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Proximate factors affecting egg volume in subarctic hole-nesting passerines

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Variation in egg volume of the Pied Flycatcher (*Ficedula hypoleuca*, n = 292 clutches), Redstart (*Phoenicurus phoenicurus*, n = 94), Siberian Tit (*Parus cinctus*, n = 31) and Great Tit (*Parus major*, n = 20) was studied in northern Finnish Lapland (69°N) from 1975 to 1987. Increased female mass and warm temperature around the time of egg-laying increased egg volume. Egg volume was not related to laying date and clutch size.

1. Introduction

Oscar Wilde once said: "An egg is always an adventure, it may be different." How large and how many eggs a female produces is certainly an adventure, since the 'decisions' made at the beginning of the breeding season may largely determine productivity and survival, and hence fitness (e.g. Trivers 1972, Schifferli 1973).

Packaging energy in eggs often involves a trade-off between the advantage a female gains from producing a large number of eggs versus the advantage of producing large but few eggs with corresponding high individual fitness (Smith & Fretwell 1974). Relatively large eggs may be particularly advantageous in the north. Large eggs tend to hatch well there because they cool slowly in cold weather. They also provide hatchlings with greater yolk reserves, thus enabling them to withstand greater periods of fasting due to poor weather (for the Pied Flycatcher *Ficedula hypoleuca*, see Järvinen & Väisänen 1983).

Despite these advantages females may have difficulty producing large eggs because of environmental constraints. In this study my emphasis is on the proximate factors that affect egg size of passerines in extremely harsh northern conditions (cf. Järvinen 1986). I approach this poorly studied problem by comparing a relatively large set of egg-volume measurements from four species of passerines in northern Finnish Lapland to such variables as laying date, clutch size, female size, temperature, and population density. The ultimate or evolutionary factors behind egg-size variation in the north are discussed elsewhere (see Ylimaunu & Järvinen 1987 and references therein).

2. Study area, material and methods

The study was conducted in subalpine mountain birch forests in NW Finnish Lapland (the Kilpisjärvi area, about 69°03′N, 20°50′E, elevation 475–600 m) from 1975 to 1987. The area is among the most 'arctic' localities in Fennoscandia with a growing season of 100 days or less (threshold +5 °C). The mean temperature during the egg-laying period of birds is given in Table 1. Snow melts from the birch forest in the beginning of June, and in 1973–1987 the date of birch leafing averaged 15 June (date of birch leafing = petioles just visible).

All nests were in nest-boxes. Only genuine first clutches are included, although some replacement clutches were laid after a nest was robbed or abandoned. The species studied were: the Pied Flycatcher (long-distance migrant and southern newcomer to northern Finnish Lapland; Järvinen 1983), the Redstart (*Phoenicurus phoenicurus*; long-distance migrant and natural inhabitant of northern Lapland), the Siberian Tit (*Parus cinctus*; resident and natural inhabitant of northern Lapland) and the Great Tit (*Parus major*; resident and southern newcomer to northern Lapland).

Analyses in this paper were on means of clutches, since individual eggs are not independent observations. Sample sizes were as follows: Pied Flycatcher 292 clutches/1679 eggs, Redstart 94/624, Siberian Tit 31/275 and Great Tit 20/192. Maximum length (EL) and breadth (EB) of each egg were measured by the author to the nearest 0.01 millimeter with sliding calipers, and

Table 1. Basic breeding data (first clutches only) for species in northern Finnish Lapland in 1975–87. M or R following species name refers to 'migrant' or 'resident'. Temperature values (°C) calculated for each clutch as explained. Egg volumes (cm^3) based on clutch means. CV = coefficient of variation. Sample sizes for body weight (g) and wing length (mm): Pied Flycatcher female 272 and 280, Pied Flycatcher male 85 and 85, Siberian Tit female 23 and 28.

