Egg and clutch sizes in four passerine species in northern Finland

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Egg and clutch size variations were studied in four passerines (breeding in nest-boxes) around Oulu (65°N, 25°30′E) in northern Finland: *Parus major, Phoenicurus phoenicurus, Ficedula hypoleuca* and *Sturnus vulgaris*. About 10 200 eggs from 1385 clutches were measured in 1969—73.

Though the trend was irregular, clutch size was found to increase towards the north in three of the species studied, the mean clutch size in Oulu being larger than in more southern areas in Europe in all except *Ficedula hypoleuca*. No geographical trends were found in egg size or shape.

The egg dimensions of *Ficedula hypoleuca* were not affected by clutch size. In *Parus major* and *Sturnus vulgaris* egg size increases with increasing clutch size and in *Phoenicurus phoenicurus* it decreases. In the three latter species the ratio of egg length to breadth was largest, on average, if the clutch size was around the median. Another peak seemed to occur in very small clutches.

To avoid weighing the results in favour of large clutches, we recommend the use of samples of clutch means, instead of samples of single eggs from separate clutches, in analyses of egg measurements. Egg measurements from small clutches are not representative of the population, as such eggs often have a very high length: breadth ratio.

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Introduction

Several studies made in recent years, especially with Laridae, show that egg size has a clear relationship with chick mortality (PARSONS 1970, NISBET 1973, DAVIS 1975, HOWE 1976, LUNDBERG & VÄISÄNEN 1978). Egg dimensions are useful indicators of geographical variation in birds (VÄISÄNEN 1969, 1977). In addition, considerable theoretical interest attaches to the genetic and environmental components of variation in egg dimensions (VÄISÄNEN et al. 1972, JONES 1973). Thus it is remarkable that, except for the study of KENDEIGH et al. (1956), there are no thorough egg dimension analyses for Passeriformes.

In spring 1969, the authors Ojanen and Orell started a study of hole-nesting birds near Oulu (65°N, 25°30′E), in northern Finland. Particular attention was paid to the variation in egg dimensions, and series of egg measurements were made in ringed populations of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. In addition, small samples of eggs of the Redstart *Phoenicurus phoenicurus* and the Starling *Sturnus vulgaris* were measured.

In this paper we present the basic information on the clutch size and egg dimensions, and examine the variation in egg dimensions in relation to clutch size.

Material and methods

In 1969, several nest-box areas were established in Oulu, Haukipudas and Ii. In 1970, the number of nest-boxes was raised from 250 to ca. 500, located in 15 separate study areas. During the years 1969—1973, a total of 10 194 eggs were measured from 1385 clutches of the Great Tit, Redstart, Pied Flycatcher and Starling. The length (EL) and breadth (EB) of the eggs were measured to the nearest 0.05 mm with a sliding caliper. The egg shape index (ES) was calculated from the formula ES = EL/EB × 100 (VÄISÄNEN 1969). The volume of an egg (EV) was estimated according to the method of VÄISÄNEN (1969): a number of museum eggs were filled with water and the regression coefficients were calculated using the obtained real volume as the dependent variable and the product $EL \times EB^2$ as the independent one. The volume coefficients are shown in TABLE 1.

The formulae explain the volume of the eggs particularly well (on average, 97 % of the variance).

Results and discussion

Geographical variation in the clutch size. The clutch sizes of the four species studied are generally of about the same magnitude in Oulu as elsewhere in Europe (Table 2). Thus our results on the relation between clutch size and egg dimensions can be applied to other European populations of these species.

Although the trends are not regular and are obscured by the tendency to lay two clutches in certain areas, it appears that clutch sizes may increase towards the north in Europe (cf. LACK 1954). In the Great Tit, the population in Oulu had the greatest clutch size so far recorded, if we exclude BUSSE's (1967) value of 10.7, calculated only from first clutches and the one-year data of WINKEL (1975). The clutch size reported for Central Sweden (JOHANSSON 1972) is astonishingly low (average of 10 years!). Our scanty data for the Redstart also give the highest average clutch recorded for Europe. PULLIAINEN (1977) has, however, reported a lower average value of 6.21 ($N=28$) from his study area in Värriö, northernmost Finland.

