62 $\pm$ 0.15 (16)	1.59 $\pm$ 0.08 (10)	1.58 $\pm$ 0.11 (10)	1.69 $\pm$ 0.10 (17)	1.71 $\pm$ 0.11 (32)	1.62 $\pm$ 0.10 (23)	*(*)
Clutch size	5.23 $\pm$ 0.82 (26)	5.38 $\pm$ 0.89 (16)	5.20 $\pm$ 0.68 (15)	5.20 $\pm$ 0.79 (10)	6.13 $\pm$ 0.78 (30)	6.24 $\pm$ 0.79 (33)	6.13 $\pm$ 0.80 (24)	***
Hatchlings	3.46 $\pm$ 1.92 (26)	4.06 $\pm$ 1.91 (16)	2.87 $\pm$ 2.36 (15)	4.00 $\pm$ 1.63 (10)	5.47 $\pm$ 1.17 (30)	5.67 $\pm$ 1.45 (33)	1.92 $\pm$ 2.62 (24)	***
Fledglings	2.23 $\pm$ 1.99 (26)	3.63 $\pm$ 1.93 (16)	2.07 $\pm$ 2.28 (15)	4.00 $\pm$ 1.63 (10)	4.80 $\pm$ 1.75 (30)	5.55 $\pm$ 1.44 (33)	1.58 $\pm$ 2.36 (24)	***

TABLE 2. Correlation coefficients between reproductive indices and related variables of Pied Flycatchers in "good" (A; 89 clutches) and "bad" years (B; 65 clutches).

	Date of laying	Female weight	Female wing length	Clutch size	Hatchlings	Fledglings	Egg length	Egg breadth	Egg volume	Egg weight
<b>A. Good years</b>										
Date of laying	1.000									
Female weight	-0.122	1.000								
Female wing length	-0.216*	0.384***	1.000							
Clutch size	-0.520***	0.257**	0.331**	1.000						
Hatchlings	-0.407***	0.170	0.170	0.647***	1.000					
Fledglings	-0.427***	0.168	0.191	0.533***	0.840***	1.000				
Egg length	-0.076	0.184	0.189	0.218*	0.107	0.106	1.000			
Egg breadth	-0.197	0.234*	0.177	0.229*	0.123	0.106	0.373***	1.000		
Egg volume	-0.179	0.242*	0.217*	0.255*	0.145	0.132	0.758***	0.874***	1.000	
Egg weight	-0.136	0.111	0.108	0.278**	0.214*	0.137	0.604***	0.742***	0.808***	1.000
<b>B. Bad years</b>										
Date of laying	1.000									
Female weight	0.174	1.000								
Female wing length	-0.052	0.302*	1.000							
Clutch size	-0.578***	0.046	-0.030	1.000						
Hatchlings	0.285*	0.252*	0.134	-0.031	1.000					
Fledglings	0.220	0.247*	0.001	0.086	0.803***	1.000				
Egg length	0.104	0.330**	0.196	-0.079	0.158	0.159	1.000			
Egg breadth	0.255*	0.201	0.032	-0.152	-0.026	0.055	0.312*	1.000		
Egg volume	0.239	0.295*	0.125	-0.159	0.066	0.127	0.696***	0.885***	1.000	
Egg weight	0.205	0.281*	0.132	-0.115	0.038	0.109	0.580***	0.767***	0.834***	1.000

