

Intraclutch Egg-size Variation in Birds: Physiological Responses of Individuals to Fluctuations in Environmental Conditions

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Slagsvold et al. (1984) analyzed intraclutch variation in egg size in 67 bird species. They felt that the percent deviation of the last egg from the clutch mean (D) was important and identified two strategies: birds that adopt the "brood-reduction strategy" have a relatively small final egg, whereas birds that adopt the "brood-survival strategy" have a relatively large final egg. They stressed that more evidence is needed, however, before the existence of the two "strategies" is accepted.

We examined the validity of using the relative size of the final egg as a measure of intraclutch egg-size variation. We present an alternative hypothesis to account for patterns in D : Cold weather causes decreases in female weight. Decreases in female weight necessarily decrease egg size (volume). No further "strategic" explanations are necessary.

Before conclusions about the reproductive strategy of a species can be made, the geographical, annual, and seasonal variations in the breeding performance of the species must be known. Although it is difficult and time-consuming to measure all eggs in many clutches according to the laying sequence, we believe that both interclutch and intraclutch egg-size comparisons should be based on such information, rather than on comparisons where the size of only some of the eggs are compared with the mean size. The last-laid egg may be larger than the mean, but it may not be the largest of all eggs within the clutch.

We have studied the population biology of the Pied Flycatcher (*Ficedula hypoleuca*) and the Redstart (*Phoenicurus phoenicurus*) in Finnish Lapland (about 69°N) since 1973 (Järvinen 1983). Egg-size variation has been a central part of our investigations, and from 1982 to 1984 we measured egg volume according to the laying sequence (see Järvinen and Väisänen 1984 for methods).

Mean egg volume of the Pied Flycatcher was consistent across years and did not differ significantly from 1982 to 1984, despite substantial variation in mean laying date, and therefore in clutch size (Table 1; cf. Järvinen and Lindén 1980). Based on combined

data from 1982-1984 (clutches with 4-8 eggs, $n = 54$ clutches), the penultimate egg of the Pied Flycatcher averaged more than the other eggs. On average the final egg was 95% of the volume of the largest egg in the clutch. However, all the eggs in a clutch had almost the same probability of being the largest one. In 13 clutches the first egg was largest, in 8 clutches the second egg was largest, in 10 clutches the penultimate egg was largest, and in 12 clutches the ultimate egg was largest. This distribution does not differ from an even distribution (G -test with Williams' correction, $G = 1.38$, $df = 3$, $P > 0.5$).

Based on data from clutches with 5-8 eggs (1980-1982, $n = 32$) in central Norway, Slagsvold et al. (1984) found that the final egg of the Pied Flycatcher averaged 2.4% above the mean volume of all eggs in the clutch. In our study area the corresponding combined figure for clutches with 5-8 eggs was only 0.4% (1982-1984, $n = 51$).

The Redstart was placed by Slagsvold et al. (1984) in the category where the relative size of the last egg is smaller than the mean ($D = -0.2\%$, $n = 4$, clutch size 7 eggs; data from central Finland after Ojanen et al. 1981). In our area the mean D -value of the Redstart was 1.8% in 1984 ($n = 10$, clutch size 5-8 eggs). In Redstart clutches with 7 eggs ($n = 4$), however, the value of D was even higher (3.1%). Thus, the final egg of the Pied Flycatcher seems to be relatively smaller in northern than in southern Scandinavia, whereas the reverse may be true for the Redstart, although the differences are not great.

Because the nesting success of the Pied Flycatcher in Lapland depends partly on egg size (Järvinen and Väisänen 1983, 1984), the young from the last-laid egg probably would benefit from a larger egg size. In 1982-1984 the final egg of the Pied Flycatcher produced a hatchling significantly less often than the other eggs (15 of 56 final eggs vs. 18 of 235 other eggs did not hatch; $G = 9.98$, $df = 1$, $P < 0.01$). In our study area predation is negligible (Järvinen 1980), and losses due to predation were excluded in this analysis.

