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Egg size in the Great Tit *Parus major*: individual, habitat and geographic differencess

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Factors affecting egg dimensions were investigated in two neighbouring Great Tit populations breeding in a poor urban and a rich rural habitat in southeast Estonia. About 80% of variation in egg size was heritable; however, the effects of female condition were also remarkable. In both populations, females laying large eggs were heavier during the second half of the nestling period, indicating that egg size reflects the component of female condition which is persistent throughout the breeding period. In the urban population, egg size decreased seasonally, most likely because of a poor phenotypic quality of late breeders. In the rural population, large clutches tended to contain small eggs, which points to a trade-off between the size and number of eggs. The analysis of literature data from 30 Great Tit populations revealed no evidence of a trade-off between egg size and clutch size at the inter-populational level, but rather a positive correlation between these traits among populations. Egg size increased with latitude.

1. Introduction

The size of eggs to lay is one of the first problems that an individual bird faces at the beginning of the reproductive cycle. Being hatched from a large egg could potentially be beneficial for a chick; from the viewpoint of the laying female, however, high investment into egg quality (size) might conflict with her own energetic demands and willingness to produce more offspring. Unveiling the causes and consequences of egg-size variation is necessary for understanding the relationship between the number and quality of offspring, a concept, central to the life-history theory.

There is little doubt that reproductive success is related to clutch size, and also some indication that egg size is closely linked to hatchling growth and survival (e.g., Ojanen 1983a, Martin 1987, Grant 1991, Magrath 1992, Potti & Merino 1994, Williams 1994). Considering that heritabilities for egg size, too, are generally higher than heritabilities for clutch size (Boag & van Noordwijk 1987), a trade-off between egg number and size in birds seems a plausible expectation. Most interestingly, however, the evidence for such a trade-off within a bird species has been claimed to be lacking (Williams 1994), and, in fact, often the positive phenotypic correlations between egg and clutch size have been found (see, e.g., Flint & Sedinger (1992) for references). Most likely, the reason for the latter is high inter-individual variation in the phenotypic quality of individuals which, according to van Noordwijk

& de Jong (1986), may lead to positive phenotypic correlations between life-history traits. Theoretically, trade-offs could be revealed by measuring genetic correlations; this, however, would require sample sizes which can seldom be obtained in field studies (see, e.g., Lessells et al. 1989).

To get an insight into the evolutionary causes and consequences of egg-size variation, alternative methods have thus to be used. One possible approach would be the study of relationships between egg and clutch size within habitats of different quality.

In this paper we examine inter-individual variation of egg size in two Great Tit populations breeding in contrasting environmental conditions in urban and rural habitats in southeast Estonia. Breeding conditions for our rural Great Tits are probably the most favourable, as indicated by large clutch sizes (one of the highest recorded for the species) and high fledging success (Hõrak 1993a). We predict that in such a situation, between-individual differences in the total amount of resources spent on reproduction are manifested to a lesser extent because individuals are less constrained by food availability in the habitat. Therefore, if there exists a trade-off between the number and size of eggs, we expect this to be revealed as a negative phenotypic correlation in our rural population. In the urban population, on the contrary, a positive correlation between egg and clutch size seems more probable, since urban Great Tits face far more difficult breeding conditions when compared to their rural conspecifics. In our study area, mean clutch size of urban Great Tits is about two eggs smaller than that of rural birds, while the nestling mortality is high (Hõrak 1993a). It is therefore tempting to suggest that between-individual differences in the phenotypic quality, leading to positive correlations between life-history traits, will be manifested in such a situation.

Another possibility for examination of the trade-off between egg and clutch size would be to study their covariation among populations breeding in different environmental conditions. The average amount of resources available for reproduction is likely to vary with respect to local breeding conditions. Hence, the optimal patterns of resource allocation between the number and quality of offspring may also depend on the locality. In this case, a trade-off at the inter-populational level could be revealed as a negative correlation between mean egg and clutch size among different geographical populations. To test this possibility, we will investigate covariation between egg and clutch size among 30 Great Tit populations breeding over a wide range of conditions in different parts of Europe. To reveal adaptive variation in egg size at the population level, we will also check for the presence of the latitudinal trend in egg size.

The second objective of our study is to extract information about the relationship between egg size and female condition. The simultaneous effect of female condition (nutritional state, phenotypic quality) on both clutch size (or laying date) and brood-rearing ability is a central element in the recent developments of the clutch-size theory (Price & Liou 1989), and in explanations for the evolution of breeding dates in birds (Price et al. 1988). Testing both of these requires the measuring of female condition at different stages of the breeding cycle, which means an examination of correlates of condition. Some authors (e.g., Ojanen et al. 1979, Murphy 1986, Järvinen & Pryl 1989) have shown that egg size might be one such correlate. In this study we test this possibility, again checking whether the relationships are similar in populations breeding in habitats of different quality.

Understanding the selective importance of variation in traits requires knowledge about the genetic basis of variation. Therefore, we will estimate repeatabilities and heritabilities of egg and clutch size in both populations. In line with other studies on egg morphology, we also examine variation in egg shape and linear measurements.

2. Material and methods

2.1. Study area and data sets

Data were collected in two main study areas: in the town of Tartu (human population about 120 000) and in the rural area of Tõrvandi, 5 km from Tartu (58°22'N 26°43'E). Egg measurements were recorded during 1987–1991. When calculating heritabilities for clutch size, we also used an enlarged data set covering eight years from 1987 to 1994. Measurements of adult morphology were started in 1990, so we had a two-year data set for examination of relationships between egg size and female morphology.

The urban study area in Tartu consisted of two large and two small parks (about 22 ha) and avenues with a total length of 9 km. The distance between the nestboxes was 30–40 m. The main tree species were *Tilia cordata, Acer platanoides, Betula pendula, Quercus robur,* and *Populus suaveolens*. All streets in the urban study area bordered on gardens where winter feeding of birds was common.

The rural study area was located at a distance of 5 km from the southern boundary of Tartu and comprised two woods (Tõrvandi and Ropka, 2.5 km apart) surrounded by cultivated land. About two-thirds of the 72 ha area of Tõrvandi wood is covered with a moist birch forest, while the remaining third accounts for a poor mixed spruce forest; the tree species include *Picea abies, Pinus sylvestris, Betula pendula* and *Populus tremula*. The 550 ha Ropka wood is mostly covered with a rich mixed spruce forest with a deciduous understory. In the understory and on roadsides *Corylus avellana* was the most common woody plant. In the rural study area the nestboxes were placed at every 40–50 meters in lines (total length 11 km) running along forest edges and roadsides.

When examining relationships between egg and clutch size we used, in addition, data on three Great Tit populations in southwest Estonia (58°09′N 24°56′E) collected in 1983. The first study site was located in the small town of Kilingi-Nõmme (human population about 2500) with a high density of breeding Great Tits. The second study site at Vanajärve was located about 20 km from Kilingi-Nõmme and consisted mainly of deciduous wood patches and strips among cultivated land. So the first two habitats were roughly analogous to our main urban and rural study areas. The third study site at the Nigula forest was in a large natural mixed forest area with a very sparse Great Tit population (Vilbaste & Leivits 1990).

2.2. Methods

The number of Great Tit pairs breeding in our study area in different years varied from 36 to 61 and from 43 to 93 in rural and urban populations, respectively (the first clutches only). The birds bred in nestboxes mounted at a height of about 2.5 m. The dimensions of the box cavity were approximately 11 × 11 × 30 cm, the diameter of the entrance hole being 3.5 cm. Old nest materials were removed every year.

Nestboxes were checked regularly to determine clutch size and laying date, assuming that one egg is laid every day. Adults were captured during the second half of the nestling period and, since 1988, were aged using plumage characteristics (see Svensson 1992).

Tarsus length was used as a measure of the overall body size of individuals. Although caution is needed for interpreting the single variables as representative to structural size in birds (e.g., Freeman & Jackson 1990), tarsus length is probably the best indicator of size among single external measures (e.g., Rising & Somers 1989, Freeman & Jackson 1990). Tarsi were measured (see fig. 18b in Svensson 1992) with a sliding caliper to the nearest 0.1 mm by the same person (PH). In an attempt to separate mass from structural size, 'condition indices' (residual weights) were computed, as the residuals from linear regressions of weight on cubed tarsus length. Diurnal weight changes were eliminated by the inclusion of weighing time into partial correlations between female weight or condition and egg size. Females were weighed with a Pesola spring balance with a precision of 0.1 g.

When collecting oomorphological data, whole clutches were photographed after the sixth day of incubation using a stand described in Mänd et al. (1986). A graphics digitizer was used for the input of egg contours from photographs, and a special program OMELETTE (Mänd et al. 1986) for smoothing data and for estimating egg dimensions and volume. The volume of an egg was calculated from the contour using trapezoidal integration instead of deriving it from linear measurements. Thus, individual differences in egg shape did not influence the accuracy of volume estimation.