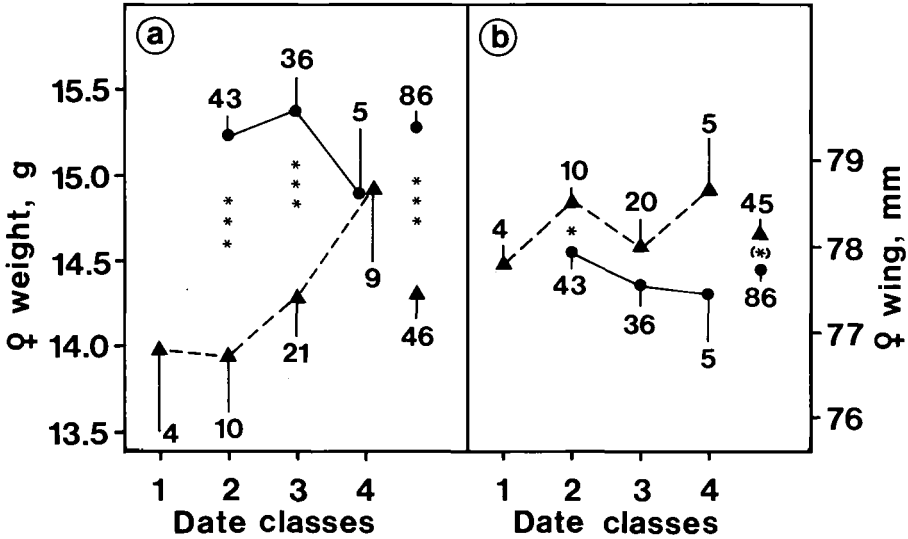


Fig. 1. Body weight (a) and wing length (b) of Pied Flycatcher females in different date classes (= date of laying of the first egg) at Kilpisjärvi in "good" (dots, continuous lines) and "bad" years (triangles, broken lines). Date classes: 1 = 21-30 May, 2 = 31 May-9 June, 3 = 10-19 June, and 4 = 20-29 June. Dots and triangles = means, vertical lines = standard errors, numbers = number of nests. To the right of each figure the total mean is given. The significance of the difference between the means in "good" and "bad" years is shown by asterisks (*t*-tests; asterisk in parentheses = 5% significance level almost reached).

years the corresponding figures were  $2.75 \pm 2.37$  ( $n = 65$ ; 50%) and  $1.95 \pm 2.18$  (71%), respectively, and differences between "good" and "bad" years were highly significant ( $t = 6.96$  and  $8.57$ , respectively,  $P < 0.001$ ). Reproductive capacity varied markedly with laying date (Fig. 2). In "good" years, numbers of hatchlings and fledglings were highest in clutches commenced early in summer; in "bad" years the reverse was apparent. Differences between "good" and "bad" years were less apparent in date class 4 (Fig. 2). The difference in reproductive capacity between "good" and "bad" years was due mainly to differences in hatching success (Fig. 2), which emphasizes the role of weather factors during egg-laying and incubation periods (cf. Järvinen 1983).

In "good" years, egg dimensions and weight were higher than in "bad" years (Table 3). In late June (date class 4), mean egg-size measurements in "bad" years were similar to those in "good" years (Fig. 3). The seasonal pattern of variation in egg weight was rather similar to that in egg volume (Fig. 3c,d), and these traits correlated significantly and positively in both "good" and "bad" years (Table 2;  $R^2 = 65.3\%$

and  $69.6\%$ , respectively,  $P < 0.001$ ). Specific density ( $\text{g}/\text{cm}^3$ ) of eggs was higher in "bad" than in "good" years [ $1.084 \pm 0.039$  (SD) vs.  $1.061 \pm 0.036$ , respectively;  $t = 3.54$ ,  $df = 132$ ,  $P < 0.001$ ].

*Breeding performance in relation to clutch size.*— In each clutch-size class, females were heavier in "good" than in "bad" years (Fig. 4a), and, especially in "good" years, the heaviest, and usually also the biggest (Fig. 4b), females laid the largest clutches. As pointed out earlier, however, in "bad" years females were not smaller than in "good" years. This means that in "bad" years big females had to lay relatively small clutches (Fig. 4b) and eggs (cf. Table 3).

The number of hatched and fledged young per a certain clutch-size class was much smaller in "bad" than in "good" years (Fig. 5). In "good" years most eggs hatched, and almost all hatchlings fledged, irrespective of clutch size.

