

## Significance of egg size on the growth of nestling Pied Flycatchers *Ficedula hypoleuca*

Antero Järvinen & Juha Ylimaunu

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The growth of nestling Pied Flycatchers in relation to egg volume was studied in NW Finnish Lapland (69° 03' N, 20° 50' E) in 1982. The nestlings were divided into two groups, those hatched from small (<1.49 cm<sup>3</sup>, n = 21) and large eggs (≥1.49 cm<sup>3</sup>, n = 41), respectively. Nestlings hatched from large eggs were heavier than nestlings from small eggs throughout the nestling period (15 days), but the weight difference between the groups was not statistically significant after the 10th day. The nestlings hatched from large eggs were larger (in terms of the wing length) at hatching than nestlings from small eggs, and the difference between the groups was significant also at fledging. Partial correlations showed that towards the end of the nestling period the larger reserves of large eggs accelerated the growth of young.

Antero Järvinen & Juha Ylimaunu, Kilpisjärvi Biological Station, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland.

### 1. Introduction

Several studies have demonstrated the effect of egg size on hatchling weight and development and survival of chicks (e.g. Parsons 1970, Schifferli 1973, O'Connor 1979, Birkhead & Nettleship 1982). Observations made at Kilpisjärvi, northern Finnish Lapland, indicate that eggs and nestlings of passerines face a critical situation during cold spells (Järvinen 1983). The smallest eggs of the Pied Flycatcher *Ficedula hypoleuca* seem to hatch poorly in the north (Järvinen & Väisänen 1983). Moreover, if weather conditions are exceptionally unfavourable during the breeding season, egg size is reduced and this seems to contribute to the relatively low breeding success in unfavourable seasons (Järvinen & Väisänen 1984). Thus, in northern Lapland large egg size seems to have positive effects on hatching success, these effects being accentuated in unfavourable (cold) physical conditions. In this paper we demonstrate the significance of large egg volume on the gain in weight and wing length in the Pied Flycatcher in northern Lapland presenting data from the whole nestling period.

### 2. Study area, material and methods

The data were collected near Kilpisjärvi Biological Station (69° 03' N, 20° 50' E) in NW Finnish Lapland in 1982. The study area is a mountain birch wood 475-600 m above sea level. The dynamics of the local Pied Flycatcher population, breeding in nest-boxes, has been monitored since 1966 (Järvinen 1983). The growth of 62 nestlings from 16 broods was studied in relation to egg volume between July 7 and 30. Nestling mortality in these broods was low: two nestlings, excluded from the analyses, died soon after hatching and one nestling died just before fledging. The mean laying date of the first egg was June 21st ± 3 days (SD, N = 16), clearly later than normal (June 13; Järvinen 1983). Eggs hatched in the second week of July (range July 7th - 15th). The mean daily air temperature in July (alt. 480 m) was +10.7° C, near the long-term average in 1966-80 (+10.9° C; Järvinen 1983). The mean precipitation in July was 41 mm, the long-term average in this month being 63 mm (Järvinen 1983).

The eggs in each brood were measured to the nearest 0.01 mm with sliding calipers and marked individually according to laying sequence. Egg volume (*EV*) was calculated from the maximum egg length (*EL*) and breadth (*EB*) with the formula:

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

where *EV* is given in cm<sup>3</sup> and *EL* and *EB* in cm. On average, this formula accounts for about 96% of the egg volume variance in the Pied Flycatcher (Ojanen et al. 1978). At the time of hatching the nests were visited once every 30 min. throughout the day (hatchings usually occurred in the

morning). Thus it was possible to determine the egg from which each young hatched. The newly hatched young (day 0) were weighed with a 10-g Pesola spring balance (accuracy 0.05 g) and their wing length was measured by the maximum chord method (Svensson 1975) to the nearest 0.5 mm. The toes of the young were coloured black with drawing ink to distinguish them until they were ringed at about a week old. On subsequent days the same nests were visited at the same time of the day (a 50-g Pesola spring balance was used after the 5th day, accuracy 0.1 g).