For describing the size and shape of eggs we used four parameters: L = egg length (mm), B = egg breadth (mm), V = egg volume (cm^3), and SPH = sphericity or the egg shape index (B/L). We preferred this ratio to the elongation index (L/B) because, in our opinion, SPH is more a figurative estimate of egg shape as it expresses egg breadth in percentages of egg length. Thus, the larger the SPH, the rounder the eggs. Measurement errors of egg dimensions (coefficient of variation of 10 measurements of the same egg) were negligible as compared to total and interclutch variation (Fig 1). Vari-

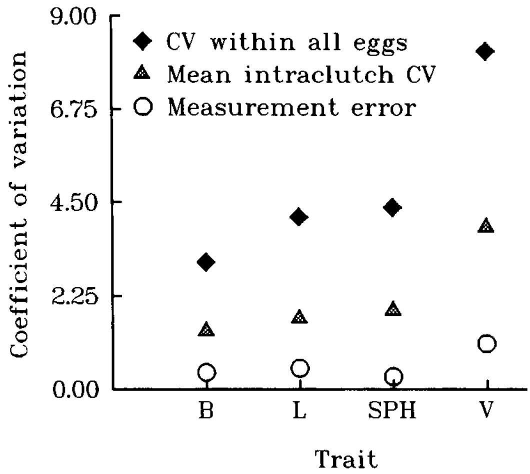


Fig. 1. Variation among egg dimensions.

ation was highest for egg volume, evidently because it is a three-dimensional trait.

To avoid pseudoreplications, the clutch means of egg parameters were used in all statistical analyses, except in Table 1. To minimize the influence of a few aberrant eggs on clutch means, one egg per clutch, the most contrasting to the others by its size, shape or appearance, was excluded before the clutch mean was calculated. The rejection was based on the preliminary visual observation of the researcher, not on the basis of calculated egg measurements.

When comparing data on egg size in literature, we recalculated egg volumes according to the formula $V = \pi/6 \times L \times B^2$, or adjusted it accordingly in case the authors had not presented original data on egg length and breadth. We consider this especially important because several authors have used different coefficients, which leads to considerable differences in estimates for egg volume.

Statistical analyses were performed using the SAS statistical package (SAS Institute 1985). All significance levels are for two-tailed tests. When pooled data were used for calculations, clutch size, laying date and egg size were yearly normalized by expressing trait values relative to the annual means of the population. Repeatabilities were calculated according to Lessells and Boag (1987). Heritabilities were estimated from mother-daughter regressions according to Falconer (1989).

Table 1. Pearson correlation coefficients between egg traits. All are significantly different from zero ($p < 0.0001$) except the correlation between SPH and egg volume. N = 3060 individual eggs.

	r	
Trait	B	V
L	0.27	0.64
B		0.87
SPH		–0.02

3. Results

3.1. Variation and relationships between egg traits

In the analysis of individual eggs, all traits except shape and size were significantly correlated with each other (Table 1), although the correlation between egg length and breadth was rather low. Variation in egg breadth was slightly lower than variation in egg length (Fig. 1; see also SD's in Table 4).

3.2. Repeatability

Repeatability expresses the proportion of the variation between measurements that is due to consistent differences between the objects measured. In quantitative genetics, repeatability provides an upper limit for the degree of genetic determination of a trait (Falconer 1989). It is calculated as the intraclass correlation coefficient, $s^2_a/(s^2 + s^2_a)$, where s^2_a is the among-groups variance component and s^2 is the within-group variance component derived from one-way ANOVA (Lessells & Boag 1987).

Egg dimensions revealed moderate to high repeatabilities in both populations when the first clutches of the same female were compared in different years (Table 2). Repeatabilities were remarkably lower when egg dimensions of individual females were compared within a year. This was evidently because egg volume and linear dimensions tended to increase from the first clutches to the repeat or second clutches. However, the difference was significant at a 5% level only in the case of egg length ($t_{19} = 2.116$, $p = 0.048$), which increased on the average by 0.26 mm (1.5%).

Repeatabilities for linear measurements were generally higher than repeatabilities for egg size.

Egg length had, on the average, about 20% higher repeatability than egg breadth.

Repeatabilities for clutch size in the data set, which was included in calculations with egg dimensions, were significantly different from zero only for the urban population ($r = 0.64$, $p < 0.0001$). The difference between the populations, however, was probably due to the smaller sample size of the rural population because in the enlarged data set (including data from three additional years) the repeatabilities of clutch size were of a similar magnitude in both populations ($r = 0.59$, $p < 0.0001$, $N = 185$ for the urban population; $r = 0.57$, $p < 0.0001$, $N = 115$ for the rural population).

To estimate the role of breeding territory quality upon the repeatabilities of breeding traits, we calculated repeatabilities for the same nestboxes inhabited by different females in different years. In none of the data sets did the repeatabilities differ significantly from zero. The result is convincing given that our sample sizes in the 8-year data set were rather large (N = 173...285 clutches).

3.3. Heritability

Since between-population differences in egg parameters were in most cases only marginally significant (see below), we found it justified, in order to increase the sample size, to rely on the data pooled over two populations. Heritability estimates for egg traits, as calculated from the pooled data, were high and significantly different from zero, although standard errors were relatively large (Table 3). Heritability estimates were generally close to repeatability estimates. Again, estimates were highly different for egg length and breadth.

In the five-year sample used for calculations with egg traits, the heritability of clutch size was not significantly different from zero in any of the

Table 2. Repeatability of egg size and shape among females. Data from 1987 to 1991. Traits are presented in descending order of repeatability value (average for four measurements). N = number of clutches, n_a = average number of observations per individual. P levels (from ANOVA) if not shown are smaller than 0.001 (in most cases smaller than 0.0001).

Trait	First clutches in different years			First vs. repeat and second clutches in the same year	
	Urban $N = 112, n_a = 2.11$	Rural $N = 43, n_a = 2.15$	Urban+Rural $N = 157, n_a = 2.12$	Urban+rural $N = 40, n_a = 2$	
SPH	0.87	0.66	0.84	0.63	
L	0.83	0.74	0.81	0.61	
V	0.64	0.69	0.64	0.34	$p = 0.064$
B	0.62	0.60	0.61	0.35	$p = 0.054$

Table 3. Heritability estimates for egg size and shape based on mother-daughter regressions. Regression coefficients and their standard errors (SE) are doubled. For individuals trapped more than once, trait values are averaged over all their breeding events. Traits are presented in descending order of their heritabilities (pooled data). Data from 1987 to 1991, first clutches only. N = number of clutches.

Trait	Urban, N = 19		Rural, N = 24		Urban + Rural, N = 43	
	h^2 (SE)	p	h^2 (SE)	p	h^2 (SE)	p
L	1.15 (0.45)	0.020	0.95 (0.44)	0.042	1.00 (0.29)	0.001
V	0.84 (0.41)	0.055	0.86 (0.44)	0.067	0.81 (0.28)	0.006
SPH	1.18 (0.50)	0.030	0.29 (0.46)	0.540	0.81 (0.32)	0.016
B	0.89 (0.47)	0.075	0.30 (0.37)	0.429	0.59 (0.29)	0.051

populations. In the enlarged data set covering eight years from 1987 to 1994 the heritability estimate for clutch size was significant for the rural population ($h^2 = 0.66 \pm 0.28$ (SE), $p = 0.021$, $N = 35$), but not for the urban birds ($h^2 = 0.48 \pm 0.38$ (SE), $p = 0.217$, $N = 39$).

3.4. Effects of year, habitat and age

Egg volume, breadth and shape (but not length) revealed slight but significant inter-annual variation (Table 4). Egg volume, length and breadth tended to be slightly larger in the rural population. The differences were, however, only marginally significant except for egg breadth. The average egg shape index (SPH) was similar for both populations. The proportion of variance in egg traits, explained by the year and habitat term together was generally low ($R^2 = 0.02...0.07$). Rural Great Tits laid, on the average, 2.3 more eggs per clutch than their urban conspecifics.

To estimate the effect of female age upon egg parameters, we compared changes in egg traits between the first and second years of breeding for the same females. By the second year of breeding, egg volume had increased on the average by 0.03 cm^3 (1.6%; $t_{35} = 2.099$, $p = 0.043$) and length on the average by 0.12 mm (0.7%; $t_{35} = 2.028$, $p = 0.050$), changes in other parameters being not significantly different from zero.

Table 4. Effect of year and habitat (urban vs. rural) on egg dimensions and clutch size of the Great Tit, estimated from ANOVA. Data from first clutches during 1987–91. In none of the models did 'year*habitat' interaction term differ significantly from zero. Sums of squares (SS) are type III of SAS allowing for an unbalanced design.