In "good" years egg size tended to increase with increasing clutch size, but in "bad" years there was no apparent trend, or it was rather a declining one (Fig. 6; cf. also the correlation coefficients in Table 2). In small clutches of 4 or 5 eggs no marked differences existed in egg

TABLE 3. Length, breadth, volume, and weight of Pied Flycatcher eggs at Kilpisjärvi in "good" and "bad" years (mean ± SD). *P* = significance level of *t*-test between means.

	"Good" ( <i>n</i> = 89)	"Bad" ( <i>n</i> = 65)	<i>P</i>
Egg length	17.91 ± 0.62 mm	17.59 ± 0.65 mm	<0.005
Egg breadth	13.45 ± 0.29 mm	13.32 ± 0.37 mm	<0.02
Egg volume	1.57 ± 0.10 cm <sup>3</sup>	1.51 ± 0.12 cm <sup>3</sup>	<0.005
Egg weight	1.67 ± 0.13 g	1.63 ± 0.13 g	<0.1

size between "good" and "bad" years. An abrupt change occurred in clutches with 6-8 eggs.

DISCUSSION

In "bad" years some females evidently started to lay too early during the period when late cold spells have a high probability of occurring (cf. Sealy 1975, Järvinen 1983). When late cold spells set in, most eggs and young are lost, which partly explains the poor breeding success in "bad" years in date classes 1-2 (Fig. 2) and the positive correlation between date of laying and number of hatchlings and fledglings in Table 2b. During cold spells, females

are known to interrupt incubation at Kilpisjärvi (Hildén et al. 1982, Järvinen 1983), and, presumably, the leaner they are the more easily they do this for their own survival. Thus, the low weight of females in early summer in "bad" years (Fig. 1a) contributes to the poor breeding success.

The negative correlation between date of laying and number of hatchlings and fledglings in "good" years was due to the general seasonal decline of clutch size and brood size of the Pied Flycatcher (cf. Järvinen 1983). In clutches commenced latest and during comparatively favorable periods of summer, the number of hatchlings and fledglings was nearly the same in "good" and "bad" years (Fig. 2). Opposing trends in breeding success in "good"

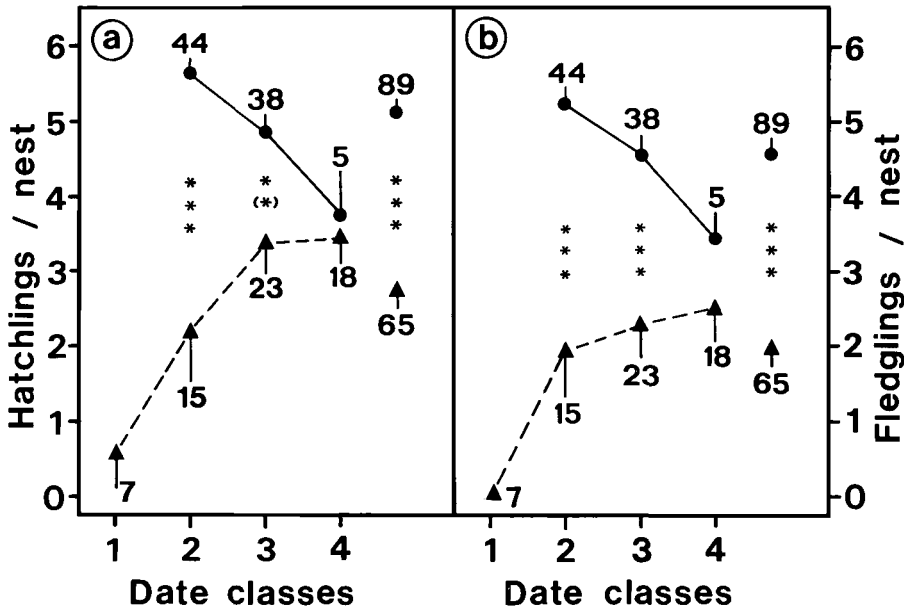


Fig. 2. Number of Pied Flycatcher hatchlings (a) and fledglings (b) per nest in different date classes at Kilpisjärvi in "good" (dots) and "bad" years (triangles). For explanation, see Fig. 1.