To study the effects of egg size on the growth of the nestlings, the nestlings were divided into two groups; i.e., those hatched from small ( $<1.49 \text{ cm}^3$ ,  $N=21$ ) and large eggs ( $\geq 1.49 \text{ cm}^3$ ,  $N=41$ ). The mean egg volume in egg category "small eggs" was  $1.40 \pm 0.06 \text{ cm}^3$  (SD), the corresponding figure for egg category "large eggs" being  $1.63 \pm 0.10 \text{ cm}^3$ . The mean brood size ( $4.05 \pm 1.12$  and  $4.07 \pm 0.98$  for egg category "small" and "large" eggs, respectively) and hatching sequence were the same in each category, so they did not affect the results obtained. A logistic equation

$$W = a / (1 + e^{-K(t-b)})$$

was fitted to the weight data using Crossner's (1977) method. Here  $W$  = weight in g at time  $t$ ,  $a$  = the upper asymptote (or the final weight) of the growth curve,  $e$  = the base of natural logarithms,  $K$  = the growth constant,  $t$  = age in days (day 0 is the day of hatching), and  $b$  = the age at the inflection point of the curve (50% of the asymptotic weight).

### 3. Results

Throughout the nestling period (15 days) nestlings hatched from large eggs were heavier than those from small eggs, but the weight difference between the groups was not significant after the 10th day (Fig. 1). However, in wing length the difference between the groups was also significant at fledging, when the average wing length of fledglings from large eggs was 72.6% of that of an adult female in 1982, the corresponding figure for fledglings from small eggs being 70.5% (Fig. 2). In both groups the original weight data (averages for 21 and 41 nestlings, resp.) fitted well to the logistic equation ( $r = 0.99$ ,  $N=12$ ,  $P<0.001$ ):

For small eggs,

$$W = 14.13 / (1 + e^{-0.473(t-4.8)})$$

and for large eggs,

$$W = 14.51 / (1 + e^{-0.474(t-4.5)}).$$

Nestlings hatched from large eggs reached a 3% higher asymptotic weight than nestlings from small eggs, but there seemed to be no differences between the groups in the growth constant ( $K$ ) or in the age at inflection point ( $b$ ).

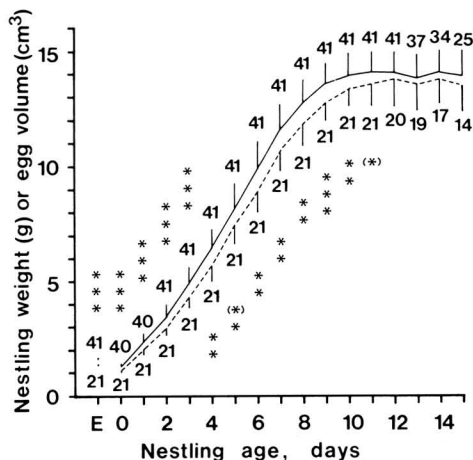


Fig. 1. Gain of body weight of nestling Pied Flycatchers (mean, SD,  $N$ ) hatching from small ( $<1.49 \text{ cm}^3$ , lower dotted line) and large eggs ( $\geq 1.49 \text{ cm}^3$ , upper continuous line), respectively. Day 0 is the day of hatching, "E" denotes to the mean egg volume in each egg volume category. \* =  $P<0.05$ , \*\* =  $P<0.01$ , \*\*\* =  $P<0.001$ .