	Siberian Tit (R)	Great Tit (R)	Redstart (M)	Pied Flycatcher (M)
No. of nests	31	20	94	292
First egg, mean	20 May	28 May	6 June	10 June
Temperature, °C	3.0	4.1	5.4	6.6
Clutch size, mean	8.9	9.6	6.6	5.8
Clutch size, range	6–11	7–13	3–8	3–8
Egg volume, mean	1.319	1.640	1.774	1.546
Egg volume, SD	0.100	0.090	0.140	0.109
CV% of egg volume	7.6	5.5	7.9	7.1
Female weight, mean	13.7	–	–	14.9
Female weight, SD	1.0	–	–	0.9
Female wing, mean	67.5	–	–	78.4
Female wing, SD	1.5	–	–	1.4
Male weight, mean	–	–	–	12.9
Male weight, SD	–	–	–	0.7
Male wing, mean	–	–	–	80.4
Male wing, SD	–	–	–	1.7

from these values egg volume (EV) was computed using the formulae:

Pied Flycatcher:

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

Redstart:

$$EV = 0.044 + 0.4752 \times EL \times EB^2$$

Great Tit and Siberian Tit:

$$EV = 0.042 + 0.4673 \times EL \times EB^2,$$

where EV is given in cm^3 and EL and EB in cm. On average, these formulae explain 96–97% of the measured egg-volume variance (Ojanen et al. 1978). I used the Great Tit egg formula for the Siberian Tit since no formula has been developed especially for the Siberian Tit. However, the correlation between fresh-egg weight and volume of the Siberian Tit eggs calculated with the Great Tit formula is very good (Pearson's correlation coefficient, $r = 0.970$, $n = 31$, $P < 0.0001$). The Great Tit formula thus seems to apply to Siberian Tit eggs as well.

Pied Flycatcher and Siberian Tit females and Pied Flycatcher males were weighed to the nearest 0.1 g with a 50-g spring balance, and wing length was measured by the maximum chord method (Svensson 1975) to the nearest millimeter with a ruler. Females were weighed during the early incubation period (days 0–5), but males usually during the nestling period (statistics in Table 1).

As most parent and nestling Pied Flycatchers and Siberian Tits were ringed, some breeding parents could be aged reliably. Adult Redstarts and Great Tits could not be captured because they tended to abandon the nest if disturbed. It is not known whether the same or different Redstart and Great Tit females nested in the boxes. In northern areas the site tenacity of passerines seems to be low (Järvinen 1983). Only about 5% of Pied Flycatcher and Siberian Tit females returned to their previous breeding sites. Low site tenacity and the fact that all the species of this long-term study are short-lived indicate that data for the same females do not bias the results.

Nests were visited regularly during the breeding season to determine the exact date of laying of the first egg and the clutch size. The number of breeding pairs in the nest-boxes was used as an estimate of population density. Temperature data were obtained from a climatological station of the Finnish Meteorological Institute (elevation 480 m) situated within the study area. Temperature values (°C) were calculated separately for each clutch and are mean daily values for the 11-day period five days before and five days after the laying of the first egg in the clutch, i.e. the main period of egg production. For details of climate, see Järvinen (1987).

3. Results

3.1. Descriptive statistics and annual variation in egg volume

For basic breeding statistics see Table 1. The Siberian Tit started to lay at a relatively low temperature, followed by Great Tit (both residents), Redstart and Pied Flycatcher (southern newcomer). Egg volume of all species was normally distributed. The relative variability (coefficient of variation, CV%) of egg volume was largest in the Redstart (Table 1).

For the Pied Flycatcher and Redstart there were enough data per year to test for annual variation in egg volume. Egg volume of Pied Flycatcher (1-way analysis of variance, $F = 2.02$, $df = 11, 280$, $P = 0.03$) and possibly of Redstart ($F = 1.79$, $df = 10, 81$, $P = 0.07$) seemed to vary significantly from year to year. In the Pied Flycatcher this result was mainly due to large eggs in 1980 (an exceptionally warm season, Järvinen & Väisänen 1984) and small eggs in 1981 (an exceptionally cold season).