Trait	Effect	DF	SS	F	P	R²	Mean ± SD (Range)	
							Urban, N = 317	Rural, N=218
V	Year	4	0.350	6.04	< 0.0001		1.69 ± 0.12	1.71 ± 0.12
	Habitat	1	0.049	3.35	0.067		(1.3–2.02)	(1.26–2.06)
	Model	5	0.403	5.56	< 0.0001	0.04		
Residual variance		529	7.677					
Total variance		534	8.081					
L	Year	4	4.126	2.13	0.076		17.92 ± 0.66	18.03 ± 0.72
	Habitat	1	1.748	3.61	0.058		(16.05–19.91)	(15.62–20.01)
	Model	5	5.706	2.36	0.039	0.02		
Residual variance		529	255.894					
Total variance		534	261.600					
B	Year	4	3.683	7.80	< 0.0001		13.60 ± 0.35	13.68 ± 0.35
	Habitat	1	0.755	6.40	0.012		(12.46–14.50)	(12.63–14.62)
	Model	5	4.590	7.77	< 0.0001	0.07		
Residual variance		529	62.466					
Total variance		534	67.056					
SPH	Year	4	0.010	2.88	0.022		0.76 ± 0.03	0.76 ± 0.03
	Habitat	1	< 0.001	0.11	0.740		(0.68–0.86)	(0.68–0.84)
	Model	5	0.010	2.31	0.043	0.02		
Residual variance		529	0.453					
Total variance		534	0.463					
Clutch size	Year	4	54.704	6.13	< 0.0001		8.80 ± 1.66	11.10 ± 1.30
	Habitat	1	634.094	284.26	< 0.0001		(3–12)	(7–14)
	Model	5	695.768	62.38	<0.0001	0.39	N = 297	N = 206
Residual variance		497	1108.63					
Total variance		502	1804.40					

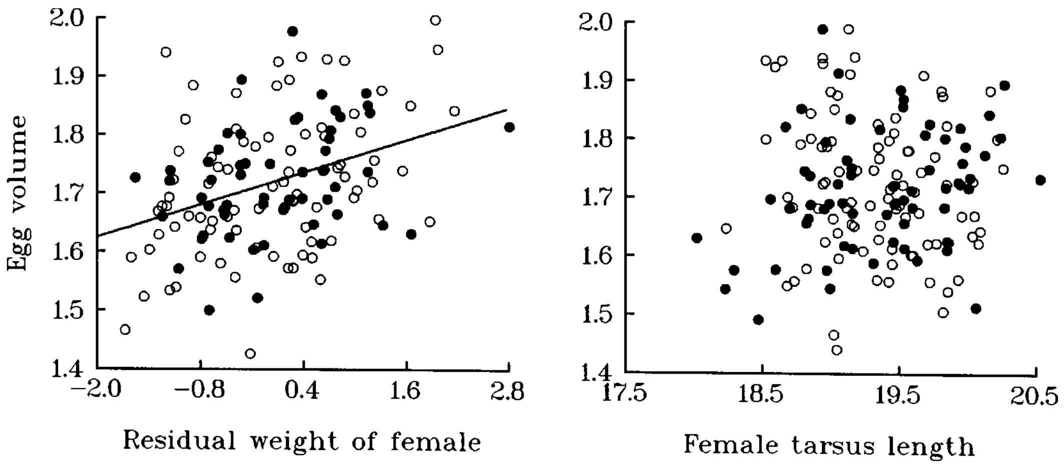


Fig. 2. Relationship between egg size and female condition (left), and between egg size and female size (right). Pooled data for 1990–91. ○ – urban population, ● – rural population. Slope for the line, calculated on data pooled over urban and rural population: $y = 1.718(\pm 0.009) + 0.046(\pm 0.010)\,x$; $p < 0.0001$, $N = 142$, $R^2 = 0.14$.

3.5. Effects of female condition and size

In both populations females laying large eggs were in a better condition (i.e., relatively heavier) in the nestling stage (Fig. 2). The partial correlation coefficient (adjusted to weighing time) between egg volume and the residual weight of a female was 0.35 ($p = 0.010$, $N = 56$) for the rural population and 0.43 ($p < 0.0001$, $N = 86$) for the urban population. Also, female weight revealed a similar relationship with egg size ($r_{partial} = 0.41$ for both populations).

We found no significant relationship between egg volume and tarsus length in either of the populations when the data were pooled for 1990 and 1991 (Fig 2). Examining the years and populations separately, however, revealed that small females laid larger eggs in the urban population in 1990 ($r = -0.29$, $p = 0.049$, $N = 46$).

3.6. Seasonal variation in egg size

Egg volume declined seasonally in the urban population when data were pooled over five years (Fig. 3; $r = -0.16$, $p = 0.006$, $N = 295$, both variables yearly normalized). For individual years, the pattern was significant only in 1991 ($r = -0.31$, $p = 0.012$, $N = 64$). Since we had female weight data for 1991, it was possible to test whether the seasonal decline in egg size could be ascribed to the poorer condition of late-breeding females. When the residual weight of the female was kept constant in the partial correlation, the relationship between egg size and laying date became insignificant: $r_{partial} = -0.15$, $p = 0.350$, $N = 40$ vs. $r = -0.36$, $p = 0.018$, $N = 40$ for ordinary Pearson correlation (sample sizes are smaller than in the previous analysis because morphometric data for all females were not known). For the rural population we found no seasonal changes in egg size.

3.7. Egg size and clutch size

Egg size decreased with increasing clutch size in the rural population of Tõrvandi (Fig. 4). The correlation between them was, however, only marginally significant in the pooled data ($r = -0.12$, $p = 0.080$, $N = 206$, both variables yearly normalized). For the individual years, the correlation between egg size and clutch size was significant in 1988 and nearly so in 1991. The latter relationship became clearer when female weight was kept constant in the partial correlation ($r_{partial} = -0.41$, $p = 0.024$, $N = 23$).

In the urban population of Tartu we found no consistent relationship between clutch and egg size, either for individual years or for pooled

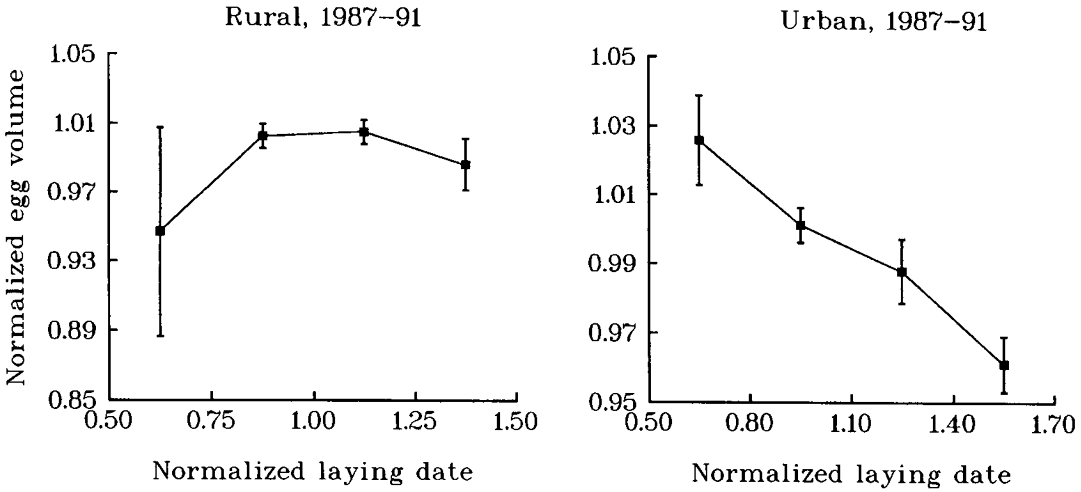


Fig. 3. Seasonal variation in egg size. Laying date and egg size are normalized by dividing the individual values to yearly averages for first clutches (i.e., expressing them in percents of yearly mean). Vertical bars denote standard errors. Grouping of data on X-axis bases on the division of total range of observations into four equal parts. Only data from first clutches are used.

data, despite the larger sample size (297 observations).

In the case of Great Tit populations from southwest Estonia, we found a negative correlation between egg and clutch size in the rural population at Vanajärve (Fig. 3). Great Tits breeding in a large forest at Nigula and in the urban population of Kilingi-Nõmme revealed no consistent relationship between egg and clutch size ($r = -0.093$, $p = 0.733$, $N = 16$ and $r = 0.07$, $p = 0.500$, $N = 93$, respectively).

