

Egg size variation within passerine clutches: effects of ambient temperature and laying sequence

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The laying sequence of the eggs was determined in 217 clutches of four hole-nesting bird species (*Parus major*, *Phoenicurus phoenicurus*, *Ficedula hypoleuca*, *Sturnus vulgaris*) in northern Finland. In all species, 50—70 % of the egg dimension variation was due to the clutches (females), about 5 % to the laying sequence within the clutch and about 5—20 % to interactions between the female and the laying sequence. The results thus confirmed that the heritability of egg size is fairly high.

Slight but statistically significant positive correlations were detected between daily temperatures (mostly mean and minimum) and egg size. The first eggs of the clutch were often affected by the temperatures occurring about a week before they were laid. These temperatures probably influence the development of the insects from eggs and pupae providing protein for the egg-forming female. The last eggs of the clutch tended to be affected by the temperatures prevailing one to three days before laying, i.e. occurring in the most intensive period of egg formation.

In the Pied Flycatcher egg size increased in the laying sequence in clutches of 6—8 eggs, but not in clutches of 4—5 eggs. The first eggs of the Redstart were slightly larger than the others. No relation between size and variation and laying order was apparent in the clutches of the Great Tit, or in the 5-egg clutches of the Starling, but in 6-egg clutches of the latter the middle eggs were largest.

These trends are compared with those found in other passerines and discussed in relation to the growth strategies suggested by O'Connor, especially clutch adjustment and brood reduction.

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Introduction

Since the pioneering research of Parsons (1970), the ecological significance of egg size variation within the clutch has been studied further in gulls and terns (e.g. Nisbet 1978, Lundberg & Väisänen 1979), in the Swift *Apus apus* (O'Connor 1979) and in two passerines.

In the Common Grackle *Quiscalus quiscula*, Howe (1976, 1978) found that egg size increased with laying sequence and that the females start to incubate before the clutch is complete. When food is short the young hatching late may starve to death, but brood reduction is slowed down by the fact that they hatch from larger eggs, and when

food is abundant the whole brood develops successfully. The presence of both egg size variation and hatching asynchrony was interpreted by Howe (1976) as a means of maximizing reproduction in unpredictable environments. His results are largely supported by the observations of Rydén (1978) on the Blackbird *Turdus merula*.

Apart from the Redstart *Phoenicurus phoenicurus*, the species studied here, the Great Tit *Parus major*, the Pied Flycatcher *Ficedula hypoleuca* and the Starling *Sturnus vulgaris*, are close to their northern limit of distribution in the Oulu area. During the early part of the breeding season cold spells occur frequently in northern latitudes (e.g. Pulliainen 1978, Ojanen 1979). The instability of bird communities increases with advancing latitude (O. Järvinen 1979), and the species are thought to evolve specific breeding strategies in order to cope with the unpredictable climate.

Temperature seems to influence egg size in some species, either by physiological stress on the females or by controlling the availability of invertebrate food (Kendeigh 1941, Perrins 1970, Jones 1973, Howe 1978). Accordingly, we have included the effect of temperature in our analysis.

The aims of this paper are (1) to split the egg dimension variation of the four species into components representing the effects of the clutches (females), the laying sequence, the interaction of these two factors and residual variation; (2) to analyse the proportion of egg size variation within the clutch that can be explained by the ambient temperatures on the days preceding laying; (3) to study trends in egg size variation within the clutch in relation to clutch size and laying period; and (4) to discuss the rôle of egg size variation in the growth strategies of nestling

passerines. According to O'Connor (1978:209—212), intra-clutch variation in egg size can be taken to enhance sibling competition and should be large in species with brood reduction strategy, intermediate in those with resource storage strategy and small in those with clutch adjustment strategy.

We have previously presented basic information on egg size variation in relation to clutch size (Ojanen et al. 1978) and studied the rôle of heredity in egg size variation in our populations (Ojanen et al. 1979b).

Materials and methods

The laying sequences in 217 genuine first clutches were determined near Oulu (65°N, 25°30'E) in northern Finland in 1969—73. The laying sequence of most eggs could be established by daily visits (Table 1). In some clutches it could be determined from the size of the air bubble in the blunt end, and the pale colour of the last eggs in the clutches of the Pied Flycatcher was occasionally used to indicate the sequence of the last two eggs (Ojanen & Orell 1978). Egg length (EL) and breadth (EB) were measured to the nearest 0.05 mm with a sliding caliper. The egg shape index (ES) was calculated from $ES = EL/EB \times 100$, and the volume (EV) estimated from $EV = a + b \times EL \times EB^2$, in which *a* and *b* are species-specific constants (see Väisänen 1969, Ojanen et al. 1978).

Two-way analysis of variance was used to separate the different components of the variation in the egg dimension variables. As the estimation of the interaction between the clutch and the laying sequence required clutches with the same number of observations (eggs measured) and replicates of measurements, the clutch size classes were analysed separately and the clutches were modified to include "replicates" of eggs. E.g. a clutch of 6 eggs was modified to comprise 3 eggs (the original 1st and 2nd eggs being taken as replicates of the new 1st egg, the original 3rd and 4th egg as replicates of the new 2nd egg, etc.). In order to obtain an even number of observations, the 3rd egg was excluded from clutches with 5 eggs and the 4th egg from clutches of 7 eggs. Clutches with 9 eggs were modified to comprise 3 eggs \times 3 replicates. Since there were only 6 clutches of the Redstart, these were modified to comprise

TABLE 1. Number of clutches measured in 1969—73. The laying sequence of the eggs was determined (A) by daily visits, (B) using the criteria presented in Ojanen & Orell (1978).