The fluctuation in the mean egg volume per year for the Pied Flycatcher was not significantly parallel with that of the Redstart ($r = 0.39$, $n = 11$, $P = 0.25$). Population size of the Pied Flycatcher (11–44 pairs annually) seemed to correlate positively with the mean egg volume per year (Spearman's rank correlation coefficient, $r_s = 0.533$, $P = 0.06$, $n = 13$).

3.2. Egg volume in relation to laying date and clutch size

Egg volume per clutch was not related to the date of laying in any species. The same conclusion was reached when the effect of year was adjusted for (multiple linear regression). In the Pied Flycatcher (n = 13) and Redstart (n = 11) there was no correlation between the mean egg volume of the population and the mean laying date of the population ($r = -0.16$, $P = 0.63$ and $r = -0.27$, $P = 0.44$, respectively).

ANOVA showed that there was no significant egg-volume variation between the different clutch sizes for any species. Mean egg volume of the population was not related to the mean clutch size of the population in either the Pied Flycatcher or Redstart ($r = 0.32$, $P = 0.30$ and $r = 0.32$, $P = 0.36$, respectively).

3.3. Egg volume in relation to female/male characteristics

For mean sizes of Pied Flycatcher and Siberian Tit parents see Table 1. Body weight and wing length of parents correlated relatively poorly (Pied Flycatcher female $r = 0.179$, $P = 0.003$; Pied Flycatcher male $r = 0.179$, $P = 0.10$; Siberian Tit female $r = 0.277$, $P = 0.20$).

Heavy and large Pied Flycatcher females laid large eggs (Table 2). Male characteristics affected egg volume less than did female characteristics (Table 2). In the Siberian Tit both female body weight and wing length affected egg volume positively, and their relative importance was more equal than for the Pied Flycatcher (Table 2). Squaring the partial correlation coefficients gives the amount of variance explained by female body weight when the effect of wing length is controlled: 9% in the Pied Flycatcher and 19 % in the Siberian Tit.

In the Pied Flycatcher (n = 13 years) the mean egg volume for the year correlated positively with the mean body weight of the females that year ($r = 0.618$, $P = 0.02$) but not with the mean wing length of the females ($r = -0.013$, $P = 0.97$).

Old Pied Flycatcher females laid slightly larger eggs (mean volume = 1.567, SD = 0.091, n = 26) than did young females (mean = 1.545, SD = 0.107, n = 4). This was also true for the Siberian Tit, but apparently due to small sample sizes these differences were nonsignificant.

3.4. Interactions between variables

Multiple linear regression showed that egg volume of the Pied Flycatcher (n = 262) increased as female body weight increased ($t = 4.80$, $P < 0.001$), as mean temperature during the 11-day period five days before and five days after the laying of the first egg increased ($t = 3.14$, $P = 0.002$), and as female wing length increased ($t = 2.22$, $P = 0.03$). The other variables included in the model (year, laying date and clutch size) were not significant. Together the three significant proximate factors explained 15% (R^2, $P < 0.001$) of the egg volume variance for the Pied Flycatcher.

Table 2. Pearson's simple (r) and partial (r_p) correlation coefficients between egg volume and parent size, Pied Flycatcher and Siberian Tit (2-tailed P values). Parents both weighed and measured included. Partial correlations used to eliminate effect of either body weight or wing length of parent bird on egg volume. F = female, M = male, n = number of nests.

		Pied Flycatcher		Pied Flycatcher		Siberian Tit	
		F weight (n=262)	F wing (n=262)	M weight (n=84)	M wing (n=84)	F weight (n=22)	F wing (n=22)
Egg volume	r	0.321	0.177	0.144	0.022	0.497	0.421
	P	<0.001	0.004	0.192	0.843	0.018	0.050
Egg volume	r_p	0.298	0.126	0.142	−0.003	0.438	0.344
	P	<0.001	0.042	0.201	0.979	0.046	0.128

Similar analyses of the factors affecting egg volume (but without female variables) revealed that temperature was nearly significant in the Redstart ($n = 94$, $t = 1.93$, $P = 0.06$), but in the Siberian Tit ($n = 31$) and Great Tit ($n = 20$) all variables were nonsignificant.