In the Pied Flycatcher, this south-north trend is far from clear, as already noted by v. HAARTMAN (1967). The greatest clutch size has been reported

TABLE 1. Regression formulae for calculating egg volume (EV, cm²) from the length (EL) and breadth (EB, cm) of an egg.

			N	% variance explained (100×r²)
Parus major	EV=	$0.042+0.4673 \times EL \times EB^2$	30	97
Phoenicurus phoenicurus	EV=	$0.044+0.4752 \times EL \times EB^2$	46	97
Ficedula hypoleuca	EV=	$-0.042+0.4976 \times EL \times EB^2$	47	96
Sturnus vulgaris	EV=	$0.455+0.4508 \times EL \times EB^2$	51	99

TABLE 2. Clutch sizes recorded for four passerine birds in different European countries.

Species, country, source	x̄	N
Parus major		
N Finland, this study	9.24	555
S Finland, v. HAARTMAN 1969	9.12	590
Sweden, JOHANSSON 1972	7.83	209[1]
USSR, near Moscov, STEPHAN 1961	8.55	95
Poland, BUSSE 1967	10.7	122[1]
West Germany, WINKEL 1975	9.39	155[2]
Holland, KLUIVER 1951	8.36	1833
England, LACK 1964	9.12	541
Czechoslovakia, BALAT 1970	8.89	417
Czechoslovakia, PIKULA & FOLK 1970	8.73	183
Phoenicurus phoenicurus		
N Finland, this study	6.67	30
(S) Finland, v. HAARTMAN 1969	6.5	114
Norway, MEIDELL 1961	6.54	26
Holland, RUITER 1941	6.27	160
Czechoslovakia, BALAT 1976	5.80	76
Ficedula hypoleuca		
N Finland Kilpisjärvi, A. Järvinen, pers. comm.	5.36	336
N Finland, this study	6.33	725
S Finland, v. HAARTMAN 1967	6.30	1210
N Sweden, HANSON et al. 1966	5.76	104
C Sweden, JOHANSSON 1972	6.20	961
S Sweden, KÄLLANDER 1975	6.49	319
Norway, MEIDELL 1961	5.95	85
USSR, near Moscow, STEPHAN 1961	5.95	546
West Germany, BERNDT & WINKEL 1967	6.30	1543
England, CAMPBELL 1955	7.12	515
Sturnus vulgaris		
N Finland, this study	5.27	78
(S) Finland, v. HAARTMAN 1969	5.0	192
East Germany, SCHNEIDER 1972	5.3	998[3]
East Germany, SCHNEIDER 1972	3.9	492[4]
Holland, LACK 1948	5.24	1592[5]
Holland, LACK 1948	4.9	?[6]
Holland, LACK 1948	4.3	193[7]
England, LACK 1948	4.9	105[5]
Czechoslovakia, PIKULA & FOLK 1970	4.69	132

Notes:

[1] only first clutches
[2] 1 year mean
[3] early broods
[4] late broods
[5] April broods
[6] May broods
[7] June broods

from England. The value for Oulu is of about the same magnitude as that for Central Europe. In mountain areas clutch sizes are low (see e.g. PULLIAINEN 1977).

The clutch size of the Starling at Oulu is the greatest recorded, but in Central Europe this species usually has two clutches; the size of the first is of the order of our sample, and the second is clearly smaller.

Geographical variation in egg dimensions. The egg dimensions of the four species studied are presented in Table 3, together with data from other European populations. Since the handbooks and many recent papers mostly present only the mean lengths and breadths and the numbers of eggs measured, their data are not suitable for statistical tests.