TABLE 1. Mean date of laying of the first egg (1 = 1 June), mean clutch size, and mean egg volume of the Pied Flycatcher in northwestern Finnish Lapland in 1982-1984 (± 1 SD).

| | 1982 | 1983 | 1984 |
|-------------------------------|-----------------|-----------------|-----------------|
| Number of nests | 17 | 18 | 26 |
| Date of first egg | 20 \pm 3 | 7 \pm 7 | 6 \pm 8 |
| Clutch size | 4.65 \pm 0.86 | 5.78 \pm 0.65 | 5.73 \pm 1.22 |
| Egg volume (cm ³) | 1.54 \pm 0.11 | 1.55 \pm 0.09 | 1.59 \pm 0.09 |

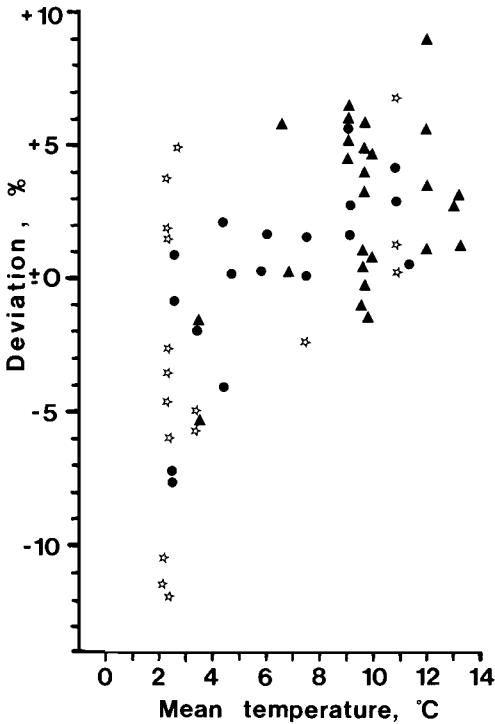


Fig. 1. The deviation (in %) of the size of the final egg laid from the mean size of all eggs in the clutch for the Pied Flycatcher in Finnish Lapland, plotted against the mean ambient temperature 1-3 days before the laying of the final egg. Stars = 1982, circles = 1983, triangles = 1984.

The character of the breeding season seems to play a role in the determination of the mean D -value of the population. In our study area, there was no pattern in D -values in 1982 (binomial test; $D > 0\%$ in 8, $D < 0\%$ in 9 cases), but in 1983 (13/5) and in 1984 (20/6) D -values greater than zero predominated ($P < 0.05$ and $P < 0.005$, respectively). Therefore, in 1983 and 1984 more Pied Flycatchers were, according to the classification of Slagsvold et al. (1984), exercising the brood-survival strategy.

Weather conditions are one possible explanation

of why the relative size of the final egg varies annually. In the late breeding season of 1982, ambient temperature during the egg-laying period was lower than in 1983, and in 1983 lower than in 1984. The relative size of the final egg of the Pied Flycatcher is related to the temperature conditions prevailing about 1-3 days before laying (Fig. 1, Table 2). The same generalization of the effect of temperature on the value of D seems to hold true within a single breeding season for the Redstart (Table 2).

Within years, this relationship also was significant for the Pied Flycatcher (1982: $r = 0.476$, $P = 0.05$; 1983: $r = 0.681$, $P < 0.005$; 1984: $r = 0.407$, $P < 0.05$; temperatures calculated for 1-3 days before the laying of the final egg). It is apparent from Fig. 1, however, that temperatures less than 4°C allow large negative D 's. Above this limit the overall relationship between temperature and D is weaker ($r = 0.300$, $n = 41$, $P = 0.06$).

Is it possible that, for example, the Pied Flycatcher is exercising a different reproductive strategy in different years (brood-reduction strategy in cold but brood-survival strategy in warm breeding seasons)? We believe not. Instead, we suggest that in cold summers females are forced to lay relatively small final eggs, whereas in warm summers they are physically able to lay relatively large final eggs. Cold breeding conditions cause a dramatic decrease in the weight of female Pied Flycatchers, which is manifested as reduced egg sizes (Järvinen and Väisänen 1984). Before inferences of "reproductive strategies" of species are made, basic physiological factors ought to be considered. If used at all, the word "strategy" preferably should be confined to situations where the ultimate (adaptive) value of a trait is apparent.

Our data are from the north, and in more favorable areas the situation may not be the same because there the temperature may never reach a level sufficient to affect egg size. This is a sound argument, although Ojanen et al. (1981) found that, in central Finland (about 65°N), the size of the final egg of the Pied Flycatcher and the Great Tit (*Parus major*) correlate with temperatures 1-3 days before laying, i.e. during the most intensive period of egg formation. These correlations, however, although significant, explained only a small proportion (1-4%) of the variation in egg size.