3.8. Inter-populational trends

Eggs tended to be larger in populations with high average clutch sizes (Fig. 5). The relationship between egg and clutch size was distorted by three observations (1, 29 and 30) which had a profound effect on the regression (absolute values of Studentized residuals > 2). When these aberrant data points were excluded from the analysis, a positive correlation between egg and clutch size at the inter-populational level was significant ($r = 0.42$, $p = 0.028$, $N = 27$).

Egg size increased towards the north (Fig. 6). A single observation (# 30) had a large Studentized residual (–2.9); however, the relationship was still significant when this point was omitted from the analysis ($r = 0.49$, $p = 0.009$, $N = 29$).

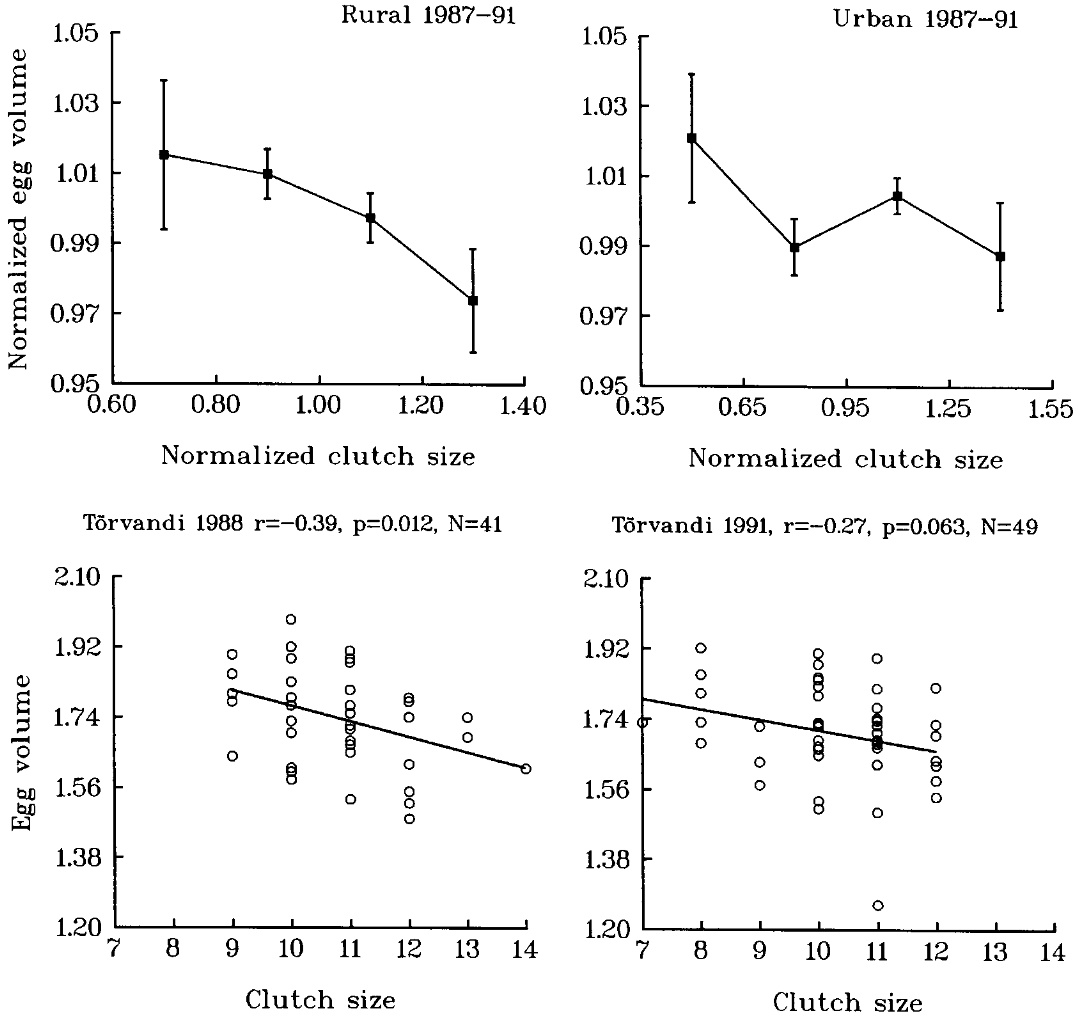
Further analysis revealed that the positive correlation between egg and clutch size might have been caused by the latitude effect. The partial correlation coefficient (adjusted for latitude) between egg and clutch size was not significant at the 5% level ($r_{partial} = 0.34$, $p = 0.092$, $N = 27$), while partial correlation between egg size and latitude (adjusted for clutch size) still was significant ($r_{partial} = 0.48$, $p = 0.020$, $N = 29$).

4. Discussion

4.1. Egg size

4.1.1. Genetic variation

Our estimates for the repeatability of egg size in the first clutches were relatively high (0.64...0.69), and similar to those recorded in other Great Tit studies (Jones 1973 cited in van Noordwijk 1987): $r = 0.72$; Ojanen et al. 1979: $r = 0.49...0.62$; van Noordwijk et al. 1981: $r = 0.59...0.80$. However, the repeatability of egg size (and linear measurements) was remarkably lower when the repeat and second clutches were compared to the first clutches of the



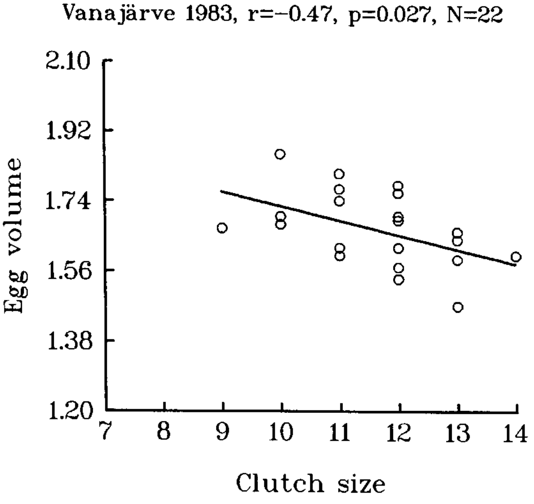


Fig. 4. Relationship between egg size and clutch size. In the upper part, clutch and egg size are normalized by dividing the individual values to yearly averages for first clutches (i.e., expressing them in percents of yearly mean). Vertical bars denote standard errors. Grouping of data on X-axis bases on the division of total range of observations into four equal parts. Only data from first clutches are used.

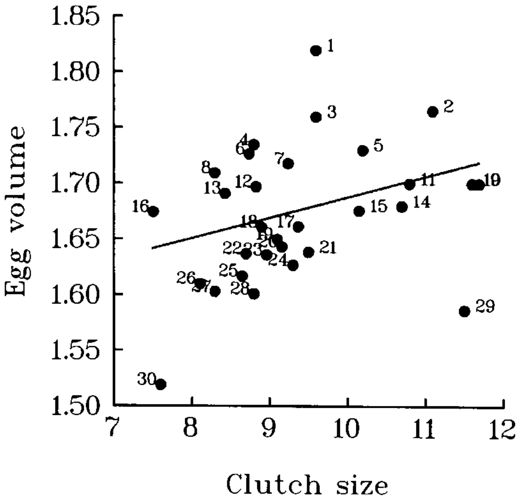


Fig. 5. Relationship between clutch size and egg size at the population level. Numbers denote ID numbers in Appendix. All egg volumes are calculated from the formula V = π/6 × L × B², or adjusted correspondingly. Slope for the line: y = 1.503(± 0.075) + 0.019(± 0.008) x. Line is fitted excluding three aberrant observations (1, 29 and 30).

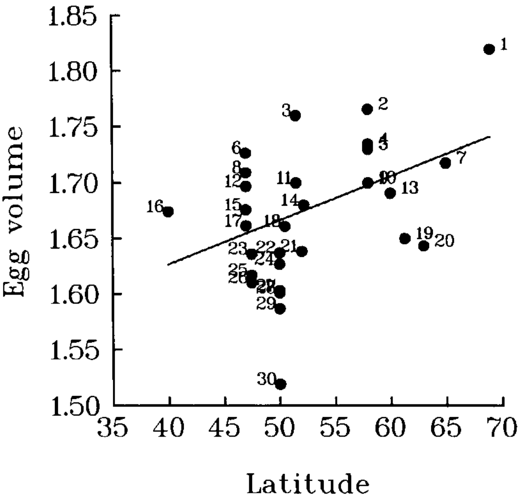


Fig. 6. Latitudinal trend in egg size. Legend as in Fig. 5. Slope for the line: y = 1.468(± 0.076) + 0.004(± 0.001) x. Line is fitted excluding the observation # 30.

same year (Table 2). A decrease of the female component in the repeat or second clutches can also be seen from the works of Ojanen et al. (1979) and van Noordwijk et al. (1981) in the Great Tit. Similarly, with other Great Tit studies (Haftorn 1985, Ojanen et al. 1979, Van Noordwijk et al. 1981, Yaremchenko 1989, Verhulst & Tinbergen 1991, Nager & Zandt 1994), we found that eggs tended to increase in the repeat/second clutches, which suggests that physiological and/or environmental processes affecting egg size and shape during the laying of the first and repeat/second clutches are different.

