Egg dimensions of the Great Tit *Parus major* in southern Finland

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Factors affecting the egg dimensions of the Great Tit in southern Finland (60°15'N) were studied in 1975–1977, using the mean clutch values of 99 first clutches. The mean egg length was 17.86 mm (SD = 0.59) and the mean egg breadth 13.45 mm (0.31). There were no annual, seasonal, clutch size-related or female age-related differences in egg dimensions. Female body weight and warm weather during the egg-laying period had positive effects on egg size.

Egg size seemed to be greater in northern Lapland (69°N) than further south in Norway and Finland. The correlation between egg length and egg breadth was the same in four different study areas, but heterogeneity was evident in the relationship between egg size and clutch size.

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Introduction

There are many studies on egg size variation in the Great Tit *Parus major* (for references, see Ojanen et al. 1978, Ojanen 1983), but in only a few cases has the study of egg dimensions been based on clutch means rather than single eggs. Data on single eggs are difficult to analyse statistically for several reasons: the eggs within a clutch are not independent, large clutches have a disproportionate effect on the results and outliers may bias the analyses.

Järvinen (unpubl.) has recorded clutch means for the egg dimensions of the Great Tit in northern Finnish Lapland (69°N) and Ojanen et al. (1978) and Ojanen (1983) give similar data for northern Finland (65°N). A useful data set is also available from central Norway (63°N; Haftorn 1985). Here, we report on egg size variation in the Great Tit in southern Finland (60°N), an area which is climatically more favourable for the breeding of the species than the areas mentioned above. First, we will analyse this single data set in isolation, to find out the most important factors affecting egg size in the local population. We will then examine whether the results are repeatable in different areas and environmental conditions, i.e. we will search for patterns of egg size variation specific to the Great Tit.

Study area, material and methods

We collected the data in southern Finland near Helsinki (south boreal zone, about 60°15'N, 24°55'E), in 1975–1977, from 99 genuine first clutches, all laid in nest-boxes in mixed or deciduous forests. During the 3-year period, the mean temperature (°C; Helsinki, Finnish Meteorological Institute) was near the long-term (1931–1960) average:

	April	May	June
1975	+3.7	+11.7	+13.9
1976	+2.3	+11.0	+13.2
1977	+1.6	+9.3	+14.5
1931–60	+2.9	+9.3	+14.5

During the 16-day period starting 10 days before and ending 5 days after the laying of the first egg in the clutches, the mean temperature in Helsinki averaged +12.8°C.

In all, 920 eggs were measured to the nearest 0.01 mm with sliding calipers. Egg volume (EV) was com-

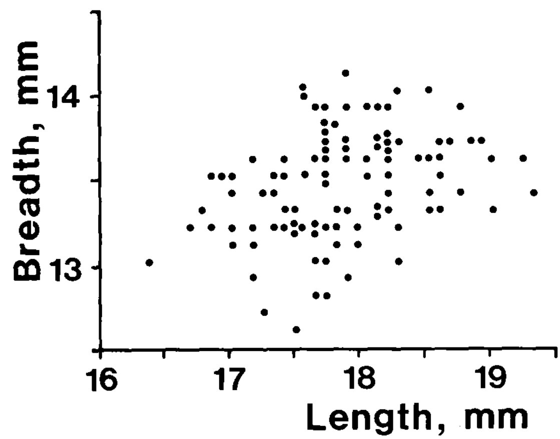

Fig. 1. The relationship between egg length and egg breadth in the first clutches of the Great Tit in Helsinki in 1975–77. Pearson's correlation coefficient = 0.361, n = 99, 2-tailed P < 0.001.

puted from the maximum length (EL) and breadth (EB) of each egg, using the formula developed by Ojanen et al. (1978):

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

where EV is given in cm^3 and EL and EB in cm. On average, this formula accounts for 97% of the overall variance in egg volume (Ojanen et al. 1978). In addition, the whole clutch was weighed with a 10-g spring balance to the nearest 0.1 g immediately after clutch completion. If not otherwise stated, clutch means are used as sampling units. In studying the effect of temperature on the within-clutch egg-size variation, the coefficient of variation (CV%) was used.