Species		Clutch size										Σ
		4	5	6	7	8	9	10	11	12		
<i>Parus major</i>	A	1	1	1	10	18	17	14	—	1	63	
<i>Phoenicurus phoenicurus</i>	B	—	1	1	4	—	—	—	—	—	6	
<i>Ficedula hypoleuca</i>	A	1	2	17	15	2	—	—	—	—	112	
	B	6	14	32	21	2	—	—	—	—		
<i>Sturnus vulgaris</i>	A	2	14	8	—	—	—	—	—	—	36	
	B	1	4	6	1	—	—	—	—	—		

6 eggs each (the measurements for the 5th egg were repeated in one clutch with 5 eggs and the 4th egg was excluded from the 4 clutches with 7 eggs).

The analysis of the effects of temperature (measured at Oulu Airport) involved the mean, minimum and maximum temperatures of each of the 10 days preceding laying. The correlations of these 30 temperatures with the dimensions of the eggs for which the exact date of laying was known were then calculated in the Great Tit, Pied Flycatcher and Starling. The effect of female-specific egg size was eliminated by expressing the dimensions (egg length, breadth and volume) as percentage differences from the clutch mean.

Results

Temperature and egg size variation. Only the data for days D1, D3, D5, D7 and D9 are presented here (D1 = the day preceding the laying of a given egg, D3 = day 3 before the laying of the egg, etc.) in order to avoid repetition of similar information caused by autocorrelation between temperatures on successive days. Correlations were calculated for all eggs within a species and also for the sequence classes E1 + E2 (the first 2 eggs in the clutch), E3 + E4 (the 3rd and 4th eggs) and E5 + E6, and in the Great Tit also E7 + E8 and E9 + E10. Unless otherwise stated, only statistically significant ($P < 0.05$) positive correlations are mentioned in the following.

In the Great Tit, egg dimensions

often correlated with the mean and maximum daily temperatures of D3—D5 in the total data (Table 2), but the daily minimum temperature seemed to have no effect. The dimensions of the first eggs of the clutch (E1 + E2) correlated only with the mean temperature of D5 ($r = 0.18^*$). The mean, minimum and maximum temperatures of D5 often had positive (but nonsignificant) correlations with egg length and (less pronounced) with egg breadth in the later eggs in the laying sequence. The breadth and volume of the last eggs of the clutch (E7 + E8 and E9 + E10) were correlated with the temperatures of the days immediately preceding laying (D1, D3, Table 3). The proportion of variance common to the egg dimensions and temperatures ($100 \times r^2$) was small for the total data (about 1%, Table 2), but larger for the last eggs in the laying sequence (as much as 10—20%, Table 3).

In the Pied Flycatcher, egg breadth and volume (but not length) were correlated with the mean temperatures of D3, D7 and D9, but not D1 and D5 (Table 2). The same correlations were also found, with a few exceptions, with the minimum and maximum temperatures. The dimensions of the first eggs (E1 + E2) correlated with the temperatures of days D7—D9, and those of the last eggs (E5 + E6) with the

TABLE 2. Correlations between daily mean (T_x), minimum (T_{\min}) and maximum (T_{\max}) temperatures of 1—9 days before laying and egg dimensions (L = length, B = breadth and V = volume) in the Great Tit, Pied Flycatcher and Starling.

Temperature	Egg dimensions	Day before laying				
		9	7	5	3	1
<i>Parus major</i> (N = 534 eggs)						
T_x	L	-0.06	0.00	0.13**	0.07	-0.04
	B	0.03	-0.01	0.05	0.09*	0.03
	V	-0.01	-0.00	0.11*	0.11*	-0.00
T_{\min}	L	-0.01	-0.04	0.03	0.05	0.07
	B	0.10*	-0.02	0.02	0.03	0.06
	V	0.08	-0.04	0.04	0.05	0.08
T_{\max}	L	-0.08	-0.00	0.13**	0.10*	-0.07
	B	0.01	0.01	0.04	0.10*	0.02
	V	-0.04	0.00	0.10*	0.13**	-0.02
<i>Ficedula hypoleuca</i> (N = 686 eggs)						
T_x	L	0.04	0.01	-0.00	0.05	-0.04
	B	0.10**	0.14***	0.05	0.09*	0.05
	V	0.10**	0.11**	0.04	0.09*	0.02
T_{\min}	L	0.04	0.05	-0.03	0.06	-0.00
	B	0.08*	0.11**	0.07	0.10**	0.12**
	V	0.08*	0.11**	0.04	0.10**	0.09*
T_{\max}	L	0.04	-0.02	-0.00	0.05	-0.04
	B	0.11**	0.13***	0.04	0.06	0.04
	V	0.10**	0.09*	0.03	0.07	0.01
<i>Sturnus vulgaris</i> (N = 193 eggs)						
T_x	L	0.00	0.22**	0.03	0.01	-0.14*
	B	0.10	0.28***	-0.01	-0.18*	-0.09
	V	0.08	0.33***	0.01	-0.14*	-0.14*
T_{\min}	L	0.03	0.11	0.10	0.01	-0.13
	B	-0.00	0.26***	0.01	-0.20**	-0.16*
	V	0.01	0.26***	0.05	-0.16*	-0.19**
T_{\max}	L	0.01	0.18**	0.01	0.04	-0.11
	B	0.11	0.26***	0.01	-0.12	-0.08
	V	0.09	0.30***	0.01	-0.08	-0.12