Heritability for egg volume was high (0.81 ± 0.28). This estimate, too, fell within the range found in other studies on the Great Tit (Jones 1973 cited in van Noordwijk 1987): $h^2 = 0.72 \pm 0.22$; Ojanen et al. 1979: $h^2 = 0.86 \pm 0.29$; van Noordwijk et al. 1981: $h^2 = 0.66 \pm 0.24...0.72 \pm 0.30$; and four other species ($h^2 = 0.55...0.99$, van Noordwijk & Boag 1987, Lessells et al. 1989). We found no effect of territory quality on egg size when repeatability of the same nestboxes with different females was calculated. This suggests that high heritability of egg size in our study was not caused by relatives sharing a similar environment. However, we concede that there might have been some hidden effect of habitat since 'nestbox quality' alone might not be a precise indicator of the quality of the breeding territory.

4.1.2. Yearly and age-related differences

In spite of highly significant inter-annual variation, the year and habitat term together explained only 4% of total variation in egg size (Table 4). Yearly differences in egg volume could have been caused by differences in air temperature (and correspondingly the development of food items) during the laying period (e.g. Ojanen et al. 1981, Järvinen 1994), while breeding density could be important, too (Perrins & McCleery 1994). However, considering high heritability of egg size, the possibility of differential elimination of genotypes as a potential source of yearly variation in egg size cannot be excluded either.

The result that egg size increased by the second year of life is in agreement with that of a Great Tit study in southwest Estonia (Mänd 1988, Mänd et al. 1990). Also, in a number of other species young females are known to lay smaller eggs than older ones (Ojanen 1983a).

4.1.3. Relationship with female condition and size

Our result that heavier and better-conditioned birds lay larger eggs, while egg volume generally does not depend on the size of the female, is in agreement with four other Great Tit studies (Ojanen et al. 1979, Mänd 1988, Järvinen & Pryl 1989, Nager & Zandt 1994). A similar tendency was found in a northern Pied Flycatcher population (Järvinen & Väisänen 1983) and in Eastern Kingbirds (Murphy 1986), Canada Goose (Leblanc 1989), Blue Tit (Nilsson & Svensson 1993), and Starling (Smith et al. 1993).

The positive correlation between egg size and female condition/weight is particularly interesting, because in our study (as well as in several others) females were weighed during the second half of the nestling period. It means that about one month after the first egg was laid, the females laying large eggs were heavier than those laying small eggs. Since females lose weight during breeding, our result indicates that either 1) females with large eggs were initially heavier, or/and 2) they lost less weight during the breeding. We therefore suggest that egg size reflects the component of female condition which is persistent throughout the breeding period.

The evidence that egg size variation within a population is related to the structural size of females is more rare. A few exceptions are the works of Larsson and Forslund (1992) in the Barnacle Goose, and Potti (1993) in the Pied Flycatcher, which found a positive correlation between egg size and female tarsus length. Several authors (e.g., Otto 1979, Järvinen & Väisänen 1984, Järvinen 1991, Potti 1993) have found positive correlations between egg size and female wing length. These studies might indicate the dependence of egg size on the structural size of the female; however, there have been claims that wing length is not a representative measure of body size (Rising & Somers 1989). It is also possible that wing length rather reflects the individual's condition during moult (see, e.g., Rätti et al. 1993).

The lack of positive correlations between female tarsus length and egg size is noteworthy in the context of another study (Hõrak 1994), which revealed positive correlations between clutch size and female tarsus length in the same populations in 1990. Since tarsus length depends on growth conditions during the nestling period, these correlations were interpreted as a possible lasting effect of the individual's ontogeny upon its reproduction. The present study suggests that growth conditions of the female do not necessarily affect her egg size.

4.1.4. Seasonal pattern

During the period of laying the first clutches, late-breeding females laid small eggs in the urban, but not in the rural population. A similar tendency has been recorded for Great Tits in southwest Estonia (Mänd 1988, Mänd et al. 1990), as well as for several other bird species (see, e.g., Ojanen 1983a, Flint & Sedinger 1992 for references).

What might cause seasonal patterns in egg size? Birkhead and Nettleship (1982) and Ojanen (1983a) have suggested that small egg size might be adaptive, allowing birds to lay early. However, Great Tits in our study clearly did not lay small eggs in early clutches. The seasonal decline of egg size in the urban population could hardly be caused by the proximate effect of food, since food availability generally increases during the laying of the first clutches. An alternative explanation would be that the quality of food decreases seasonally (e.g., vegetation growth and drying of soil could possibly make it more difficult for birds to find gastropods and other calcium-rich food items). This explanation, however, contradicts the finding that egg size increases again during the laying of repeat and second clutches. In addition, our personal observations confirm that snails are abundant during the whole Great Tit breeding period in our urban study area. Therefore, we suggest that small eggs in late first clutches just reflect the poor phenotypic quality of late-breeding females. This explanation is convincingly supported by the fact that the significant relationship between egg size and laying date vanished when the residual weight of the female was included in the analysis.

It is probably symptomatic that seasonal decline in egg size was revealed only in the urban population breeding under more unfavourable conditions than their rural conspecifics. Under harsh conditions individuals are likely to experience considerable energetic limitation in their activities, and, therefore, differences in their physiological condition will affect reproduction most prominently. In line with this explanation, the seasonal decline in clutch size, too, was steeper in our urban population than in the rural population (Hõrak 1993b).

4.1.5. Relationship with clutch size within populations

When data were pooled over five years, rural Great Tits at Tõrvandi tended to lay small eggs in large clutches. A similar pattern was present also during two individual years and in the rural population of Vanajärve in 1983. A negative correlation between clutch and egg size has been also reported in three other Great Tit studies (Jones 1973, cited in Ojanen et al. 1978; Haftorn 1985; Järvinen & Pryl 1989, but see Busse 1967 and Ojanen et al. 1978 for the opposite), and some other passerines (Ojanen et al. 1978, Greig-Smith et al. 1986, Hillström 1992) and non-passerines (Koskimies 1957, Myrberget 1977, Manning 1978).

Positive correlations between egg and clutch size have been recorded in the Starling (Ojanen et al. 1978, Smith et al. 1993) and several non-passerine species (Coulson 1963, Batt & Prince 1979, Rohwer & Eisenhauer 1989, Lessells et al. 1989, Flint & Sedinger 1992). Still, most egg size studies have revealed no clear trend in the relationship between egg size and number.

Two points can be made on the basis of these data: 1) Although it has been claimed that the evidence for a trade-off between egg size and clutch size within a bird species is lacking (Williams 1994), some populations do reveal negative correlations between clutch size and egg size. 2) Although the trade-off between clutch size and egg size is most likely to be expected in 'capital breeders' (*sensu* Drent & Daan 1980) who lay their eggs on the basis of a fixed amount of resource, the evidence of such a trade-off has been found also in small passerines laying eggs on the basis of daily energetic income.

We suggest that this is so because small passerines, in spite of being 'income breeders', also deplete their body reserves to a remarkable extent during laying (e.g., Jones & Ward 1976, Pinowska 1979, Ojanen 1983b). Since the laying of large eggs is energetically more demanding, the laying of smaller eggs in large clutches can be adaptive for 'income breeders', if it enables a female to start incubation with a lesser extent of depletion of body reserves during egg-laying. Thus, there is reason to expect a conflict between the number and size of eggs. We propose that the mechanism for a trade-off between egg size and clutch size works as follows: selection has fixed alleles for the strategy, which allows the clutch size to increase by laying small eggs. Clutch size, however, approaches its genetically determined maximum (upper limit of reaction norm) only under the most favourable environmental conditions. If a female is not in the best possible trim during the laying period, laying will cease before the maximum possible clutch size is attained, and the bird ends up with a small or average clutch containing small eggs. This explanation agrees with the fact that heritabilities for egg size are always higher than for clutch size (Boag & van Noordwijk 1987, Lessells et al. 1989, this study). In this context, it is noteworthy that in our study, the heritability estimate for clutch size was significantly different from zero in the rural, but not in the urban, population with small clutches. Negative correlations between egg and clutch size occurred only in the rural habitats of Tõrvandi and Vanajärve where breeding conditions are probably among the best recorded for the Great Tit (compare clutch sizes in Appendix).