Females were weighed to the nearest 0.1 g with a 50-g spring balance. Only females which were weighed 0–5 days after the clutch was completed were included. Female wing length was measured by the maximum chord method to the nearest 1 mm and the female's age (1-year-old vs. over 1-year-old) was determined from the primary coverts (Svensson 1975).

The term "laying date" is defined as the date of laying of the first egg in a clutch. For each clutch, the mean daily temperatures were calculated in the period from 10 days before to 5 days after the laying date.

The statistical methods used are explained in Zar (1984) and Hedges & Olkin (1985).

Table 1. Dimensions of eggs and the body weight and wing length of the Great Tit females in Helsinki in 1975–77. Only first clutches included; clutch used as sampling unit.

Variable	Mean	SD	Range	n
Egg length, mm	17.86	0.59	16.38–19.33	99
Egg breadth, mm	13.45	0.31	12.60–14.06	99
Egg volume, cm^3	1.553	0.099	1.344–1.740	99
Egg weight, g	1.68	0.12	1.40–1.90	85
Female weight, g	20.8	1.5	17.3–24.4	40
Female wing length, mm	74.3	1.9	70.0–78.0	70

Results

Mean values and correlations between egg-size variables

Egg length averaged 17.86 mm, egg breadth 13.45 mm, egg volume 1.553 cm^3 and egg weight 1.68 g (Table 1). The between-clutch coefficient of variation was 3.3% for egg length, 2.3% for egg breadth, 6.4% for egg volume and 7.2% for egg weight.

Egg length and egg breadth tended to increase together (Fig. 1), as did also egg volume and egg weight (Pearson's correlation, $r = 0.933$, $n = 85$, $P < 0.001$). However, among short eggs (≤18 mm) the correlation between egg length and egg breadth was stronger ($r = 0.270$, $n = 60$, $P = 0.037$) than among long (> 18 mm) eggs ($r = 0.005$, $n = 39$, $P = 0.98$). Also, there was a significant correlation between within-clutch CV% for egg length and egg breadth (Spearman's rank correlation, $r_s = 0.336$, $n = 99$, $P < 0.001$), i.e. if the within-clutch variation in egg length was large, it tended to be large in egg breadth as well.

Egg size in relation to year, female characteristics, laying date and clutch size

The egg dimensions did not differ significantly between the years (Table 2). Only female body weight had significant positive effects on egg breadth and egg volume (and possibly female wing length on egg breadth, Table 3): about 15% of the variation in mean egg breadth and egg volume was explained by female body weight. There were no differences in egg size between the different clutch-size classes (Table 4).

In 32 cases the female was one-year-old ("young" females, born the previous summer), in 39 cases more

Table 2. Annual variation in the egg dimensions of the Great Tit in Helsinki in 1975–77. Only first clutches included. Differences between means tested by 1-way analysis of variance (only probabilities are given).

Year	Egg length, mm		Egg breadth, mm		Egg volume, cm^3	
	Mean	SD	Mean	SD	Mean	SD
1975 (n = 42)	17.76	0.52	13.46	0.35	1.548	0.102
1976 (n = 41)	17.90	0.66	13.40	0.30	1.547	0.101
1977 (n = 16)	18.02	0.56	13.50	0.26	1.579	0.089
P (ANOVA)	0.29		0.51		0.51	

Table 3. Spearman's rank correlation coefficients (2-tailed P's) between egg dimensions and some reproductive variables in the first clutches of the Great Tit in Helsinki. Before the correlations were calculated, the laying date was standardized (mean = 0, SD = 1) within each year.