temperatures of D1 (Table 4). The dimensions of E3 + E4 showed no significant correlation with temperature. As in the Great Tit, the highest correlations explained only a small proportion of the variation in the total data (about 1%), and the values were not much higher for the first or last eggs (about 4%).

In the Starling, the temperatures of

D7 correlated closely with egg length and breadth, and therefore also with volume (Table 2). The correlation was especially strong in the first eggs (E1 + E2, $r \cong 0.4^{**}$). Using partial correlations it was found that the negative correlations between egg dimensions and the temperatures of D1—D3 were caused by high temperatures on D7, and these correlations were reduced to

TABLE 3. Correlations between daily mean (T_x), minimum (T_{\min}) and maximum (T_{\max}) temperatures on days 3 and 1 before laying and the dimensions of the last eggs in the clutches of the Great Tit. E7—8 = 7th and 8th egg, E9—10 = 9th and 10th eggs.

Egg dimension	Temperature	Eggs	N	Day before laying	
				3	1
Breadth	T_x	E7—8	110	0.20*	0.20*
		E9—10	47	0.30*	0.14
	T_{\min}	E7—8	110	-0.01	0.30**
		E9—10	47	0.48***	0.06
	T_{\max}	E7—8	110	0.24*	0.14
		E9—10	47	0.21	0.14
Volume	T_x	E7—8	110	0.25**	0.16
		E9—10	47	0.24	0.22
	T_{\min}	E7—8	110	0.05	0.30**
		E9—10	47	0.37**	0.25
	T_{\max}	E7—8	110	0.28*	0.08
		E9—10	47	0.15	0.17

TABLE 4. Correlations between daily mean (T_x), minimum (T_{\min}) and maximum (T_{\max}) temperatures on days 7 and 1 before laying and the dimensions of the first (E1—2) and last (E5—6) eggs in the clutches of the Pied Flycatcher.

Egg dimension	Temperature	Eggs	N	Day before laying	
				7	1
Breadth	T_x	E1—2	224	0.22**	0.01
		E5—6	194	-0.04	0.15*
	T_{\min}	E1—2	224	0.14*	0.13
		E5—6	194	-0.13	0.20**
T_{\max}	E1—2	224	0.21**	-0.03	
	E5—6	194	-0.03	0.16*	
Volume	T_x	E1—2	224	0.16*	-0.03
		E5—6	194	-0.06	0.13
	T_{\min}	E1—2	224	0.14*	0.10
		E5—6	194	-0.05	0.16*
T_{\max}	E1—2	224	0.14*	-0.05	
	E5—6	194	-0.05	0.13	

almost zero by keeping the D7 temperatures constant. In Starlings laying is highly synchronized (see e.g. Ojanen et al. 1979a). During the springs in which the Starling data were collected, the temperature was high for about a week before the first eggs were laid, but then decreased by several degrees. This was perhaps the cause of the odd negative correlations between egg dimensions and temperature. The proportion of the variation explained was largest in this species, reaching about 10—15 %.

Other weather variables were also analysed (accumulated temperatures of the 10 days preceding laying, daily temperature ranges and precipitation), but these did not more explain the variation in egg dimensions in the species studied.

Effect of laying sequence on egg dimensions. In the Great Tit there was little within-clutch variation in clutches of 7—10 eggs (abbreviated C7—C10; data for C9 and C10 given in Fig. 1). The clutch component of variance was large in all dimensions (56—86 %, Table 5), except in breadth in the smallest clutches (C7). Negative estimates of variance were caused by minor deviations from the assumptions of the analysis of variance. The effect of the laying sequence was generally small, but more important in some clutches, as interactions between clutches and sequences of eggs were often significant. The proportion of error variance (between "replicated" eggs within clutches) averaged about 20 %.

In the Redstart, clutches contributed most to the variation in egg dimensions

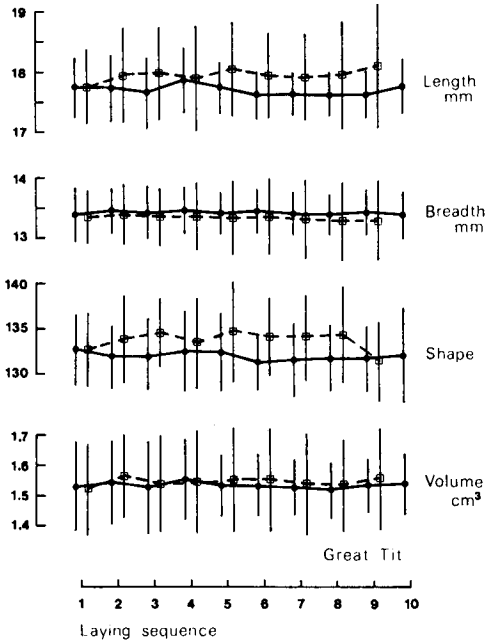


FIG. 1. Mean \pm SD of egg dimensions in clutches of nine (\square , $N = 17$) and ten (\bullet , $N = 14$) eggs, the two most common clutch sizes in the Great Tit.