4.1.6. Inter-populational trends

The study of 30 Great Tit populations revealed no evidence of a trade-off between egg size and clutch size at the inter-populational level (Fig. 5). This suggests that in the Great Tit, adaptations to locally prevailing breeding conditions do not involve different resource allocation patterns between the number and size of eggs at the population level.

Great Tits tended to lay larger eggs in populations with large average clutch sizes. To some extent, the phenomenon might be explained by proximate food limitations on both clutch and egg size at the population level. Proximate food limitations is a plausible explanation for the coexistence of very small eggs and clutches in Frankfurt on Main where breeding conditions for Great Tits seem to be poorest among the populations studied. On the other hand, the partial correlation analysis revealed that the simultaneous increase of egg and clutch size might have been largely due to latitude effect. In this case, the phenomenon can have a different reason: if individuals in northern populations of Great Tit have larger body size (Bergmann's rule) and also the clutch size increases towards the north, then the positive correlation between egg and clutch size would result as a byproduct of geographic trends in body size and clutch size. Whether the latitudinal trend in body size occurs in the Great Tit would require a further research; for the clutch size trend the evidence is contradicting (see Orell & Ojanen 1983 and references therein).

4.2. Egg shape

Like other researchers (Preston 1969, Ojanen et al. 1978, van Noordwijk et al. 1981, Järvinen & Väisänen 1983, and references in these) we found that egg length was more variable than breadth. Theoretically, the higher repeatability of egg length in comparison with that of egg breadth could, to some extent, be caused by its higher variation, because repeatabilities generally tend to be higher with greater differences between individuals in a sample (e.g., Harper 1994). Nevertheless, we believe that this was not the case, since the repeatability of egg volume, which showed the highest variation among egg traits, was much lower than that of egg length. Our data suggest, therefore, that among egg dimensions egg length possesses the highest level of genetic determination. This conclusion is convincingly supported by the comparison of heritability estimates from mother-daughter regressions (Table 3.).

Our finding about the high repeatability/heritability of egg length compares favourably with the results of Ojanen et al. (1979) and Mänd (1988) on the Great Tit. A similar tendency has been found also in some other species (Ojanen et al. 1979, Potti 1993 — Pied Flycatcher; Hendricks 1991 — American Pipit). Another Great Tit study (van Noordwijk et al. 1981), however, revealed the highest repeatability/heritability for the egg shape index, while heritabilities for egg length (but not breadth) were not significantly different from zero in one of the two study areas.

Grant (1982; see also Järvinen & Väisänen 1983, Hendricks 1991) suggested that egg shape is a function of egg size and female body size, mediated by the maximum extensibility of the oviduct. According to Grant's hypothesis, the maximum width of the oviduct sets an upper limit to egg breadth among eggs of various sizes, egg length being not so constrained.

The results of this study agree with those of many others which have shown that egg length is more variable than breadth. However, in our study egg length had also the highest heritability. This finding seems to be at odds with Grant's hypothesis, which suggests that egg length is most sensitive to non-genetic variation. Contrary to this expectation, we found that the most plastic egg trait was breadth (Tables 2 and 3), suggesting that the oviduct diameter is highly dependent on the physiological condition of the female, while factors determining egg length are most constant within individuals. Grant's hypothesis also suggests that small eggs must be more spherical in shape than large ones. Several authors (e.g., Myrberget 1977, van Noordwijk et al. 1981, Järvinen & Pryl 1989, Potti 1993) have presented similar evidence. Nevertheless, we failed to find any consistent relationship between egg size and shape in a sample of 3060 eggs (Table 1). Our result is similar to that of Mänd (1988) and Mänd et al. (1990).

Another explanation for differences in the female component among egg dimensions is the notion of van Noordwijk et al. (1981), who suggested on the basis of high repeatabilities of egg shape that it is not the diameter but the expansibility of the oviduct that is under genetic control. This can explain why we, too, found the highest repeatabilities for egg shape. The heritability estimate for the egg shape index, however, had only a penultimate rank among other egg dimensions in our study (Table 3).

An ultimate explanation for the higher heritability of egg length as compared to that of breadth agrees with the popular interpretation of Fischer's Fundamental Theorem: egg breadth is more directly related to egg volume than egg length, and since egg volume most likely has a fitness value, one can expect that directional selection has weeded out more genetic variation in egg breadth than in egg length (see also Hendricks 1991).

4.3. Conclusions

Egg size in the Great Tit is highly heritable but also sensitive to the female condition. The component of the female condition affecting egg size is persistent also about one month later, during the second half of the nestling period. The relationship between egg size and female condition was similar for populations breeding in rich and poor habitats, which suggests that egg size may be potentially useful for the examination of differences in the phenotypic quality of individuals. Nevertheless, egg size reflects the female condition probably best in the poor habitat, as indicated by the seasonal decline in egg size in our urban but not in the rural population.

Within populations, a trade-off between egg size and clutch size in small passerines is possible, as far as negative correlations have been observed between these traits. However, the trade-off can become apparent only when the female condition during egg laying is sufficient to approach the upper limit of the reaction norm for clutch size.

A trade-off between egg size and clutch size is not likely to occur at the inter-populational level in the Great Tit. On the contrary, egg and clutch size tend to correlate positively among populations. This might indicate that both egg size and clutch size are proximately food-limited in some populations. Alternatively, a simultaneous increase of egg and clutch size might be a by-product of latitudinal trends in body size and clutch size.

The genetic component is much higher for egg length than for egg breadth, possibly because egg length is more neutral in respect to fitness than breadth which is more strongly related to egg volume.

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Selostus: **Talitiaisen munan koko: yksilöiden, elinympäristöjen ja eurooppalaisten populaatioiden erot**

Minkä kokoinen muna naaraan tulisi munia? Poikaselle on edullista, jos se on kuoriutunut suuresta (laadukkaasta) munasta, koska se saattaa lisätä myöhempää hengissä selviytymisen mahdollisuutta, mutta naaraalle suuren munan tuottaminen voi olla energeettisesti rankkaa ja pienentää munalukua. Munakoon vaihtelun syiden ja seurausten tutkiminen on tärkeää, jotta ymmärrettäisiin jälkeläisten lukumäärän ja laadun välistä yhteyttä.

Pesimistulos liittyy ilman muuta jälkeläismäärään, mutta myös munakokoon, jos se vaikuttaa poikasen kasvuun ja selviytymiseen. Ottaen huomioon, että munan koon periytyvyys on yleensä suurempaa kuin pesyekoon, on oletettavissa, että nämä rajoittavat toisiaan (eli niiden välillä tulisi olla negatiivinen korrelaatio), mistä ei kuitenkaan ilmeisesti ole todellista tietoa. Päin vastoin: muna- ja pesyekoko ovat useissa tutkimuksissa korreloineet keskenään positiivisesti. Tämä johtunee yksilöiden välisistä fenotyyppisistä eroista, jotka voivat korreloida geneettisten elinkierto-ominaisuuksien kanssa.

Tietoa muna- ja pesyekoon keskinäisestä rajoittavuudesta on saatavissa tutkimalla niiden suhdetta yhtenäisten elinympäristötyyppien sisällä ja välillä. Me tutkimme kaupunkilaistuneiden ja maaseutuympäristössä pesivien talitiaisnaaraiden munakoon vaihtelua Kaakkois-Virossa. Tutkimme myös munakoon ja naaraan kunnon välistä suhdetta, jolla teoriassa on keskeinen merkitys sekä pesyekoon että jälkeläisten kasvatuskyvyn ja lisäksi pesintäajankohdan evoluution kannalta. Näiden testaaminen edellyttää naaraiden kunnon mittaamista pesintäkierron eri vaiheissa. Me tutkimme mahdollisuutta, että munan koko kuvastaisi naaraan kuntoa erilaisten ympäristöjen populaatioissa.

Aineisto kerättiin pääosin Tarton puistoissa ja puistokatujen varsilla sekä lehti- ja sekametsissä Tõrvandissa Tarton läheisyydessä vuosina 1987–91, pesyekoon perityvyyden arviointia varten vuoteen 1994 asti.

Maaseututalitiaistemme pesimisympäristöt ovat luultavasti mitä suotuisimmat, koska niiden pesyekoko on suuri (yksi suurimmista on talitiaisella on havaittu) ja pesintätulos erinomainen. Näissä oloissa ennustimme, että yksilöiden väliset erot lisääntymiseen käytettyjen resurssien määrässä ovat vähäisiä, koska ravintoa on tarjolla riittämiin. Siksi odotimme, että munien koon ja lukumäärän välillä on negatiivinen fenotyyppinen korrelaatio, jos niiden välillä ylipäätään on toisiaan rajoittava suhde.