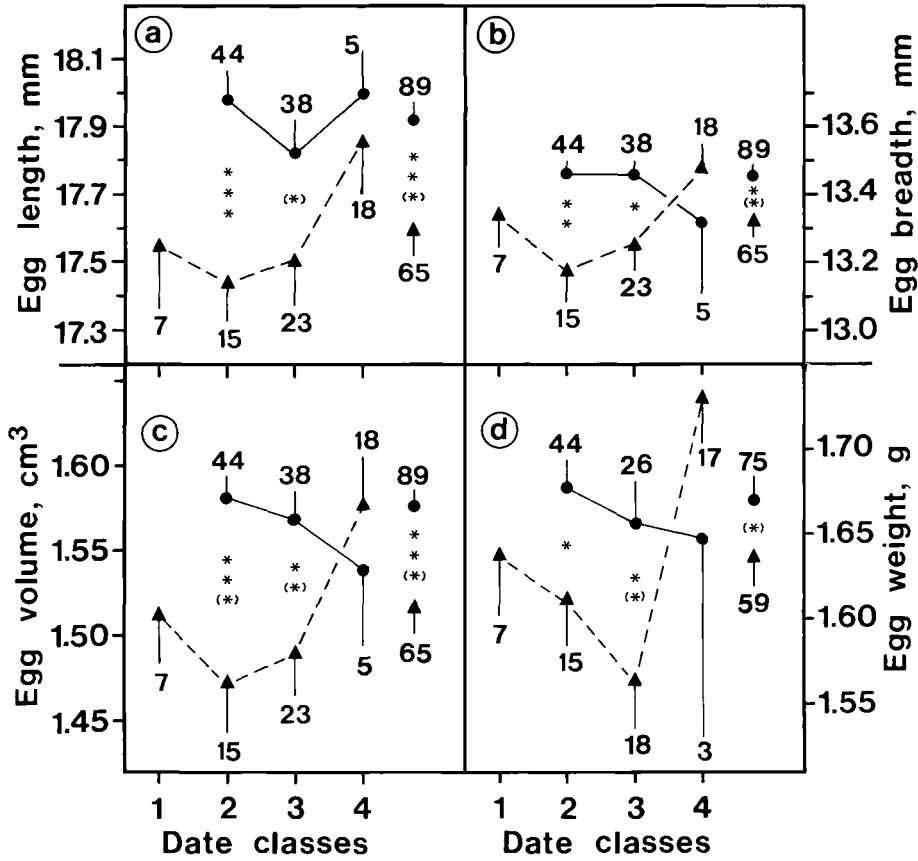


Fig. 3. Length (a), breadth (b), volume (c), and weight (d) of Pied Flycatcher eggs in different date classes at Kilpisjärvi in "good" (dots) and "bad" years (triangles). For explanation, see Fig. 1.

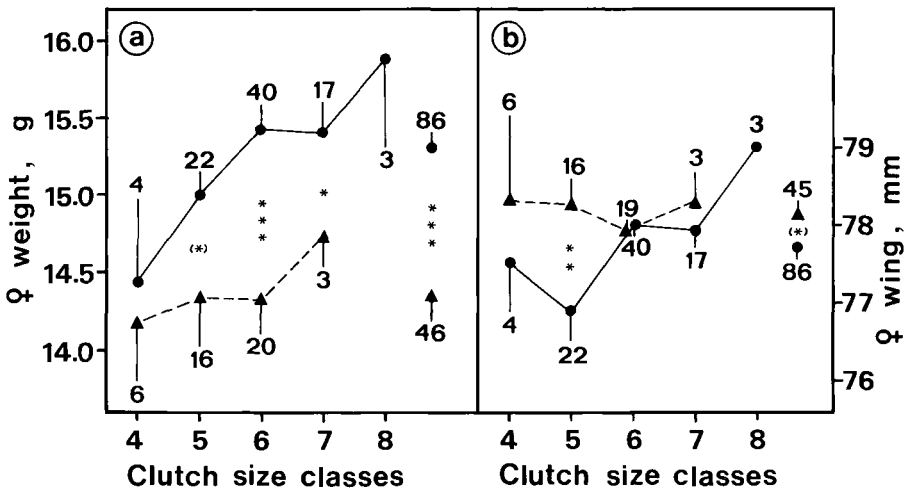


Fig. 4. Body weight (a) and wing length (b) of Pied Flycatchers in different clutch-size classes at Kilpisjärvi in "good" (dots) and "bad" years (triangles). For explanation, see Fig. 1.