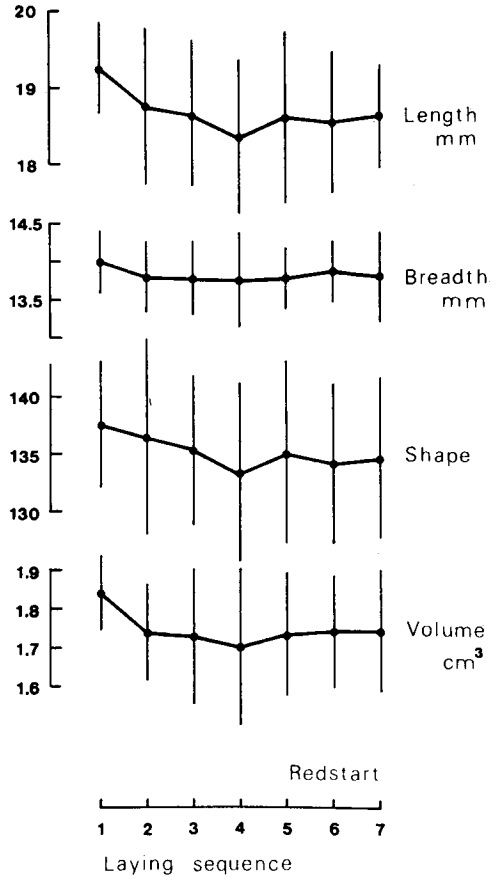


FIG. 2. Mean \pm SD of egg dimensions in clutches of seven eggs ($N = 4$) in the Redstart.

(70–80 %, Table 6). The laying sequence had a significant effect on egg length and shape (about 9 %). This was caused by the first egg of the clutch, which was 3.1 % longer and 5.5 % larger in volume than the clutch mean (Fig. 2). In a total of 12 clutches in which the first egg was known, this egg was the longest in six cases, the shortest once and intermediate in five cases. The interaction between clutches and laying sequence was negligible (Table 6).

In the Pied Flycatcher the effect of the laying sequence was significant for egg breadth and volume in the largest clutches, C6–C8 (Table 7, Fig. 3). Regression analysis showed that volume in particular increased significantly ($P < 0.05$) between successive eggs in

C6 (0.015 cm³ per egg), C7 (0.011 cm³) and C8 (0.008 cm³). The laying sequence did not affect the egg dimensions in the smallest clutches (C4–C5, Table 7). The differential response within the clutch size classes was also related to the date of laying, as the small clutches were laid late in the season. The female component of the variation ranged from 49 to 77 %, except for the breadth and shape index in C8, where it was 22–37 % (Table 7). In the latter cases the residual component was un-

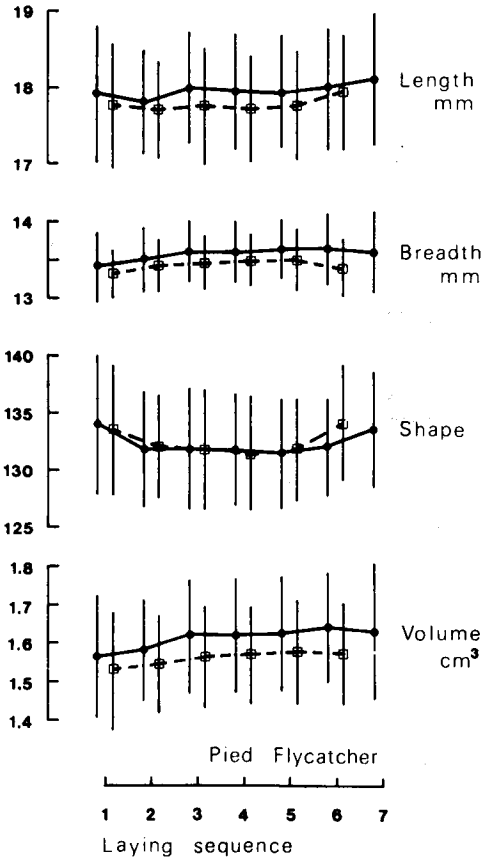


FIG. 3. Mean \pm SD of egg dimensions in clutches of six (\square , $N = 49$) and seven (\bullet , $N = 36$) eggs, the two most common clutch sizes in the Pied Flycatcher.

usually large. The large interactions indicated that the effect of the laying sequence differed between females.