If only female body weight and temperature were considered, in the Pied Flycatcher egg volume was more strongly correlated with female body weight (partial correlation coefficient, $r_p = 0.314$, $df = 261$, $P < 0.001$) than with mean temperature during the period five days before and five days after the laying of the first egg ($r_p = 0.187$, $P = 0.002$). Using the same variables for the Siberian Tit gives the following result: egg volume vs. female body weight $r_p = 0.493$ ($df = 19$, $P = 0.02$) and egg volume vs. temperature $r_p = 0.047$ ($P = 0.84$).

Thus, in both species the female factor seems to be more important than the temperature factor, but in the southern species (Pied Flycatcher) temperature also significantly affected egg size.

4. Discussion

Egg volume of hole-nesting passerines in northern Lapland was affected by only a few of the factors measured. In fact, only two factors stand out, i.e. female body weight and temperature (Table 3) but even these variables were not significant in every species.

Between-year differences in egg volume were small. This is in accordance with many earlier studies, including those of the Pied Flycatcher and Great Tit (Ojanen 1983). Only very harsh weather conditions seem to cause significant annual differences in egg size (cf. Järvinen & Väisänen 1984, Hildén et al. 1982).

Pied Flycatchers tended to lay large eggs when the population size was large. This correlation is probably spurious and merely reflects the fact that a favourable (warm) season is manifested in numerous breeding pairs and large eggs.

Greater egg size might be predicted for a later laying date due to general amelioration of weather as the breeding season progresses. However, egg volume was not related to laying date. This was possibly due to cold spells that often occur relatively late in northern Lapland. In central Norway (Haftorn 1985), but not in southern Finland (Järvinen & Pryl 1989), egg size of the Great Tit seemed to increase with the progress of the season.

No clear trade-offs between egg size and clutch size were observed. Ojanen et al. (1978) classified the Redstart as a species in which egg dimensions decrease with increasing clutch size ($n = 30$ clutches). My larger material does not confirm such a classification. In West Germany, egg size of the Pied Flycatcher was not related to laying date or clutch size (Sternberg & Winkel 1970) but in a one-year study, average-sized Great Tit clutches seemed to contain bigger eggs than did very small or very large clutches (Winkel 1970). In southern Finland there were no clutch-related differences in egg dimensions of the Great Tit (Järvinen & Pryl 1989).

The species studied laid their eggs in cold weather (mean daily air temperature between +3 and +7 °C, Table 1). Temperature around the date of egg-laying was among the two most important factors affecting egg size (Table 3). In more southern regions, however, egg size has usually not been very susceptible to temperature (Ojanen 1983). It is impossible to say whether cold temperature affected the females directly (increased

Table 3. Summary of statistically significant factors affecting egg volume of hole-nesting passerines, northern Finnish Lapland. + = positive effect, 0 = no effect and ? = no data available. Two symbols means (e.g. +/0), case uncertain.

Variable	Pied Flycatcher	Redstart	Siberian Tit	Great Tit
Year	+	+/0	?	?
Population size	+/0	0	?	?
Laying date	0	0	0	0
Clutch size	0	0	0	0
Temperature	+	+/0	0	0
Female weight	+	?	+	?
Female wing	+	?	0	?
Male weight	0	?	?	?
Male wing	0	?	?	?

costs of thermoregulation) or indirectly via the lack of food. Possibly both direct and indirect pathways are involved. For instance, cold breeding conditions cause a dramatic decrease in the body weight of Pied Flycatcher females, which is manifested as reduced egg sizes (Järvinen & Väisänen 1984).

Heavy females laid large eggs in the Pied Flycatcher and Siberian Tit (Table 2), and the female condition seemed to be a relatively more important factor than temperature. Similar correlations between female weight and egg volume or egg weight have been found earlier (Askenmo 1977, Ojanen et al. 1979, Järvinen & Pryl 1989). Strong effects of age on egg size have not been found in the species studied in the present paper (Sternberg & Winkel 1970, Ojanen 1983, Järvinen & Pryl 1989).