The eggs of the Great Tit at Oulu are perhaps longer than the average for Europe. The other egg dimensions are about the same as elsewhere in Europe. The eggs of the Redstart are shorter in Scandinavian populations than in Central Europe. The mean dimensions of the eggs of the Pied Flycatcher and Starling are about the same throughout Europe. In the Starling, the volume for the Shetlands and Outer Hebrides is very high, and that for Central Europe is especially low (Table 3), but both these values were obtained from rather small samples of eggs (*N* about 50).

Judging from the present material, we can conclude that the egg dimensions of the four passerine species studied do not differ between the North and Central European populations.

TABLE 3. Egg dimensions (mean ± *SD*) of four passerine birds in some European populations. Calculations are made from single eggs. Shape index and volume are calculated by us.

	Length mm	Breadth mm	Shape	Volume cm³	*N*
Parus major					
1. Finland	17.93±0.70	13.53±0.40	132.6±5.5	1.58±0.12	5007
2. Sweden	17.75	13.57	130.8	1.57	179
3. Poland	17.61	13.49	130.5	1.55	1289
4. West Germany	17.70	13.30	133.1	1.50	424
5. England	17.3	13.7	126.3	1.61	50
6. England	17.98	13.62	132.0	1.60	100
6. Central Europe	17.69	13.93	127.0	1.65	470
6. France	17.45	13.47	129.5	1.52	137
7. USSR (Ukraine)	17.9	13.7	130.7	1.61	70
Phoenicurus phoenicurus					
1. Finland	18.46±0.79	13.96±0.36	132.3±5.6	1.76±0.13	200
2. Sweden	18.14	13.75	131.9	1.67	78
6. England	18.7	13.9	134.5	1.76	100
8. Central Europe	18.7	13.8	135.5	1.74	61
6. Central Europe	18.65	14.13	132.0	1.81	218
Ficedula hypoleuca					
1. Finland	17.78±0.71	13.43±0.39	132.4±5.3	1.56±0.13	4576
2. Sweden	17.14	13.50	127.0	1.51	129
9. West Germany	17.84	13.45	132.6	1.56	1025
6. England	17.93	13.42	133.6	1.56	100
8. Central Europe	17.16	13.47	127.4	1.51	39
6. Central Europe	17.80	13.39	132.9	1.55	268
Sturnus vulgaris					
1. Finland	29.47±1.30	21.11±0.82	139.7±6.0	6.40±0.63	411
2. Sweden	29.58	21.41	139.6	6.57	80
6. Shetlands and Hebrides	31.13	21.99	141.6	7.24	52
6. England	30.20	21.20	142.5	6.57	100
8. Central Europe	28.83	20.84	138.3	6.10	51
6. Central Europe	29.65	21.11	140.5	6.41	72
7. USSR (Ukraine)	29.4	21.3	138.0	6.47	59

Sources:

1. This study. 2. ROSENIUS 1926—29. 3. BUSSE 1967. 4. WINKEL 1970. 5. WITHERBY et al. 1940. 6. MAKATSCH 1976. 7. DEMENT'EV et al. 1954. 8. REY 1912. 9. STERNBERG & WINKEL 1970.

Thus, in passerines the selection pressures on egg dimensions do not appear to be related with geographical gradients, as they were found to be by VÄISÄNEN (1969, 1977) in European waders.

Variation within and between clutches. The species-specific egg parameters were computed separately for eggs, using the total material, and for clutches, using clutch means or females as units. The strength of egg dimension variation in the four species was compared by calculating the coefficients of variation. The values for the different egg dimensions are:

	Coefficient of variation between clutches CV_c%	Coefficient of variation between eggs CV_e%
Egg length	3.5—4.0	3.9—4.4
Egg breadth	2.3—3.6	2.6—3.9
Egg shape	3.5—3.9	4.0—4.3
Egg volume	6.8—9.0	7.5—9.9

The breadth varied least; the length and shape varied 0.3—1.4 % units more than the breadth, and the variation of volume was about twice that of length and shape. The same sequence in respect to variation has been reported for the egg dimensions of waders (VÄISÄNEN 1969), and the breadth varies less than the length in various other bird species, as well (e.g. NICE 1937, KENDEIGH et al. 1956, KOSKIMIES 1957, COULSON 1963, GROMADSKI 1966, STERNBERG & WINKEL 1970, MYRBERGET 1977).