Kaupunkipopulaatiossa munakoon ja pesyekoon välille on odotettavissa positiivinen korrelaatio, koska kaupunkilaistalitaiset elävät paljon vaikeammissa oloissa kuin lajitoverit maalla. Tutkimusalueellamme kaupunkilaistalitiaisten pesyekoko on suunnilleen kahta munaa pienempi kuin maalla ja poikaskuolleisuus on suurta. Siksi on odotettavissa, että yksilöiden väliset fenotyyppiset laatuerot, jotka voisivat johtaa elinkierto-ominaisuuksien positiiviseen korrelaatioon, korostuvat.

Suunnilleen 80% munan koon vaihtelusta oli periytyvää, mutta myös naaraan kunnon vaikutus oli huomattava. Molemmissa populaatioissa suuria munia munineet naaraat olivat painavia myös poikaskauden jälkipuoliskolla. Tämä osoittaa, että munan koko heijastaa naaraan kuntoa, joka pysyy samanlaisena läpi pesimäkauden. Kaupunkipopulaatiossa keskimääräinen munakoko pieneni munintakauden edistyessä luultavimmin siksi, että myöhäiset munijat olivat varhaisia huonokuntoisempia. Maaseutupopulaatiossa suurten pesyeiden munat olivat pieniä, mikä viittaa (ennustettuun) munaluvun ja -koon keskiseen rajoittavuuteen.

Toinen mahdollisuus tutkia muna- ja pesyekoon keskinäistä rajoittavuutta on selvittää, miten ne vaihtelevat toisiinsa nähden erilaisissa pesintäoloissa. Keskimääräinen pesintään käytettävien resurssien määrä luultavasti vaihtelee kunkin paikan olojen mukaan. Siten resurssien optimaalisen jakamisen jälkeläisten laadun ja lukumäärän kesken tulisi riippua paikasta. Tällöin muna- ja pesyekoon keskinäisen rajoittavuuden voi olettaa ilmenevän negatiivisena korrelaationa eri maantieteellisten populaatioiden välillä. Kirjallisuudesta eri puolilta Europpaa 30 populaatiosta kerättyjen tietojen pohjalta ei löytynyt todisteita siitä, että munakoon ja -luvun välillä olisi populaatiotasolla rajoittavuutta, ennemminkin näiden välillä oli positiivinen korrelaatio. Tutkimme myös munan koon etelä-pohjoissuuntaista vaihtelua, selvittääksemme, onko siinä havaittavissa sopeutuneisuutta populaatiotasolla. Munakoko kasvoi leveyspiirien suuntaisesti etelästä pohjoiseen.

Tutkimuksemme perusteella munakoko ja -luku rajoittavat toisiaan, mutta vain niin hyvissä olosuhteissa, että ravinnon saanti ei ole esteenä naaraan hyvälle kunnolle.

References

Batt, B. D. I. & Prince, H. H. 1979: Laying dates, clutch size and egg weight of captive Mallards. — Condor 81:35–41.

Báldi, A. & Csörgö, T. 1993: Effect of habitat on the clutch size and egg dimensions of the Great Tit (Parus major). — Aquila 100:201–209.

Birkhead, T. R. & Nettleship, D. N. 1982: The adaptive significance of egg size and laying date in Thick-billed Murres (Uria lomvia L.). — Ecology 63:300–306.

Boag, P. T. & van Noordwijk, A. J. 1987: Quantitative Genetics. — In: Cooke, F. & Buckley, P. A. (eds.), Avian Genetics:45–78. Academic Press, London.

Busse, P. 1967: Zmiennosc wielkosci, ksztaltu i ubarwienia jaj podvarszawskich populacji sikor: Parus major L. i Parus caeruleus L. — Notatki Orn. 8:33–50.

Coulson, J. C. 1963: Egg size and shape in the Kittiwake (Rissa tridactyla) and their use in estimating age composition of populations. — Proc. Zool. Soc. Lond. 140:211–227.

Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — Ardea 68:225–252.

Eeva, T. & Lehikoinen, E. 1995: Egg shell quality, clutch size and hatching success of the Great Tit (Parus major) and the Pied Flycatcher (Ficedula hypoleuca) in air pollution gradient. — Oecologia:102:312–323.

Freeman, S. & Jackson, W. M. 1990: Univariate metrics are not adequate to measure avian body size. — Auk 107:69–74.

Falconer, D. S. 1989: Introduction to quantitative genetics., 3rd ed. — Longman. New York.

Flint, P. L. & Sedinger, J. S. 1992: Reproductive implications of egg-size variation in the Black Brant. — Auk 109:896–903.

Grant, M. C. 1991: Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel Numenius phaeopus. — Ibis 133:127–133.

Grant, P. R. 1982: Variation in the size and shape of Darwin's Finch eggs. — Auk 99:15–23.

Greig-Smith, P. W., Feare, C. J., Freeman, E. M. & Spencer, P. L. 1986: Causes and consequences of egg size variation in the European Starling Sturnus vulgaris. — Ibis 130:1–10

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

Hamann, H.-J., Schmidt, K.-H. & Simonis, S. 1989: Der Einfluss der Höhenlage auf Ei- und Gelegegrösse bei Kohlmeisen (Parus major). — J. Ornithol. 130:69–74.

Harper, D. C. G. 1994: Some comments on the repeatability of measurements. — Ringing & Migration 15:84–90.

Hendricks, P. 1991: Repeatability of size and shape of American Pipit eggs. — Can. J. Zool. 69:2624–2628.

Hillström, L. 1992: Patterns of hatching and adult body mass change in the Pied Flycatcher Ficedula hypoleuca: adaptations and constraints. — Ph. D.-thesis, University of Uppsala.

Hõrak, P. 1993a: Low fledging success of urban Great Tits. — Ornis Fennica 70:168–172.

— 1993b: Age-related differences in seasonal pattern of clutch size in the Great Tits (Parus major): proximate vs. ultimate explanation. — In: Proceedings of the

Fourth Congress of the European Society for Evolutionary Biology:179. Montpellier.

— 1994: Effect of nestling history on adult size and reproduction in the Great Tit. — Ornis Fennica 71:47–54.

Järvinen, A. 1991: Proximate factors affecting egg volume in subarctic hole-nesting passerines. — Ornis Fennica 68:99–104.

— 1994: Global warming and egg size of birds. — Ecography 17:108–110.

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.

Jones, P. J. 1973: Some aspects of the feeding ecology of the Great Tit Parus major. — Ph. D.-thesis, University of Oxford.

Jones, P. J. & Ward, P. 1976: The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea Quelea quelea. — Ibis 118:547–574.

Kiziroğlu, I. 1982: Brutbiologische Untercuchungen an vier Meisenarten (Parus) in der Umgebung von Ankara. — J. Ornithol. 123:409–423.

Koskimies, J. 1957: Variation in size and shape of eggs of the Velvet Scoter, Melanitta fusca (L.). — Arch. Soc. Vanamo 12:58–69.

Larsson, K. & Forslund, P. 1992: Genetic and social inheritance of body and egg size in the Barnacle Goose (Branta leucopsis). — Evolution 46:235–244.

Leblanc, Y. 1989: Variation in size of eggs of captive and wild Canada Geese. — Ornis Scand. 20:93–98.

Lessells, C. M. & Boag, P. T. 1987: Unrepeatable repeatabilities: a common mistake. — Auk 104:116–121.

Lessells, C. M., Cooke, F. & Rockwell, R. F. 1989: Is there a trade-off between egg weight and clutch size in wild Lesser Snow Geese (Anser c. caerulescens)? — J. Evol. Biol. 2:457–472.

Magrath, R. D. 1992: The effects of egg mass on the growth and survival of Blackbirds: a field experiment. — J. Zool., Lond. 227:639–653.

Manning, T. H. 1978: Measurements and weights of eggs of the Canada Goose Branta canadensis, analyzed and compared with those of other species. — Can. J. Zool. 56:676–687.

Martin, T. E. 1987: Food as a limit on breeding birds: a life-history perspective. — Ann. Rev. Ecol. Syst. 18:453–487.

Murphy, M. T. 1986: Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. — Auk 103:465–476.

Mänd, R. 1988: Intrapopulational variation of avian eggs (In Russian with English summary). — Valgus. Tallinn.

Mänd, R., Nigul, A., & Sein, E. 1986: Oomorphology: A new method. — Auk 103:613–617.

Mänd, R., Vilbaste, H. & Leivits, A. 1990: The effect of ecological factors on the variability of eggs of the Great Tit. — In: Viksne, J. & Vilks, I. (eds.), Proceedings of the Fifth Conference on the Study and Conservation of Migratory Birds of the Baltic Basin:266–269., Vol. I. Zinatne Publishers, Riga.

Myrberget, S. 1977: Size and shape of eggs of Willow Grouse Lagopus lagopus. — Ornis Scand. 8:39–46.