In the Starling, the laying sequence affected egg breadth and volume in C6, but not in C5 (Table 8, Fig. 4). Eggs in the middle of the sequence tended to have the greatest breadth and volume, the 3rd eggs of C6 being significantly larger in volume than the 1st or 6th ones ($P < 0.05$, t -test). The corresponding difference in egg shape was also

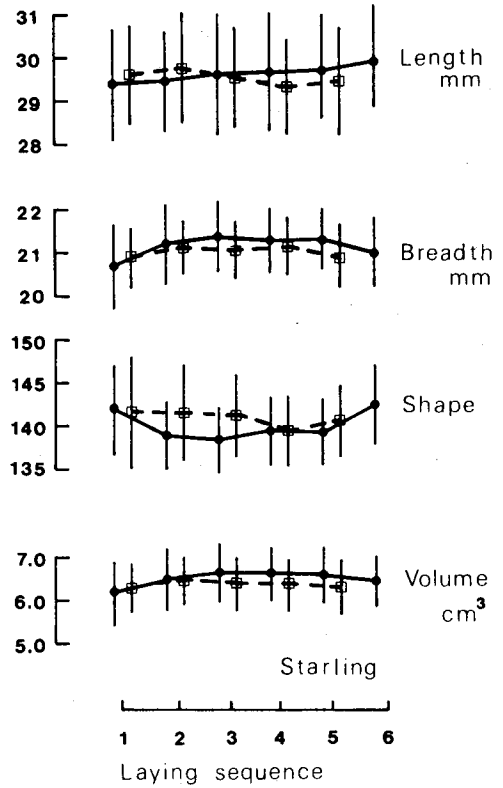


FIG. 4. Mean \pm SD of egg dimensions in clutches of five (\square , $N = 18$) and six (\bullet , $N = 14$) eggs, the two most common clutch sizes in the Starling.

significant ($P < 0.05$), the 1st and 6th eggs being more elongated than the 3rd ones. The female component of the variation in the shape index was very small (38–49%, Table 8), and the interactions were again large, indicating that the effect of the laying sequence differed between females.

Discussion

Egg size has generally been found to be a good predictor of hatchling weight (Schifferli 1973, Howe 1976).

TABLE 5. Variation in egg dimensions in the Great Tit in relation to sequence in the clutch. Two successive eggs are used as replicates (see text). Two-way analysis of variance (mixed model); percentage estimates given for components of variation, and the significance of *F* tests shown by stars.

Variable	Clutch size	Replicates	No. of clutches	Variation components (%)			
				Clutches	Sequence of eggs	Interaction	Residual
Length	7	3×2	10	80***	—0	—0	20
	8	4×2	18	75.9***	1.6*	2.6	19.9
	9	3×3	17	65***	—0	6*	29
	10	5×2	14	63***	—0	17***	20
Breadth	7	3×2	10	25***	—0	43***	32
	8	4×2	18	75.0***	0.3	6.1*	18.6
	9	3×3	17	86***	—0	6***	8
	10	5×2	14	79***	—0	5*	16
Shape	7	3×2	10	70***	—0	11*	19
	8	4×2	18	72.9***	3.4***	1.7	21.9
	9	3×3	17	84***	—0	5	11
	10	5×2	14	66***	—0	10*	24
Volume	7	3×2	10	56***	—0	16*	28
	8	4×2	18	76***	—0	6*	18
	9	3×3	17	84***	—0	7***	9
	10	5×2	14	76***	—0	9**	15

Thus egg volume, calculated from length and breadth measurements, can be used as a practical index of hatching size (Nolan & Thompson 1978, Lundberg & Väisänen 1979). Since the heritability of a number of ecologically important characteristics, including egg size, has been found to be high in the few wild bird species studied (for the Great Tit, see Jones 1973, Perrins & Jones 1974, Garnett 1976, Ojanen et al.

1979b, van Noordwijk et al. 1980; for other species see e.g. Boag & Grant 1978, Smith & Zach 1979), the mean values of a population can be changed by natural selection (van Noordwijk et al. 1980).

The large clutch (female) component of egg size variation (50—70 %) fits with our previous observations on the high heritability of egg size variation in the four species studied (Ojanen et

TABLE 6. Variation in egg dimensions in the Redstart in relation to sequence in the clutch. Two successive eggs are used as replicates (see text). For other explanations, see Table 5.

Variable	Clutch size	Replicates	No. of clutches	Variation components (%)			
				Clutches	Sequence of eggs	Interaction	Residual
Length	5—7	3×2	6	70.3***	9.2***	1.4	19.0
Breadth				79***	—0	6	16
Shape				74.3***	8.9**	1.2	15.6
Volume				76.0***	1.8	4.3	17.9

TABLE 7. Variation in egg dimensions in the Pied Flycatcher in relation to sequence in the clutch. Two successive eggs are used as replicates (see text). For other explanations, see Table 5.