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Selostus: **Koloissa pesivien varpuslintujen munan tilavuuteen vaikuttavat tekijät Kilpisjärvellä**

Munan tilavuuteen vaikuttavia tekijöitä tutkittiin Kilpisjärven biologisella asemalla vuosina 1975–1987. Analyysien perustana käytettiin pesyeiden munan tilavuuksien keskiarvoja (292 kirjosiepon, 94 leppälinnun, 31 lapintiaisen ja 20 talitiaisen pesää; taul. 1). Tilavuutta lisäsivät naaraan suuri paino ja ulkoilman korkea keskilämpötila muninta-aikana (taul. 2–3). Muninta-ajankohdalla ja munamäärällä ei ollut vaikutusta.

References

Askenmo, C. 1977: Some aspects of the reproduction of the pied flycatcher Ficedula hypoleuca (Pallas). — Ph. D. Thesis, Dept. of Zoology, Univ. of Gothenburg.

Haftorn, S. 1985: Variations in clutch size and egg dimensions of the great tit Parus major. — Fauna Norv. Ser. C, Cinclus 8:106–115.

Hildén, O., Järvinen, A., Lehtonen, L. & Soikkeli, M. 1982: Breeding success of Finnish birds in the bad summer of 1981. — Ornis Fennica 59:20–31.

Järvinen, A: 1983. Breeding strategies of hole-nesting passerines in northern Lapland. — Ann. Zool. Fennici 20: 129–149.

— 1986: Clutch size of passerines in harsh environments. — Oikos 46:365–371.

— 1987: Basic climatological data on the Kilpisjärvi area, NW Finnish Lapland. — Kilpisjärvi Notes 10:1–16.

Järvinen, A. & Pryl, M. 1989: Egg dimensions of the Great Tit Parus major in southern Finland. — Ornis Fennica 66:69–74.

Järvinen, A. & Väisänen, R. A. 1983: Egg size and related reproductive traits in a southern passerine Ficedula hypoleuca breeding in an extreme northern environment. — Ornis Scand. 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. 1983: Significance of variation in egg traits in birds, with special reference to passerines. — Acta Univ. Ouluensis. A 154, Biol. 20.

Ojanen, M., Orell, M. & Väisänen, R. A. 1978: Egg and clutch sizes in four passerine species in northern Finland. — Ornis Fennica 55:60–68.

— 1979: Role of heredity in egg size variation in the great tit Parus major and the pied flycatcher Ficedula hypoleuca. — Ornis Scand. 10:22–28.

Schifferli, L. 1973: The effects of egg weight on subsequent growth of nestling great tits Parus major. — Ibis 115:549–558.

Smith, C. C. & Fretwell, S. D. 1974: The optimal balance between size and numbers of offspring. — Amer. Nat. 108: 499–506.

Sternberg, H. & Winkel, W. 1970: Über die Ei-Grösse des Trauerschnäppers (Ficedula hypoleuca) und ihre Beziehung zu Zeit, Alter und Biotop. — Vogelwarte 25:260–267.

Svensson, L. 1975: Identification guide to European passerines. — Naturhistoriska Riksmuseet, Stockholm.

Trivers, R. L. 1972: Parental investment and sexual selection. — In: Campbell, B. (ed.), Sexual selection and the decent of man 1871–1971:136–179. Aldine, Chicago.

Winkel, W. 1970: Experimentelle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise (Parus major und P. caeruleus). Über Legeperiode, Eigrösse, Brutdauer, Nestlingsentwicklung und Reaktion bei Veränderung der Eizahl. — J. Orn. 111:154–174.

Ylimaunu, J. & Järvinen, A. 1987: Do pied flycatchers Ficedula hypoleuca have a brood-survival or brood-reduction strategy? — Ornis Fennica 64:10–15.