Nager, R. G. & Zandt, H. S. 1994: Variation in egg size in Great Tits. — Ardea 82:315–328.

Nilsson, J.-Å: & Svensson, E. 1993: Causes and consequences of egg mass variation between and within Blue Tit clutches. — J. Zool., Lond. 230:469–481.

van Noordwijk, A. J., Keizer, L. C. P., van Balen, J. H. & Scharloo, W. 1981: Genetic variation in egg dimensions in natural populations of the Great Tit. — Genetica 55:221–232.

van Noordwijk, A. J. 1987: Quantitative ecological genetics of Great Tits. — In: Cooke, F. & Buckley, P. A. (eds.), Avian Genetics: A Population And Ecological Approach:363–380. Academic Press, London.

van Noordwijk, A. J. & de Jong, G. 1986: Acquisition and allocation of resources: their influence on variation in life history tactics. — Am. Nat. 128:137–141.

Ojanen, M. 1983a: Significance of variation in egg traits in birds, with special reference to passerines. — Ph. D.-thesis, Dept. of Anatomy and Dept. of Zoology, University of Oulu.

— 1983b: Egg development and the related nutrient reserve depletion in the Pied Flycatcher, Ficedula hypoleuca. — Ann. Zool. Fennici 20:293–300.

Ojanen, M., Orell, M. & Väisänen, R. A. 1978: Egg and clutch sizes of 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.

— 1981: Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. — Ornis Fennica 58:93–108.

Orell, M. & Ojanen, M. 1983: Effect of habitat, date of laying and density on clutch size of the Great Tit Parus major in northern Finland. — Holarct. Ecol. 6:413–423.

Otto, C. 1979: Environmental factors affecting egg weight within and between colonies of Fieldfare Turdus pilaris. — Ornis Scand. 10:111–116.

Perrins, C. M. & McCleery, R. H. 1994: Competition and egg-weight in the Great Tit Parus major. — Ibis 136:454–456.

Pinowska, B. 1979: The effect of energy and building resources of females on the production of House Sparrow (Passer domesticus (L.)) populations. — Ekol. Polska 27:363–393.

Potti, J. 1993: Environmental, ontogenetic, and genetic variation in egg size of Pied Flycatchers. — Can. J. Zool. 71:1534–1542.

Potti, J. & Merino, S. 1994: Heritability estimates and maternal effects on tarsus length in Pied Flycatchers, Ficedula hypoleuca. — Oecologia 100:331–338.

Preston, F. W. 1969: Shapes of birds' eggs: extant North American families. — Auk 86:419–428.

Price, T. & Liou, L. 1989: Selection on clutch size in birds. — Am. Nat. 134:950–959.

Price, T., Kirkpatrick, M. & Arnold, J. 1988: Directional selection and evolution of breeding date in birds. — Science 240:798–799.

Rising, J. D. & Somers, K. M. 1989: The measurement of overall body size in birds. — Auk 106:666–674.

Rätti, O., Dufva, R. & Alatalo, R. V. 1993: Blood parasites and male fitness in the Pied Flycatcher. — Oecologia 96:410–414.

Rohwer, F. C. & Eisenhauer, D. I. 1989: Eggs mass and clutch size relationships in geese, eiders, and swans. — Ornis Scand. 20:43–48.

SAS Institute 1985: SAS User's Guide, Version 6 Edition. — SAS Institute Inc., Cary, NC.

Smith, H. G., Ottosson, U. & Ohlsson, T. 1993: Interclutch variation in egg mass among Starlings Sturnus vulgaris reflects female condition. — Ornis Scand. 24:311–316.

Svensson, L. 1992: Identification guide to European passerines. 4th edn. L. Svensson. Stockholm.

Török, J. & Csörgö, T. 1988: Breeding ecology of hole-nesting passerines in different habitats in the Pilis mountains. — Aquila 95:67–76.

Verhulst, S. & Tinbergen, J. M. 1991: Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit Parus major major. — J. Anim. Ecol. 60:269–282.

Vilbaste, H. & Leivits, A. 1990: Programmes for long-term observations of dynamics of bird populations in the Nigula Nature Reserve (In Russian with English summary). — In: Renno, O. (ed.), Communications of the Baltic Commission for the Study of Bird Migration, Vol. 22:64–83.

Williams, T. D. 1994: Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. — Biol. Rev. Cambridge Phil. Soc. 69:35–59.

Winkel, W. 1970: Experimentelle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise (Parus major und P. caeruleus). — J. Ornithol. 111:154–174.

Yaremchenko, O. A. 1989: Reproduction of the Great Tit in artificial nests (In Russian). — In: Shurakov, A. I. (ed.), Gnezdovaja zhizn ptits:133–142. Pedagogical Institute of Perm, Perm.

Appendix

Data used in Figures 5 and 6. Egg sizes are presented in descending order. All egg volumes are calculated from the formula $V = \pi/6 \times L \times B^2$, or adjusted correspondingly. N is the number of clutches if not otherwise indicated.

L	B	V Mean ± SD (N)	Clutch size Mean ± SD (N)	N. Latitude	ID	Source
		1.82 ± 0.09 (20)	9.6 (20)	69°03'	1	Järvinen 1991
18.03	13.68	1.77 ± 0.12 (218)	11.10 ± 1.30 (206)	58°22'	2	This study, Tõrvandi
		1.76 ± 0.90 (13)	9.6 ± 1.1 (13)	51°	3	Verhulst & Tinbergen 1991
17.92	13.60	1.74 ± 0.12 (317)	8.80 ± 1.66 (297)	58°22'	4	This study, Tartu
17.90	13.60	1.73 ± 013 (93)	10.21 ± 1.27 (93)	58°09'	5	This study, Kilingi-Nõmme
18.02	13.53	1.73 ± 0.11 (51)	8.74 ± 1.42 (61)	47°15'	6	Báldi & Csörgö 1993
17.93	13.53	1.72 ± 0.12 (5007)*	9.24 (55)	65°00'	7	Ojanen et al. 1978
		1.71 ± 0.29 (414)*	8.30 ± 1.31 (54)	47°	8	Hamann et al. 1989
17.80	13.50	1.70 ± 0.11 (16)	11.69 ± 1.78 (16)	58°09'	9	This study, Nigula
17.60	13.60	1.70 ± 0.10 (22)	11.60 ± 1.67 (22)	58°09'	10	This study, Vanajärve
		1.68 ± 0.10 (10)	10.8 ± 1.1 (10)	51°	11	Verhulst & Tinbergen 1991
18.03	13.41	1.70 (168)*	8.83	57°	12	Török & Csörgö 1988
17.86	13.45	1.69 ± 0.10 (99)	8.43** (89)	60°15'	13	Järvinen & Pryl 1989
17.61	13.49	1.68 (1289)*	10.7 (122)	52°	14	Busse 1967
17.86	13.39	1.68 (147)*	10.15	57°	15	Török & Csörgö 1988
17.95	13.35	1.52 (45)*	7.51 (193)	40°	16	Kiziroğlu 1982
17.76	13.37	1.66 (120)*	9.37	47°	17	Török & Csörgö 1988
		1.66 ± 0.15 (479)*	8.9 ± 1.53 (73)	50°30'	18	Hamann et al. 1989

contd.

contd.

		1.65 ± 0.02 (78)*,†	9.10 ± 0.11 (213)	61°20'	19	Eeva & Lehikoinen 1995
17.54	13.38	1.64 ± 0.11 (11)	9.16 ± 1.04 (31)	61°25'	20	Haftorn 1985
17.70	13.30	1.64 (42)	9.5	58°18'	21	Winkel 1970
		1.64 ± 0.15 (716)*	8.7 ± 1.57 (69)	50°	22	Hamann et al. 1989
		1.64 ± 0.10 (93)	8.97 ± 1.33 (93)	47°33'	23	Nager & Zandt 1994 + unp.
		1.63 ± 0.15 (2380)*	9.3 ± 1.48 (182)	50°	24	Hamann et al. 1989
		1.62 ± 0.11 (187)	8.65 ± 1.31 (187)	47°33'	25	Nager & Zandt 1994 + unp.
		1.61 ± 0.12 (137)	8.11 ± 1.45 (137)	47°33'	26	Nager & Zandt 1994 + unp.
		1.60 ± 0.14 (1993)*	8.3 ± 1.54 (227)	50°	27	Hamann et al. 1989
		1.60 ± 0.14 (1816)*	8.8 ± 1.46 (183)	50°	28	Hamann et al. 1989
17.40	13.2	1.59 (569)*	11.5	50°	29	Yaremchenko 1989
		1.52 ± 0.15 (497)*	7.6	50°	30	Hamann et al. 1989

*– number of eggs, not clutches; **– value calculated by us, possibly not exact; †– only unhatched eggs measured