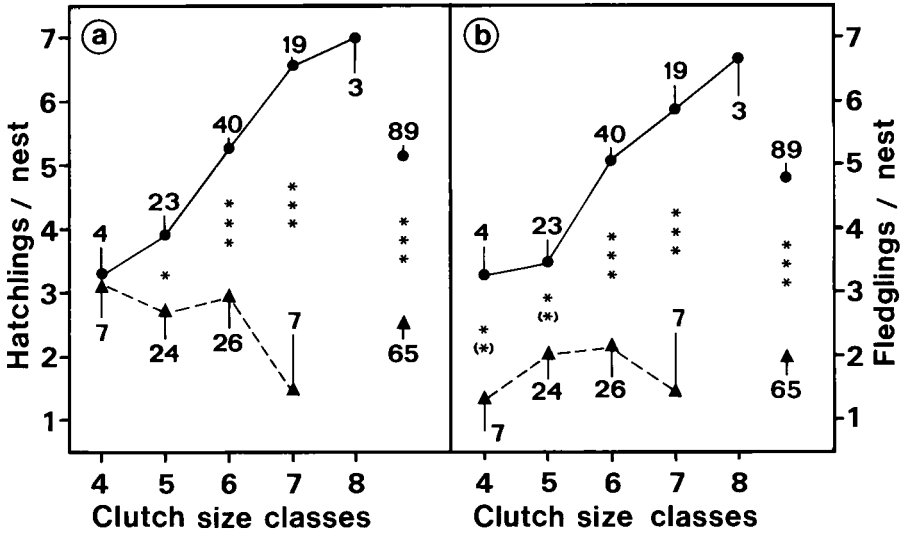


Fig. 5. Number of Pied Flycatcher hatchlings (a) and fledglings (b) per nest in different clutch-size classes at Kilpisjärvi in "good" (dots) and "bad" years (triangles). For explanation, see Fig. 1.

versus "bad" years explain why date had no significant effects on breeding success when data for all years were combined (Järvinen and Väisänen 1983).

In another paper (Järvinen and Väisänen 1983), we demonstrated that the smallest eggs of the Pied Flycatcher do not hatch well at Kilpisjärvi. In "bad" and cold years, when food was apparently also scarce, eggs were much smaller than in "good" years in our study area (Figs. 3 and 6). Siivonen (1957) published evidence that eggs of pen-reared Ring-necked Pheasants (*Phasianus colchicus*) in poor nutritional condition at the time of laying were smaller than those produced by hens in good condition. He also correlated this difference with the occurrence of "good" and "bad" breeding success. Later, Högstäd (1981) showed experimentally that Black-billed Magpie (*Pica pica*) pairs supplied with extra food started to lay earlier, had larger clutches, heavier eggs, and greater hatching success, and produced more fledglings than did control pairs. We believe, however, that the physiological condition of females is a more crucial factor in determining nesting success than is egg size (cf. correlation coefficients in Table 2b).

It has been suggested that, early in the breeding season when food conditions are poor, smaller females are at an advantage, because

they have fewer basal energy requirements and lay smaller eggs than larger birds do (Perrins 1970, Jones 1973, Svensson 1978). Our results from Pied Flycatchers in northern Lapland indicate that first-laying females are not smaller than those laying later (Fig. 1b; in our study area wing length is not related to age; A. Järvinen unpubl. data). It is true that in "bad" years egg size seems to be smaller early in the summer (Fig. 3). At Kilpisjärvi, Pied Flycatcher females are known to die in nests in years of very inclement weather and poor food conditions (Hildén et al. 1982). Laying smaller, as well as fewer, eggs might increase females' chances of survival (Moss et al. 1981).