The coefficients CV_e and CV_c have a high correlation within species (r= 0.999***), and CV_c is about 11 % smaller than CV_e. Thus, if we know the standard deviation of a certain egg size or shape variable, calculated from single egg measurements, we can obtain the deviation between females (or clutches) from the formula $SD_c = 0.89 \times SD_e$.

As the clutch size of the species studied varies greatly, e.g. 2—14 in the Great Tit, clutch-specific means give the most reliable estimates for the parameters, especially when the sample is small (pooling all the eggs in the sample gives more weight to the large clutches than to the small ones).

Clutch size and egg dimensions. In the Great Tit, two regular trends appear in the variation of the egg shape index (Fig. 1). The shape index decreases at a constant and statistically significant rate from clutch size class 8 (C8) to 13 (C13) (r=0.15***, N=489). In smaller clutches the curve is U-shaped: the mean is great at C4, reaching the lowest point at C6 and rising again to C8. This disagrees with the limited data of BUSSE (1967), according to which the shape index does not correlate at all with clutch size in Poland.

If the smallest clutch size class (C4), which has four observations and a very large egg volume, is excluded, the small clutches (C5-C8) have about 1 % smaller egg volume, on average, than the larger clutches (C9-C13) (from C5 to C13 r=0.09*, N=549). The egg length, breadth and volume probably increased with clutch size in Poland, too (BUSSE 1967). In contrast, JONES (1973), who studied the egg weight of the Great Tit in Oxford found "a significant, though small inverse correlation between clutch size and egg weight". In some populations, however, average egg size might be maximal if clutch size is around the median (see GIBB 1950 and WINKEL 1970; their data are nevertheless scanty or poorly analysed from the statistical point of view).

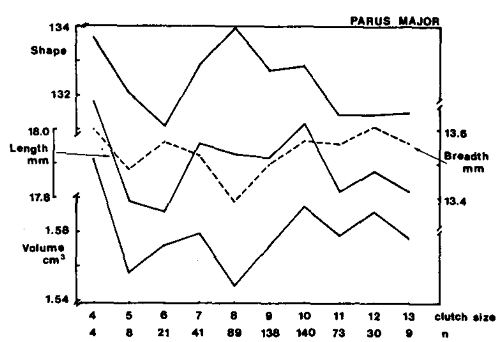

FIG. 1. Mean egg length, breadth, shape index and volume in clutch size classes of the Great Tit *Parus major* in Oulu.

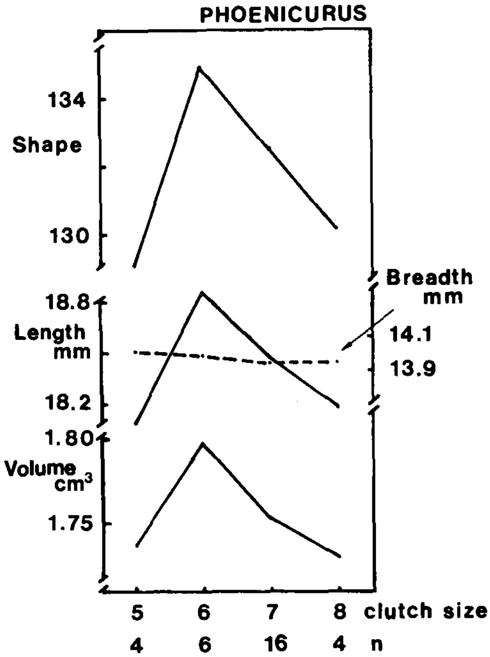

FIG. 2. Mean egg length, breadth, shape index and volume in clutch size classes of the Redstart *Phoenicurus phoenicurus.*