Variable	Egg length		Egg breadth		Egg volume	
	r_s	P	r_s	P	r_s	P
Female weight (n = 40)	0.228	0.157	0.382	0.015	0.404	0.010
Female wing length (n = 70)	0.031	0.787	0.231	0.052	0.192	0.107
Laying date (n = 87)	0.121	0.264	-0.002	0.933	0.092	0.403
Clutch size (n = 89)	–0.028	0.787	0.114	0.287	0.077	0.481

Table 4. Egg dimensions of the Great Tit in Helsinki in different clutch-size classes in 1975–77. Only first clutches included.

Clutch size	Egg length, mm		Egg breadth, mm		Egg volume, cm^3	
	Mean	SD	Mean	SD	Mean	SD
6–8 (n=18)	17.80	0.54	13.40	0.31	1.538	0.092
9 (n=38)	17.98	0.61	13.46	0.27	1.566	0.094
10 (n=18)	17.88	0.63	13.40	0.36	1.545	0.110
11–12 (n=15)	17.73	0.57	13.57	0.30	1.569	0.103
P (ANOVA)	0.49		0.35		0.69	

than one-year-old ("old" females, born before the previous summer) and in 28 cases the age of the female was unknown. The eggs were largest in the "unknown" age group and smallest in the "old" group (Table 5), but the differences in egg length and egg volume were significant only at the 10% level (differences between "young" and "old" were all clearly non-significant).

Table 5. Egg dimensions of the Great Tit in different female-age groups in Helsinki in 1975–77. Only first clutches included.

Age of female	Egg length, mm		Egg breadth, mm		Egg volume, cm^3	
	Mean	SD	Mean	SD	Mean	SD
Unknown (n=28)	18.02	0.51	13.54	0.25	1.586	0.080
1-year (n=32)	17.89	0.70	13.40	0.31	1.547	0.109
>1-year (n=39)	17.72	0.52	13.41	0.35	1.533	0.100
P (ANOVA)	0.099		0.192		0.086	

Table 6. Egg dimensions of the Great Tit in different study areas in Fennoscandia (n = number of clutches). In Norway some replacement clutches were included. In all areas egg volume was computed by the same formula (see Study area, material and methods).

Area	Egg length, mm		Egg breadth, mm		Egg volume, cm^3	
	Mean	SD	Mean	SD	Mean	SD
1) N Lapland, 69°N (n=20)	18.34	0.48	13.65	0.31	1.64	0.09
2) N Finland, 65°N (n=555)	17.93	0.62	13.53	0.36	1.58	0.11
3) Norway, 63°N (n=36)	17.71	0.52	13.55	0.35	1.56	0.10
4) S Finland, 60°N (n=99)	17.86	0.59	13.45	0.31	1.55	0.10

1) A. Järvinen (unpubl.), 2) Ojanen et al. (1978), 3) Haftorn (1985), 4) present study. According to the Bonferroni corrected t tests (six 2-tailed tests/variable) the following pairwise comparisons of the mean egg length and egg breadth values showed significant differences: egg length N Lapland vs. N Finland ($P = 0.020$), egg length N Lapland vs. Central Norway ($P < 0.001$), egg length N Lapland vs. S Finland ($P = 0.004$), egg breadth N Lapland vs. S Finland ($P = 0.050$).

Egg-size variation in relation to temperature

Egg length and egg breadth were most strongly affected by the temperature 6 days before the laying of the first egg in the clutches (Fig. 2A). Egg length was more sensitive to temperature than egg breadth, but the correlation coefficients varied similarly (r_s = 0.627, n = 16, P = 0.009). The within-clutch variation (CV%) in egg breadth and egg volume was most strongly affected by the temperatures prevailing 1–2 days after the laying of the first egg (Fig. 2B). This suggests that the size of last-laid eggs is likely to be affected by temperature.