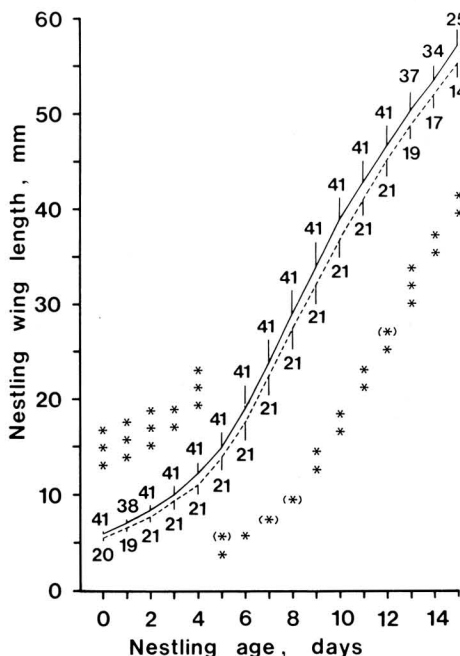


Fig. 2. Wing length of nestling Pied Flycatchers (mean, SD,  $N$ ) hatching from small ( $<1.49 \text{ cm}^3$ , lower dotted line) and large eggs ( $\geq 1.49 \text{ cm}^3$ , upper continuous line), respectively. Day 0 is the day of hatching.

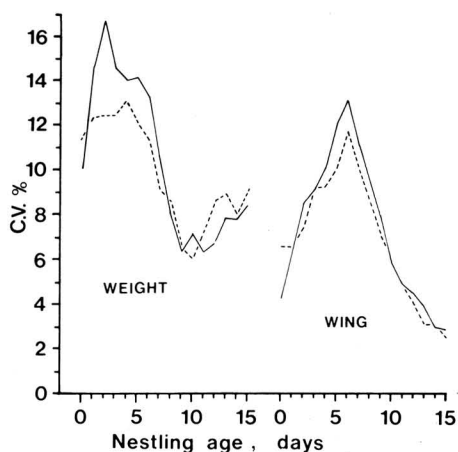


Fig. 3. Coefficient of variation in body weight (left) and wing length (right) of nestling Pied Flycatchers hatching from small ( $<1.49\text{ cm}^3$ , dotted line) and large eggs ( $\geq 1.49\text{ cm}^3$ , continuous line), respectively. Day 0 is the day of hatching.

At the time the sheaths of feather cylinders split (about day 8) the difference in average wing length was statistically least significant between the groups (Fig. 2). About that time the coefficient of variation in wing length was also the largest (Fig. 3). The CV in nestling weight was declining after the inflection point was passed (Fig. 3; days 4–5, i.e. the age when the absolute maximum growth rate in weight was attained), but rose again somewhat at the time of fledging. During the early part of the nestling period CV tended to be higher in nestlings hatched from large eggs than from small eggs (Fig. 3), but in no case was the difference significant (F tests). Using all data, the CV of the mean daily weight (days 0–15) was greater ( $10.1 \pm 3.0\%$ ) than that of the wing length ( $7.2 \pm 3.0\%$ ;  $t=3.96$ ,  $df=62$ ,  $P<0.001$ ).

The correlation coefficients of body weight with egg volume became weaker toward the end of the nestling period. In nestlings 0–9 days old correlation coefficients varied between  $+0.5$  and  $+0.6$  ( $N=62$ ,  $P<0.001$ ), but in nestlings 10–14 days old between  $+0.3$  and  $+0.4$  ( $P<0.05$  or  $<0.01$ ). However, in wing length there seemed to be no age-related change in the correlations:  $r$ -values, though lower than the corresponding values in weight during the early part of the nestling period, remained at a rather constant level of  $+0.45$  ( $P<0.001$ ) throughout the nestling period.