TABLE 2. Correlation coefficients between the mean air temperature before the laying of the final egg and the relative size of the final egg (D , %) for the Pied Flycatcher (1982-1984) and the Redstart (1984) in Finnish Lapland.

| | 1 day before | 1-3 days before | 1-7 days before | 1-10 days before |
|---------------------------------|----------------------|----------------------|----------------------|----------------------|
| Pied Flycatcher ($n = 61$) | 0.562 $P < 0.001$ | 0.624 $P < 0.001$ | 0.525 $P < 0.001$ | 0.412 $P = 0.001$ |
| Redstart ($n = 10$) | 0.695 $P < 0.05$ | 0.685 $P < 0.05$ | 0.284 NS | -0.150 NS |

Olli Järvinen, Jake Rice, Tore Slagsvold, and two anonymous reviewers offered useful comments on an earlier draft of the manuscript. This study was supported by grants from the Academy of Finland, the Finnish Cultural Foundation, and the Emil Aaltonen Foundation.

LITERATURE CITED

- JÄRVINEN, A. 1980. Population dynamics in the Pied Flycatcher *Ficedula hypoleuca* at subarctic Kilpisjärvi, Finnish Lapland. *Ornis Fennica* 57: 17-25.
- . 1983. Breeding strategies of hole-nesting passerines in northern Lapland. *Ann. Zool. Fennici* 20: 129-149.
- , & H. LINDÉN. 1980. Timing of breeding and the clutch size in the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland. *Ornis Fennica* 57: 112-116.
- , & R. A. VÄISÄNEN. 1983. Egg size and related reproductive traits in a southern passerine *Ficedula hypoleuca* breeding in an extreme northern environment. *Ornis Scandinavica* 14: 253-262.
- , & ———. 1984. Reproduction of Pied Flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. *Auk* 101: 439-450.
- OJANEN, M., M. ORELL, & R. A. VÄISÄNEN. 1981. Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. *Ornis Fennica* 58: 93-108.
- SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, Ö. LORENTSEN, & M. HUSBY. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101: 685-697.

Received 9 April 1985, accepted 3 September 1985.

Nutrient Reserves of Premigratory Brant During Spring

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Brant (*Branta bernicla*), like other arctic-nesting geese, rely heavily on stored nutrient reserves during reproduction. Brant arrive on the nesting grounds with large lipid and protein reserves and metabolize substantial portions of these reserves during egg-laying and incubation (Ankney 1984). Because of their small body size, however, Brant must rely on exogenous sources of nutrients because they cannot store enough reserves to fast throughout incubation. Spring weather conditions on the arctic nesting grounds have substantial influence on Brant reproductive success. During late springs, when Brant arrive on snow-covered nesting grounds, they metabolize lipid reserves for maintenance until the snow disappears and nest sites and food become available. Consequently, nests are initiated later, clutch sizes are reduced, and the proportion of non-nesting Brant increases (Barry 1962).

Ebbinge et al. (1982) found that Brant that were heavier on the spring staging grounds on the Wadden Sea area in western Europe had a greater probability of returning the following fall accompanied

by young. They also found that during 1978 and 1979, when 35 and 33%, respectively, of fall populations were immatures, the rate of fattening and departure weights on the staging grounds were greater than in 1977, when no immatures were observed in the fall population. Although alternative explanations can be proposed, Ebbinge et al.'s (1982) results suggest that nutrient reserves acquired before arrival on nesting grounds may also influence reproductive success of Brant. Similar studies on North American populations of Brant have not been conducted on either the wintering or staging grounds.

Brant exhibit a rather protracted spring migration. Some Brant may begin the northward trek as early as late March to early April, while others do not leave wintering areas until mid-May (Palmer 1976). During aerial surveys of Brant conducted from 16 to 23 May 1977, 35,513 were counted. These Brant were distributed from New Jersey northward along the Atlantic coast (27% mostly on Long Island and in New Jersey), in the maritime provinces of Canada (14%), in the Gulf and estuaries of the St. Lawrence (36%), on Lake Ontario (12%), and on James Bay (10%) (Reed 1977). By comparing nutrient reserves of Brant that were collected on the most northerly of the major wintering areas during or immediately before spring migration with that of prelaying Brant collected by Ankney (1984) on the nesting grounds, we sought to determine whether Brant depart the wintering grounds with substantial nutrient reserves or

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