Discussion

The mean egg dimensions of Great Tit clutches are given for different study areas in Table 6. Usually the differences between areas were small, but the size, especially egg length, seems to be greater in northern Lapland than elsewhere (see footnote in Table 6).

The relatively large eggs in the far north may have survival value, since losses due to hatching failure are more common there than in the south at least in the Pied Flycatcher *Ficedula hypoleuca*, and small eggs tend to hatch poorly in the north (Järvinen & Väisä-

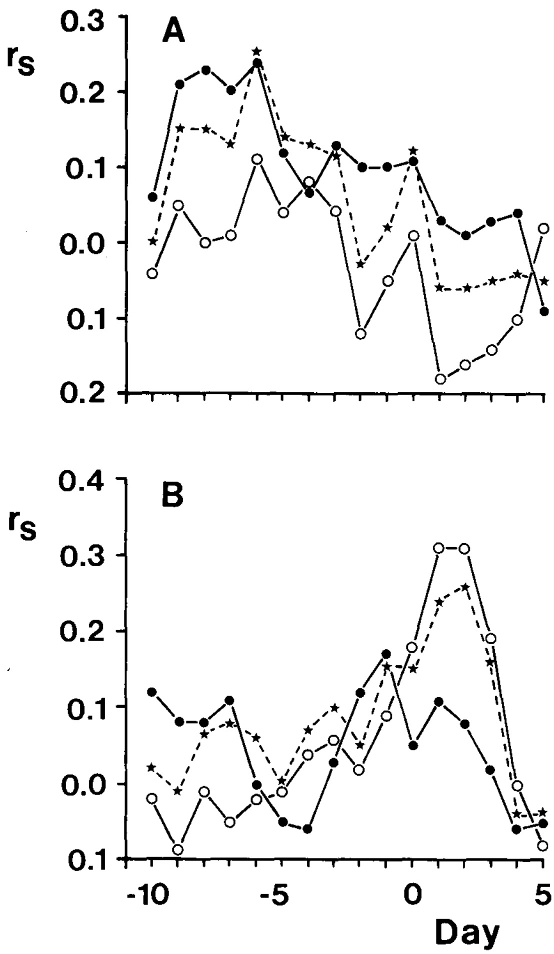

Fig. 2. Spearman's rank correlation coefficients between egg-size variables and the mean temperature on different days during the period 10 days before and 5 days after the laying of the first egg in the clutch. Only first clutches included. (A) Correlations for mean egg length (dots), mean egg breadth (circles) and mean egg volume (stars, broken line) in each clutch (n=84). (B) Correlations for the within-clutch variation (CV%) in egg length (dots), egg breadth (circles) and egg volume (stars, broken line). For n = 84 the nominal 5% significance level of Spearman's correlation is 0.215. However, more important than this level is the general pattern of the correlation coefficients.

nen 1983). Thus selection may favour large egg size in the north.

In northern Lapland the correlation between egg length and egg breadth is 0.21 (n = 20, P = 0.38; A. Järvinen, unpubl.), in central Norway 0.35 (calculated for single eggs, n = 321, no. of clutches = 36; Haftorn 1985) in southern Finland 0.36 (n = 99, P < 0.001; present study, Fig. 1) and in West Germany (52°N) 0.31 (calculated for single eggs, n = 424, no. of clutches about 42; Winkel 1970). These correlations do not differ from each other ($\chi^2 = 0.43$, df = 3, P = 0.93), and can thus be combined: the common, weighted correlation coefficient of the four studies is 0.33 (n = no. clutches in each area, P < 0.001). However, it should be remembered that the correlation between egg length and egg breadth may vary with egg length: in long eggs this correlation may be near zero (see Results) or even negative (van Noordwijk et al. 1981).