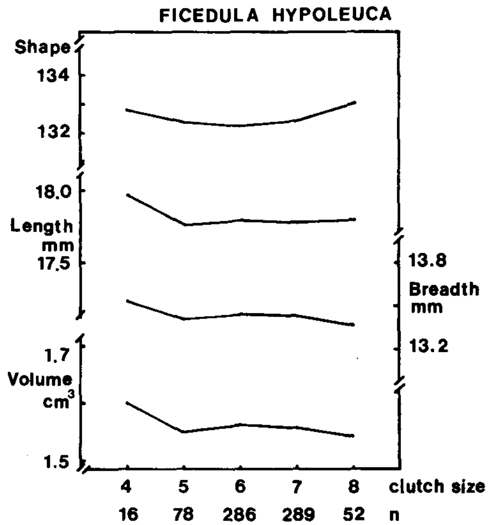

FIG. 3. Mean egg length, breadth, shape index and volume in clutch size classes of the Pied Flycatcher *Ficedula hypoleuca.*

The shape index of the Redstart is related with clutch size (Fig. 2). As in the median clutch size classes of the Great Tit, the curve has a peak. The decrease from C6 to C8 is not significant, though it reaches directional probability ($P=0.10$). The mean egg breadth is surprisingly constant throughout the range of clutch sizes, the variation of egg volume being mainly influenced by that of egg length.

The most frequent clutch sizes of the Pied Flycatcher (C5-C8) do not differ from each other in their egg dimensions (Fig. 3). On average, the smallest clutches (C4) have the largest eggs.

The eggs of the Starling are shortest in C3, the length then increasing significantly towards C7 ($r=0.225^*$, $N=77$) (Fig. 4). The egg shape index varies in the same manner as in the Great Tit; it rises from C4 to C5-6 and then sinks to C7. Egg volume grows significantly from C3 to C7 ($r=0.28^*$, $N=77$).

Conclusions

According to our data, the eggs in small clutches are often long. This causes a deviating shape index and large volume. It is possible that a bird producing a small clutch is in an abnormal physiological condition, which is reflected not only in clutch size, but also in the dimensions of the eggs. These females are most probably strongly affected by external factors.

When analysing the inheritance of clutch size in the Great Tit, PERRINS & JONES (1974) excluded clutches smaller than 6.5 eggs (corrected value) from their material. In this way they obtained a normal distribution instead of

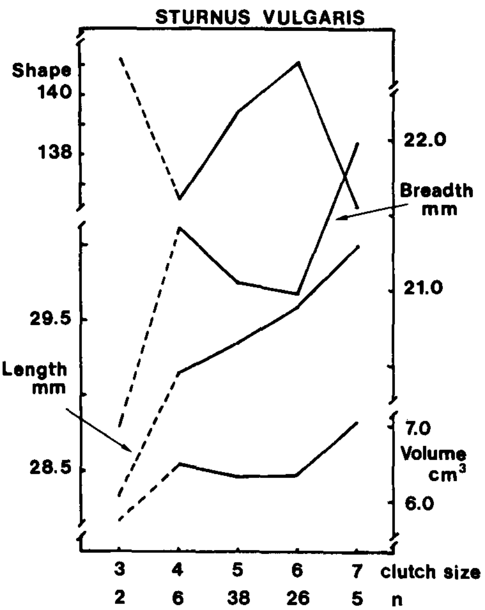

FIG. 4. Mean egg length, breadth, shape index and volume in clutch size classes of the Starling *Sturnus vulgaris*.

a positively skewed one. Our observations of the deviating egg dimensions in small clutches strongly support this practice.