This is not to say that small egg size is a favorable reproductive trait in unfavorable conditions, however (cf. Schifferli 1973). If we compare Figs. 1-3 with one another, we find a similarity in the form of the curves. These data suggest that gains in female weight and egg volume are essential for successful breeding in the north. A fat female, which produces large eggs, may incubate and feed young effectively without long breaks for her own feeding (cf. White and Kinney 1974). A large egg, with a small surface-area-to-volume ratio, is probably relatively well "buffered" against chilling, and it may contain larger food reserves for the hatched young than does a small egg (for a



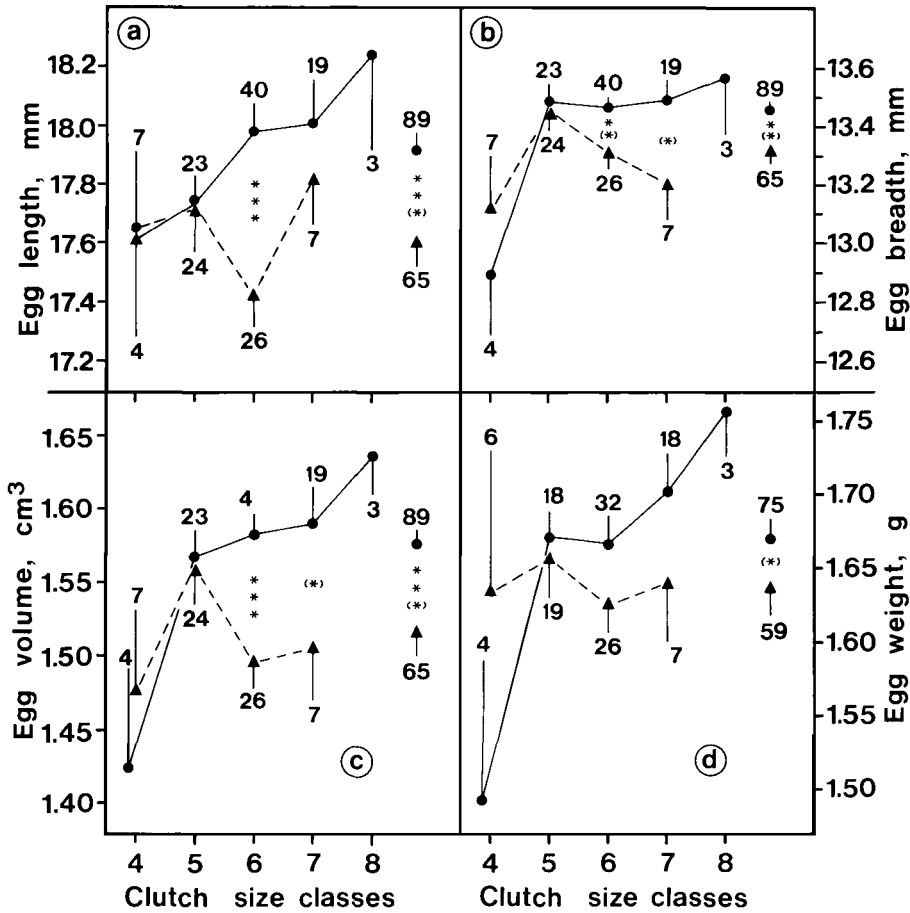


Fig. 6. Length (a), breadth (b), volume (c), and weight (d) of Pied Flycatcher eggs in different clutch-size classes at Kilpisjärvi in "good" (dots) and "bad" years (triangles). For explanation, see Fig. 1.

thorough review, see Ojanen 1983a; for the Pied Flycatcher in Lapland, see Järvinen and Ylimaunu in press).