According to Winkel (1970), the eggs of the Great Tit are largest in medium-sized clutches. In central Norway (Haftorn 1985), egg volume correlated negatively, though not significantly, with clutch size (r = –0.25, n = 36, P = 0.14). In northern Finnish Lapland this correlation was –0.37 (P = 0.109), and in the present study almost zero (Table 3). In contrast, in northern Finland Ojanen et al. (1978) found a slightly positive correlation between egg volume and clutch size (r = 0.09, n = 549, P = 0.03). It should be noted that in the latter study the sample size is very large, and in such material even a small correlation coefficient is statistically significant. The correlation coefficients between egg volume and clutch size in northern Lapland, northern Finland, central Norway and southern Finland are possibly not homogeneous ($\chi^2 = 7.211$, df = 3, P = 0.065) and a common correlation coefficient cannot be calculated.

In the areas mentioned above, the clutch size-related differences in egg size are small, which suggests that the Great Tit females invest the same amount of energy in their eggs, irrespective of clutch size. Their investment is accordingly larger in large clutches.

The most important factors affecting egg size in southern Finland were female weight and the ambient temperature during the egg-laying period. Egg breadth seemed to be related to female weight and egg length to temperature (Table 3, Fig. 2A). There is little information in the literature on the effects of female size on egg size in the Great Tit (see Ojanen 1983). In Oulu, egg breadth correlated slightly with wing length (r = 0.16, n = 241, P < 0.05; Ojanen et al. 1979). The correlation between female body weight and egg length was 0.15 (n = 223, P < 0.05), and for egg breadth and egg volume the corresponding correlation coefficients were 0.21 (P < 0.01) and 0.22 (P < 0.01), respectively. However, in Oulu the females were not weighed in the same phase of the breeding cycle and the correction for weight decrease during the nestling period was done with a relatively poorly fitting regression equation (Ojanen et al. 1979).

According to Ojanen et al. (1981), the ambient temperature about 5 days before egg-laying seems to affect the egg size of the Great Tit in northern Finland. This seems to apply to egg volume in southern Finland (Fig. 2A).

No annual differences in egg size were found (Table 2), despite the fact that there were great annual differences in the mean date of egg-laying in the population (1975 7 May; 1976 13 May; 1977 22 May). This accords with the result of Ojanen et al. (1979) from northern Finland.

Neither we (Table 5) nor Ojanen et al. (1979) and Ojanen (1983) found significant differences in egg size between 1-year-old and over 1-year-old females. However, the result of our analysis, i.e. larger egg sizes in young females, suggests the same trend as those of Winkel (1970) and Jones (1973); we do not know, however, why egg size was largest among females of unknown age (Table 5).

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Selostus: **Talitiaisen munamittavaihtelusta Helsingissä**

Talitiaisen munamittavaihteluun vaikuttavia tekijöitä tutkittiin Helsingissä 1975–1977 käyttäen pesyekohtaisia munamittojen keskiarvoja (99 ensimmäistä pesyettä). Munamittojen tunnusluvut ovat taulukossa 1. Munamittavaihtelussa ei havaittu tilastollisesti merkitseviä vuosittaisia, vuodenaikaisia, pesyekokokohtaisia tai naaraan ikään liittyviä eroja (taulukot 2–5). Naaraan suuri paino (taulukko 3) ja lämmin sää muninta-aikana (kuva 2A) kasvattivat munan kokoa.

Helsingin munamittoja verrattiin mm. Kilpisjärven, Oulun ja Keski-Norjan mittoihin (taulukko 6). Kilpisjärvellä munat olivat suurempia kuin muualla. Eri alueilla munan pituuden ja leveyden välinen korrelaatio (Helsingin osalta ks. kuva 1) oli yhtä voimakas (neljän alueen yhdistetty korrelaatiokerroin 0.33). Sen sijaan eri alueilla munamitat vaihtelivat eri tavalla suhteessa pesyekokoon.

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Erratum. Due to an editorial mistake the legends of Fig. 1 and Fig. 8 in A. Järvinen: Patterns and causes of long-term variation in reproductive traits of the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland (OF 66:24–31) had changed places.