Variable	Clutch size	Replicates	No. of clutches	Variation components (%)			
				Clutches	Sequence of eggs	Interaction	Residual
Length	4	2×2	7	64***	—0	17*	19
	5	2×2	16	62.1***	0.3	14.9*	22.7
	6	3×2	49	77.2***	0.5	10.0***	12.3
	7	3×2	36	72.5***	1.4*	7.7**	18.4
	8	4×2	4	65***	—0	16*	19
Breadth	4	2×2	7	64***	—0	8	28
	5	2×2	16	50***	—0	31***	19
	6	3×2	49	69.9***	2.4***	3.5	24.3
	7	3×2	36	70.5***	5.2***	9.2***	15.1
	8	4×2	4	22.5**	43.1**	3.5	30.8
Shape	4	2×2	7	65***	—0	8	27
	5	2×2	16	48.7***	0.9	10.4	40.0
	6	3×2	49	66.7***	0.9*	7.3**	25.1
	7	3×2	36	59.2***	0.6	5.3	34.9
	8	4×2	4	37.2***	4.9	17.6	40.4
Volume	4	2×2	7	64***	—0	16*	20
	5	2×2	16	63***	—0	23***	14
	6	3×2	49	77.6***	1.4**	7.3***	13.6
	7	3×2	36	74.8***	4.5***	9.8***	10.9
	8	4×2	4	59.3***	21.3**	7.1	12.4

al. 1979b). Similar values have been obtained for the clutch component in many species (see Ojanen et al. 1979b for further discussion). The eggs of some other passerine species are per-

haps more susceptible to environmental factors, for instance those of the Fieldfare *Turdus pilaris* (Otto 1979) and the Eastern Bluebird *Sialia sialis* (Pinkowski 1979), but more data are needed.

TABLE 8. Variation in egg dimensions in the Starling in relation to sequence in the clutch. Two successive eggs are used as replicates (see text). For other explanations, see Table 5.

Variable	Clutch size	Replicates	No. of clutches	Variation components (%)			
				Clutches	Sequence of eggs	Interaction	Residual
Length	5	2×2	18	67.1***	2.3	13.0*	17.6
	6	3×2	14	78.4***	1.2	12.5**	8.0
Breadth	5	2×2	18	84***	—0	0	16
	6	3×2	14	76.7***	5.4**	1.5	16.4
Shape	5	2×2	18	49.3***	3.9	7.7	39.1
	6	3×2	14	37.9**	2.3	18.8*	41.0
Volume	5	2×2	18	85***	—0	5*	10
	6	3×2	14	83.8***	4.0**	3.2	9.0

Högstedt (1981) has shown that if extra food is given to the Magpie *Pica pica*, it lays heavier eggs.

In the present species, the component of variation due to the laying sequence was in most cases only 0—4 %, although the components of the interaction between clutches and laying sequence were frequently 5—20 %, indicating that egg size was affected by laying sequence in a number of females. In the following we shall discuss the biological implications of these percentages.

Effect of temperature on egg size. In small passerines, the rapid growth of the yolk begins 3 or 4 days before ovulation and presumably 4 or 5 days more are needed to achieve body fat and protein reserves, the latter of which are stored in the flight muscles (Kendall et al. 1973, Jones 1973, Jones & Ward 1976, 1979). Statistically significant positive correlations were found here between egg size and daily temperature about 7 days (Starling) or 7 to 9 days (Pied Flycatcher) before the laying of an egg, which agrees with the period of accumulation of these body reserves. The most likely interpretation of these facts is that the temperatures in question are correlated with the development of insects from eggs and pupae (e.g. Jones 1973), which probably takes about a week in the most important prey species. These temperatures thus affect the food resources of the female in the most intensive egg formation period, one or two days before laying.

This hypothesis could be tested in nature by following the development of the most important groups of prey insects in relation to egg size variation in the laying sequence. Such tests might also explain why the correlations with temperature appeared later in the

Great Tit than in the other species studied, about 5 days before laying, and were highest in the first eggs of the clutch. (The Great Tit deviates from the other species studied in the fact that the male feeds the female even before the first egg is laid and also brings food during the laying period, which covers the extra demands of forming an egg each day (Royama 1966, Krebs 1970).)

The second set of correlations between egg size and ambient temperatures appeared 1 to 3 days before laying in the Great Tit and the Pied Flycatcher, at the period of rapid growth of the yolk. Interestingly, these were detected only in the last eggs of the clutch, indicating that environmental factors affected the laying female more easily at the end of the laying cycle, when she had spent the majority of the fat and protein reserves stored for egg production. These late correlations could not be studied in the Starling, due to the masking effect of temperatures about a week before laying (see the results section).

Correlations between egg size and temperature might be explained by the need for thermoregulation in our northern study area, where cold spells during laying are not uncommon. Increased demand of calories for basal metabolism most probably decreases investments in eggs. Indirect evidence of the effect of air temperature on the onset of laying is provided by correlations between the onset of egg-laying and the air temperature on the previous 3—4 days (e.g. Kendeigh 1941, 1963, Kluyver 1951, Tanner 1966, Pinowski 1968). A cold period after the onset of laying may also arrest follicular development and interrupt egg-laying (e.g. Nice 1937, Myres 1955, Winkel 1970, Winkel & Winkel 1974, O'Connor 1979). Thus in critical situations a bird

does not reduce the size of the egg below a given minimum, but instead ceases laying.

Kendeigh (1941) and Jones (1973) have stated previously that egg size in a passerine species is correlated with the temperatures of the 3 or 4 days preceding laying. Lack of statistical details makes these studies difficult to compare with our results. Howe (1978) used polynomial curve fitting to show covariation between egg weight and the temperature of the day before laying in the Common Grackle, and found a marked effect of the minimum temperature on the fresh and dry weight.