Three types of variation might be distinguished among passerines on the basis of the correlation between clutch size and egg size (the reality of these types remains to be confirmed). In the first group, egg dimensions are not affected by clutch size; e.g. in *Troglodytes aedon* (KENDEIGH et al. 1956), *Turdus philomelos* (PIKULA 1971), *T. merula* (PIKULA 1974, calculated from values in his Table 11) and *Ficedula hypoleuca* (our data). The second group is formed by species in which the egg dimensions increase with increasing clutch size: *Sturnus vulgaris* (our data), *Parus major* (BUSSE 1967 and our data) and *Spinus tristis* (HOLCOMB 1969). The third group consists of species in which the egg dimensions decrease with increasing clutch size: *Phoenicurus phoenicurus* (our data) and the British population of *Parus major* (JONES 1973).

The ecological significance of the variation of egg shape with clutch size is not clear. However, the Great Tit female saves calcium when laying rounded eggs in large clutches, for rounded eggs have least surface area in relation to volume. Rounded eggs also require less space than elliptical ones and so are better covered by the incubating female, which probably makes the incubation of large clutches more efficient.

The heritability of the clutch size of the Great Tit is high ($h^2 = 0.51$, PERRINS & JONES 1974). Although the mean clutch of the population varies from year to year, the clutch size of individual females is fairly stable compared with the population mean.

The heritability of the egg size of the Great Tit has also been found to be high (JONES 1973, our unpubl. data). The relationships discovered here between the clutch size and egg size of the four hole-nesters studied suggests that the genes regulating these properties may be partly dependent.

Selostus: **Talitiaisen, leppälinnun, kirjosiepon ja kottaraisen pesyekoosta ja munankoosta Oulun seudulla**

Vuosina 1969—73 mitattiin Oulun lähistöllä 15 eri tutkimusalueella, joilla on n. 500 pönttöä, n. 10 200 munaa 1385 pesyeestä. Pääosa aineistosta kertyi talitiaisesta ja kirjosieposta, vähäisemmät näytteet leppälinnusta ja kottaraisesta.

LACK'in (1954) säännön varpuslintujen pesyekoon kasvamisesta pohjoista kohti todettiin kolmen lajin osalta pitävän suurinpiirtein paikkansa. Keskimääräiset pesyekoot (taul. 2) olivat Oulussa yleensä suuremmat kuin etelämpänä Euroopassa lukuun ottamatta kirjosieppoa, jonka pesyekoko on suurin Englannissa. Poikkeuksena säännöstä todettiin Keski-Ruotsin talitiais-

populaatiossa alhainen pesyekoko ja toisaalta kahdessa lajin keskieurooppalaisessa populaatiossa (tosin vajavaiseen aineistoon perustuen) suuri pesyekoko. Kottaraisen pesyekoko on Oulussa aineiston mukaan suurin, mutta vertailua vaikeuttaa se, että osa Keski-Euroopan populaatiosta pesii kahdesti vuodessa ensimmäisen pesyeen pesyekoon ollessa lähes sama kuin Oulussa. Munankoossa ei tutkituilla lajeilla havaittu maantieteellisiä suuntauksia (taul. 3).

Kirjosiepon pesyekoon ja munankoon välillä ei havaittu yhteyttä. Sen sijaan talitiaisen ja kottaraisen munan tilavuus kasvaa ja leppälinnun munan tilavuus pienenee pesyekoon kasvaessa (kuvat 1—4). Kolmen viimeksi mainitun lajin munan muotoindeksi (100×munan pituus/leveys) vaihtelee säännönmukaisesti pesyekoon mukaan. Suurimmat muotoindeksit havaitaan keskimäärin yleisimmissä pesyekokoluokissa. Hyvin pienten pesyeiden muotoindeksien keskiarvot ovat usein varsin suuria, mikä johtuu normaalia pitkulaisemmista munista.

Käsiteltäessä munamitta-aineistoja tilastollisesti tulee yksikkömittana käyttää pesyeen keskiarvomittoja yksittäisten munien sijasta. Vaikka havaintojen lukumäärä näin pieneneekin, vältetään aineiston painottuminen suurten pesyeiden mitoilla.

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