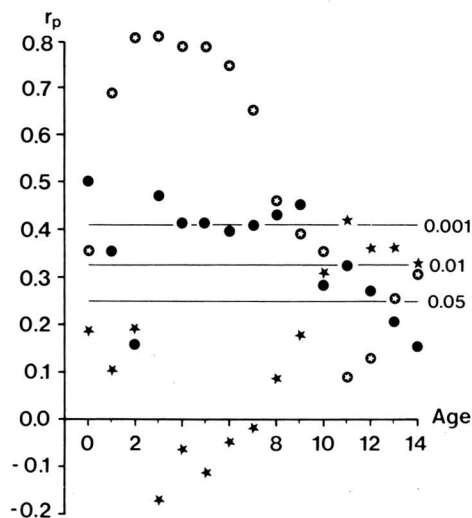


Fig. 4. Age change in partial correlations between nestling weight and egg volume, holding wing length constant (black dots), between nestling wing length and egg volume, holding weight constant (black stars) and between nestling weight and wing length, holding egg volume constant (white stars). The significance levels are indicated by horizontal lines.

During the early part of the nestling period (days 0–9) the relation between wing length and egg volume, holding weight constant, was not significant (partial correlations,  $P>0.1$ ), whereas the relationship between weight and egg volume, holding wing length constant, was significant ( $P<0.01$  or less; Fig. 4). In addition, the relationship between weight and wing length, holding egg volume constant, was significant ( $P<0.01$  or less). A change occurred on the 10th day, when the relationship between wing length and egg volume was significant for the first time ( $r_p=0.306$ ,  $N=62$ ,  $P<0.05$ ), and stronger than the relationship between weight and egg volume ( $r_p=0.284$ ,  $N=62$ ,  $P<0.05$ ). From this day onwards, the young from large eggs were better developed (larger) than those from small eggs ( $P<0.01$  or less), but had only slightly larger reserves ( $P<0.05$  or NS; Fig. 4). At the same time the correlation between weight and wing length, when egg volume was held constant, became low (Fig. 4).

#### 4. Discussion

The development of the young was related to

the size of the egg. The implications of this result for nesting success and population dynamics are of obvious importance. A small egg probably contains less energy for a hatchling than a large egg and a smaller embryonic capital may place a hatchling in the brood at a competitive disadvantage in the struggle for existence. Development in the nest may be crucial for the survival of the young after leaving the nest as well, but in 1982 we failed to obtain enough data on the post-fledging survival of the young in relation to egg size.

According to Ojanen (1983), a large egg size is a good predictor of a high energy content of the egg in the Pied Flycatcher; in a one-year-study (1978) in Central Finland he found egg albumen to be the main contributor to the positive correlation between egg size and energy content. As pointed out by Schifferli (1973) and Birkhead & Nettleship (1982), shortage of food or a late breeding season may accentuate the influence of egg size on chick development and survival. At Kilpisjärvi the breeding season of 1982 was late due to cold weather in June. Especially in cold and late years it seems to pay to lay large eggs in our northern study area, since the change of population numbers may be at the expense of females laying small eggs (Järvinen & Väisänen 1983, 1984; present study). Although selection pressure for large egg size seems to be strong in the north (Järvinen & Väisänen 1983), in severe environmental conditions females probably often fail to find enough food to fulfil the energy requirements of both laying large eggs, and of maintaining their metabolic rate. It is suggestive that in severe conditions eggs are smaller but also females are lighter than in favourable conditions (Järvinen & Väisänen 1984).

The changes in the partial correlations (Fig. 4) paralleled the changes in the significance levels in Figs. 1-2. After the 10th day the weight difference between the egg-volume groups was no longer significant (Fig. 1), but the difference in wing length remained significant even after this day (Fig. 2). To conclude, at hatching, when weight was held constant, the young from large eggs were apparently not much larger in body-size than young from small eggs, having only larger food or energy reserves (cf. Table 1 in Birkhead & Nettleship 1982). However, toward the end of the nestling period their larger reserves apparently accelerated the growth of the young

hatched from large eggs and this was manifested in better developed (larger) young at fledging. Because the reserves of even a large egg are depleted as the nestlings grow, it is understandable that the partial correlations between nestling weight and egg volume decreased toward the end of the nestling period. We believe there is at least one major message borne out by our results: To make valid generalizations about the effects of egg size on the growth and development of nestlings, measurements covering the whole nestling period are needed.

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