Egg traits may be considered to be very conservative. Ricklefs (1974) stated that, when the female has insufficient energy, the size and quality of her eggs are not altered appreciably, only the number. Our results indicate that in severe stress, when females are in lean condition, at least egg size may be reduced (Figs. 3 and 6). This is important, because very small eggs seem to hatch poorly (Järvinen and Väisänen 1983), and young from large eggs seem to be better developed at fledging than are young from small eggs, particularly if feeding conditions are poor (Schifferli 1973, Järvinen and

Ylimaunu in press). It is conceivable that variations in the energy balance of laying females also affect egg formation and thereby modify egg dimensions (cf. Kendeigh et al. 1956, Koskimies 1957). At Kilpisjärvi there was a general correlation between female weight and egg volume ( $R^2 = 12.0\%$ ,  $n = 132$ ,  $P < 0.001$ ), whereas egg volume was apparently not much affected by the size (wing length) of the bird ( $R^2 = 1.5\%$ ,  $n = 131$ ,  $P > 0.1$ ).

No common rules seem to exist regarding the relationship between clutch size and egg size in passerines. For instance, van Noordwijk et al. (1981b) found that clutch size and egg volume of Great Tits (*Parus major*) were not correlated, although a major proportion (60–80%)

of the phenotypic variation in egg volume was genetic. There is also a geographical factor involved: the egg size of Pied Flycatchers correlated negatively with clutch size in southern Finland, but the correlation changed to positive towards the north (Järvinen and Väisänen 1983). At Kilpisjärvi these variables were positively correlated in "good" years but not in "bad" years (Table 2, Fig. 6c).

Physiological mechanisms regulating egg size may be found in the water balance of eggs. An increase in egg size with laying sequence in large clutches (Ojanen et al. 1981) seems to be due mainly to the inclusion of water into the albumen (Ojanen 1983b). In "bad" years females were probably incapable of "pumping" water into eggs, because under prevailing conditions the specific density of eggs increased at Kilpisjärvi.

By plotting the number of hatchlings and fledglings against clutch size (Fig. 5), one can see that the reproductive capacity of Pied Flycatchers varies according to the quality of the breeding season (cf. also the correlation coefficients in Table 2). In "good" years large clutches produce more fledglings than do smaller ones, and in every clutch-size class almost all hatchlings fledged. In contrast, in "bad" years large clutches do not produce more hatchlings and fledglings than do smaller ones.

In theory, when an environment is predictably cyclic, it is usually advantageous for an organism to anticipate events rather than to respond to them (Levins 1968). If female Pied Flycatchers could predict the quality of the coming breeding season with reasonable accuracy, they should lay more eggs in "good" than in "bad" years to ensure a maximum reproductive output over their lifetime. To allocate more energy for reproduction in "bad" years would be disadvantageous: this effort would be wasted to a large extent, and the production of extra eggs would be an especially great strain for the female and would reduce her chances of survival (e.g. Murray 1979: 83).

Hirshfield and Tinkle (1975) suggested that selection for high levels of reproductive effort should occur in years favorable to juvenile survivorship in a variable environment, provided that the relative quality of the year is predictable by adults. Does the reproductive effort of Pied Flycatchers vary annually according to prevailing conditions, or is their effort at a constant level, matching the availability of

resources? We cannot give a definite answer to this question, because detailed energy budgets are not available for this species. The ratio of clutch weight to body weight suggests about the same effort in "good" (65%) and "bad" years (63%). This index is not very useful, however, because individuals "could devote the same quantity of energy to reproduction at equivalent body sizes, but differ greatly in the absolute amount of energy gathered or in the time during which it was gathered" (Hirshfield and Tinkle 1975).

How could reliable information be obtained about the quality of the coming season? In northernmost Finnish Lapland there was considerable unpredictability in weather conditions within each year, but in "good" years the conditions were less severe than in "bad" years. "Good" breeding seasons were preceded by relatively early and warm springs (A. Järvinen, unpubl. data). In fact, in 1966–1981 there was only one clear exception to this rule: in 1981 a warm period at the turn of May–June came to a sudden end in early June, and the weather remained cold thereafter, causing serious nesting losses for Pied Flycatchers (Hildén et al. 1982).