High temperatures have been reported to reduce egg size (Bennion & Warren 1933, Kendeigh 1941), but no such effects were observed in the present study area; in all the species studied intensive laying occurred within the mean temperature range of 4–18°C.

Trends and strategies in egg size variation within the clutch. Mensural differences relating to the laying sequence have been reported in many passerines, although there are few cases in which the data have been appropriately analysed. In several papers clutches representing different parts of the breeding season and different clutch sizes have been grouped together, only mean values have been calculated, and statistical tests may be lacking. In most species for which data are available, egg size tends to increase during the laying sequence, although there are some species in which it decreases or shows no variation (Table 9).

Rydén (1978), following the ideas of Pinkowski (1975) and Howe (1976), concluded that the increase of egg weight in the laying sequence in the Blackbird can be interpreted as moderating the effects of asynchronous hatching in such a way that the surviv-

al of the last-hatched young bird is prolonged. The disappearance of this adaptation later in the breeding season is thought to reflect a decline in the predictability of food resources.

The predictability and stability of food resources for the nestlings was the cornerstone of the theory of O'Connor (1978), with its three extremes of breeding strategy. He postulated that food supplies for nestlings may or may not be predictable at the time of egg-laying, and may or may not fluctuate during the nestling period. When they are both predictable and stable, *clutch size adjustment*, the prior adjustment of clutch size, is appropriate. When they are unpredictable at egg laying but stable during the nestling period, *brood reduction* is appropriate, i.e. starvation of the smallest nestlings until the brood size matches the parental foraging rate. When food levels fluctuate during the nestling period, *resource storage*, the accumulation of fat or other reserves, is most appropriate. (This strategy is not valid for the species studied here, and is not discussed further.)

O'Connor (1978) took variation in egg size as enhancing sibling competition, which should be high in brood reduction and small in clutch adjustment. A typical representative of the brood reduction strategy, the House Sparrow *Passer domesticus*, had a coefficient of variation for egg weight of 10.2%, while in a typical clutch adjustment strategist, the Blue Tit *Parus caeruleus*, it was 6.8% (values from O'Connor 1978). The brood reduction strategy involves a high rate of starvation mortality, e.g. 33% in the House Sparrow (Dawson 1972). In this species a sibling hierarchy is ensured by marked hatching asynchrony (O'Connor 1978).

The Jackdaw *Corvus monedula*, in

TABLE 9. Trends in egg size variation within the clutch in certain passerine species.

Species	Country	Source
A. Increasing (or last egg(s) larger than others)		
<i>Alauda arvensis</i>	England	Delius 1965
<i>Parus major</i>	England	Gibb 1950
<i>Parus major</i>	West Germany	Winkel 1970
<i>Parus caeruleus</i>	West Germany	Winkel 1970
<i>Troglodytes aedon</i>	USA	Kendeigh et al. 1956
<i>Turdus merula</i>	Czechoslovakia	Pikula 1971
<i>Turdus merula</i>	Sweden	Rydén 1978
<i>Sialia sialis</i>	USA	Pinkowski 1975
<i>Luscinia luscinia</i>	Finland	Pryl 1980
<i>Phylloscopus collybita</i>	Germany	Groebbels et al. 1930
<i>Ficedula hypoleuca</i>	Finland	This study
<i>Passer domesticus</i>	USA	Murphy 1978
<i>Dendroica petachia</i>	USA	Schrantz 1943
<i>Dendroica discolor</i>	USA	Nolan 1978
<i>Quiscalus quiscula</i>	USA	Howe 1976
<i>Spinus tristis</i>	USA	Holcomb 1969
B. Decreasing (or first egg(s) larger than others)		
<i>Corvus monedula</i>	West Germany	Zimmermann 1951
<i>Corvus monedula</i>	Finland	Antikainen 1978
<i>Phoenicurus phoenicurus</i>	Finland	This study
<i>Passer domesticus</i>	India	Pinowski & Myrcha 1977
<i>Emberiza citrinella</i>	West Germany	Winkel 1970
C. No regular trend		
<i>Delichon urbica</i>	England	Bryant 1975
<i>Parus major</i>	Finland	This study
<i>Sturnus vulgaris</i>	Finland	This study
<i>Melospiza melodia</i>	USA	Nice 1937

which egg size is reported to decrease within the clutch, shows adjustments very close to those of the House Sparrow; nestling mortality of 36 %, marked hatching asynchrony, and a CV for egg volume of 9.3—10.7 % (data from Antikainen 1978; partly recalculated).

The coefficients of variation for egg size in the four species studied here were: Starling 9.8 %, Pied Flycatcher 8.3 %, Great Tit 7.6 % and Redstart 7.4 % (Ojanen et al. 1978). Although the values do not differ significantly (F test), they represent a continuum

along the brood reduction — clutch adjustment gradient.

The brood reduction strategy of the Starling is shown not only in the large CV for egg size, but also in the high nestling mortality (Ojanen et al. 1979a) and commencement of incubation before the clutch is complete; all of these imply selective starvation of the youngest members of the brood when food is scarce. In the Pied Flycatcher nestling mortality is low in the main parts of the breeding range (e.g. v. Haartman 1951, Curio 1959, Källander 1975)

but higher at its northernmost extreme (Pulliainen 1978, A. Järvinen 1980). Egg size increased in the largest clutches, but not in the late ones with only 4 or 5 eggs. These observations indicate that Pied Flycatchers have a clutch adjustment strategy in the early part of the breeding season and a brood reduction strategy later on.

O'Connor (1978) writes of the Great Tit at Oxford that "... early broods have a stable predictable food supply and are hatched from phenotypically adjusted clutches ... while the late broods encounter rapidly declining, and therefore unpredictable, food levels and show characteristics of brood reduction". In Finland the situation is unclear. Clutch size fluctuates markedly from year to year (authors' unpubl. data), no regular trends are evident in egg size within the clutch and the *CV* for egg size is only 7.6 %, all of which indicates a clutch adjustment strategy. Nestling mortality is high, however, about two chicks per brood in southern Finland (v. Haartman 1969) and at Oulu (authors' unpubl. data), which points to a brood reduction strategy.

The seasonal change from clutch adjustment to brood reduction strategy in the Great Tit seems to be caused mainly by hatching asynchrony, the effect of which is more pronounced in continental populations than in that of Oxford. Females start incubation earlier in late clutches in the Netherlands (van Balen 1973), West Germany (Neub 1979) and Oulu (our own observations), and the later the brood is hatched, the more pronounced are the age differences. The effect of hatching asynchrony in late clutches has also been observed at Oxford (Perrins 1970), but because of the very peaked laying period there (see references in Ojanen 1979b:27) the asynchrony is less likely to be effective. When food

is scarce even slight asynchrony in hatching leads to a weight hierarchy within the brood, and the runts die rapidly (Neub 1979, our own observations).

Our limited data on the Redstart are difficult to interpret. Low nestling mortalities have been reported (Meidell 1961), but high mortalities sometimes occur in the northernmost populations during occasional cold spells (A. Järvinen 1978, Pulliainen 1978). The *CV* for egg size was low, pointing to a clutch adjustment strategy, but the large first egg may generate size differences between the siblings and implies a component of brood reduction.

Northern environments are unpredictable and provide many "evolutionary bottlenecks" (Wiens 1977), which must test the reproductive strategies of organisms. This makes population parameters very variable in northern latitudes and as such highly interesting.

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Selostus: Lämpötilan ja munintajärjestyksen vaikutuksesta varpuslintujen munamittoihin

Neljän kolopesijän (talitiainen, leppälintu, kirjosiippo ja kottarainen) pesyeensisäistä munamittamuuntelua tutkittiin Oulun lähistöllä. Yhteensä 217 ensimmäisen pesyeen munien munimjärjestys määritettiin joko päivittäin seuraten tai ns. ilmakuplamenetelmällä (taul. 1). Munien pituus ja leveys mitattiin työntötkillä ja näiden perusteella laskettiin muotoindeksi ja tilavuus.

Pesyeen sisällä munan tilavuus korreloi munintaa edeltävien vuorokausien lämpötiloihin (erityisesti keski- ja minimilämpötiloihin, taul. 2). Pesyeen munien koko oli usein yhteydessä noin viikkoa aikaisemman ajan lämpötilaan, todennäköisesti siksi, että tällöin kehittyi muni-

van naaraan tarvitsema hyönteisravinto munaja kotelovaiheista. Pesyeen viimeisiin muniin vaikutti erityisesti edeltävän 3—1 vuorokauden lämpötila (taul. 3 ja 4). Tähän aikaan keskittyy varsinainen munan muodostaminen.

Kun lajinsisäinen munamittavaihtelu pilkottiin osiin, saatiin pesyeiden välisen muuntelun osuudeksi 50—70 %, munimisjärjestyksen osuudeksi noin 5 % sekä pesyeiden ja munimisjärjestyksen vuorovaikutuksen osuudeksi 5—20 % (taulukot 5—8). Perimän vaikutuksesta kukin naaras siis yleensä muni mittasuhteiltaan tyyppillisiä muniä.

Munimisjärjestyksen vaikutus munankokoon oli pienehkö. Suuret vuorovaikutukset kertoivat kuitenkin, että tutkituissa populaatioissa oli naaraita, joiden pesyeissä munimisjärjestys vaikutti huomattavasti munamittoihin.

Kirjosiepon munankoko kasvoi munimisjärjestyksessä 6—8 munan pesyeissä, mutta ei 4—5 munan pesyeissä (kuva 3). Leppälinnulla pesyeen ensimmäiset munat olivat muita suurempia (kuva 2). Talitaisen munankoko ei muuttunut munien munimisjärjestyksessä (kuva 1). Sama päti 5-munaisiin kottaraispesyeisiin, mutta 6-munaisissa keskimmäisten munien koko oli suurin (kuva 4). Näiden suuntausten evolutiivista merkitystä tarkastellaan O'Connorin kehittämien varpuslinnunpoikasten kasvustrategioiden valossa. Erityisesti verrataan munamittamuuntelun yhteyttä pesyekokostrategiaan (*clutch adjustment*) ja poikueen pienentämistästrategiaan (*brood reduction*). Munankoonhan on todettu useissa tutkimuksissa olevan hyvä poikaseen koon ja menestymisen tunnus.

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