It has been shown that the average laying date of Pied Flycatchers is significantly ( $R^2 = 66.7\%$ ,  $P < 0.001$ ) retarded at Kilpisjärvi when the mean spring temperature is low (Järvinen and Lindén 1980). The mean daily air temperature during the main prelaying and egg-laying period of Pied Flycatchers (1–15 June) was correlated significantly with the mean air temperature during the main incubation and nestling period (16 June–15 July) in 1966–1980 ( $R^2 = 36.5\%$ ,  $P < 0.02$ ;  $R^2$  was almost the same if the mean temperature during 1–31 July was used as the dependent variable,  $40.0\%$ ,  $P < 0.02$ ). This suggests that in northern Lapland warm weather in early June predicts higher than average temperatures during later parts of the breeding season.

Thus, if spring is early and warm, it seems probable that the breeding season will be "good," and then flycatchers might "know" that it is advantageous to lay large clutches. The risk that this warning system does not function in the north seems to be very small (one case in 16 yr,  $P < 0.001$  according to the binomial distribution). Cohen (1967), Slagsvold (1977), O'Connor (1978), and Askenmo (1982) have pointed out the possibility that temperatures

and phenophases experienced by birds in early spring might provide a means for making predictions.

The above hypothesis of the existence of a "warning system" clarifies one detail in the breeding biology of Pied Flycatchers, i.e. the calendar effect of the clutch size (von Haartman 1967, Järvinen and Lindén 1980): in a large geographical area all females tend to lay approximately equally large clutches on a certain calendar day (clutch size decreases seasonally by an average number of 0.08 eggs/day; Järvinen and Lindén 1980). We think that this mechanism may be a preadaptation for optimizing clutch size closer to the value that produces most the offspring under certain conditions. So, in late and cold years, which are probably "bad" in terms of breeding success, females start with fewer eggs.

#### CONCLUSIONS

In the far north small passerine birds are likely to encounter harsh and capricious physical conditions that seriously affect several important reproductive traits. During inclement weather, those females with poor fat reserves seem particularly to be in difficulties. Our results (Fig. 5) agree with those of Mountford (1973), Murray (1979), van Noordwijk et al. (1980), and Moss et al. (1981) in that, in varying environments, the clutch size that produces the most chicks in one year may not do so in another year. However, the difference in productivity between different clutch sizes of Great Tits in central Europe seemed to arise after fledging (van Noordwijk et al. 1980), but in the Pied Flycatcher in northernmost Europe a considerable proportion of it seemed to arise before fledging or even before hatching.

Moss et al. (1981) concluded that "hens with a successful gene may lay a range of clutch sizes, thus ensuring that the gene does relatively well each year. It is immaterial to this mechanism whether the variation is environmental or genetic." Högstedt (1980) proposed that in a bird population there is not a single optimal clutch size but many. According to him, the optimal strategy for birds in high-quality territories is to lay large clutches and for birds in poor territories to lay small clutches. Our results agree with Högstedt (1980), if we replace the word "territory" with the word "year" in his hypothesis.

The energetic constraints of "bad" (cold) breeding conditions seem to cause a dramatic reduction in the weight of the females (Figs. 1a and 4a). In "bad" years light-weight females lay smaller eggs than in "good" years (Figs. 3 and 6), and hatching and fledging success of lighter birds is also reduced (Figs. 2 and 5). Thus, the following general pattern emerges from our results: early and warm spring, "good" breeding season, heavy females, early date of egg-laying, large eggs, large clutches, good hatching success, and good fledging success.

In the north the influence of "bad" years on population dynamics is probably considerable; Järvinen (1983) estimated that the long-term breeding result is insufficient to maintain the Pied Flycatcher population at Kilpisjärvi without immigration. Spring weather may provide a means of obtaining information about the character of the future breeding season, which may help the birds to maximize their lifetime production of young.

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