Egg dimension variation in five wader species: the role of heredity

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Indirect methods (i.e. not by crossing experiments), mainly the analysis of variance, were used to estimate the effect of heredity on the variability of the egg dimensions of waders. Several 4-egg clutches of marked females of five species were measured on the coasts of Western Finland (29 females of *Charadrius hiaticula,* 17 *Calidris temminckii,* 35 *C. alpina,* 7 *Phalaropus lobatus*) and Germany (11 *Tringa totanus*), mainly in one population per species.

There are species-specific variations in the egg size and shape of individual females (1) according to egg laying sequence within the clutch, (2) between clutches of the same year, and (3) between the clutches of consecutive years. This variation is small, however, the greatest deviations from the clutch mean being only 1—2 %. Few interactions were observed between females and clutches. The main reason for these in *Calidris alpina* seemed to be very late laying, which may cause an abrupt change in egg dimensions. Female body size and egg size were positively correlated in three species. Egg dimension variances within a species were partitioned by the hierarchical analysis of variance. In four species about 60 % of the variance of egg volume was attributable to the females, but no more than 20 % to the clutches. In the fifth species, *C. temminckii,* the corresponding figures were 45 % and 15 %. In this species, which lays two immediately successive clutches in 10 days, egg size steadily increases in the 4+4 egg sequence.

By comparing our results with those obtained by crossing experiments made with *Gallus domesticus,* we concluded that the role of heredity in determining egg size is as great in waders as in the Domestic Fowl. Published data for variations in egg dimensions, for the effect of selection on egg size, and for phenotypic and genotypic correlations between female body size and egg size, warrant the following conclusion: the more precocial a species, the more suitable indices egg dimensions are for taxonomic and evolutionary studies, and the more altricial a species, the more egg dimensions depend upon the age of the female and influence the young's chance of surviving.

1. Introduction

Avian egg dimensions — usually related to female body size — have in recent years been used as indicators of several biological phenomena (BARTH 1967/68, LACK 1968, COULSON *et al.* 1969, VÄISÄNEN 1969, ANDERSON & HICKEY 1970, PARSONS 1970, RATCLIFFE 1970).

Table 1. Data of populations studied.

Species	Location	Years of study	Studied by	Number of			References
				Clutches measured	Females with several clutches	Females measured	
Ringed Plover *Charadrius hiaticula*	Norrskär (island) (63°14′N, 20°38′E) Finland	1966—71	S. V. R. A. V.	97	16 13 * } 29	37	Väisänen 1969
Redshank *Tringa totanus*	Wangerooge (island) (53°47′N, 7°55′E) West-Germany	1956—57	G. Grosskopf	84	11	71	Grosskopf 1958—59, 1970
Temminck's Stint *Calidris temminckii*	Kokkola (coast) (63°50′N, 23°05′E) Finland	1965—71	O. H.	133	17	30	Hildén 1965, 1970
Dunlin *C. alpina*	Pori (coast) (61°30′N, 21°40′E) Finland	1966—69	M. S.	154	35	67	Soikkeli 1966, 1967, 1970a, 1970b
Red-necked Phalarope *Phalaropus lobatus*	Norrskär (island) (63°14′N, 20°38′E) Finland	1967—71	O. H. S. V.	61	7	9	Vuolanto 1968 (study area)

* 13 females from Kuusamo and the Gulf of Bothnia in the years 1966—67 (Väisänen 1969).

The genetic basis of egg size and shape has, however, received but little attention in these studies, because in nearly all studies under natural conditions heritability estimates suffer greatly because of the difficulty of obtaining sufficient numbers of crossings. Laboratory crosses are, for practical reasons, impossible in most species.

In numerous studies of the Domestic Fowl *Gallus domesticus*, heritability estimates for body weight and egg weight have been high. According to Hill *et al.* (1966), phenotypic and genotypic correlations tend to be similar within each of the components of egg contents, hatch and body weights. In contrast, phenotypic and genotypic correlations between the above traits and the egg number and survival were generally quite different in magnitude and sometimes in sign. Birds producing few or many eggs laid smaller eggs than birds with intermediate productivity. — Directional selection may, however, cause differences between the phenotypic and genotypic correlations for body size and egg size, and low values for these, as body weight and egg weight are evidently controlled by both independent and pleiotropic genes (Festing & Nordskog 1967).

Our aim is to estimate, by indirect methods, the heritable component influencing variation in the egg dimensions of five wader species. In the following, several clutches laid by colour-marked females are studied mainly by variance analysis. Two advantages are gained by using only four-egg clutches: (a) the number of replications is the same for factorial arrangement and (b) complications arising from correlations between egg size and clutch size (Hill *et al.* 1966) are avoided.

2. Material and methods

Clutches of colour-marked females of five wader species were measured usually from only one population per species. Length and breadth measurements are accurate to within 0.1 mm. Research work in the Ringed Plover *Charadrius hiaticula,* the Temminck's Stint *Calidris temminckii,* the Dunlin *C. alpina,* and the Red-necked Phalarope *Phalaropus lobatus* was performed on the west coast of Finland over a period of 4—7 years between 1965—71. Data for the Redshank *Tringa totanus* were obtained from Wangerooge in the Frisian Islands, and are from the years 1956—57. They have been partly discussed by GROSSKOPF (1958—59), and those for the Ringed Plover by VÄISÄNEN (1969). The location of study areas, number of clutches and literature references for the populations studied are given in Table 1.

An improved version of the methods used by VÄISÄNEN (1969) was applied in the basic treatment and coding of the data. Statistical analyses were performed using the BURROUGHS 67000 computer and multivariate library programs of the HYLPS-package of the University of Helsinki. For the applications of the variance analysis used in the present study see e.g. SIMPSON *et al.* (1960, p. 258—305).

Because all computer programs did not give exact risk values for rejecting the null hypothesis in the output, the following signs are used:

risk level	*mark*	*significance of the result*
$P < 0.05$	*	fairly significant
$P < 0.01$	**	significant
$P < 0.001$	***	highly significant

Egg shape index (ES) was calculated using the formula

$$ES = 100 \times EL/EB$$

where EL is the length and EB the breadth of the egg. Egg volume (EV) formulae were obtained by means of regression analysis (VÄISÄNEN 1969, p. 17—19). A number of eggs from museum collections (mainly Museum Oologicum, R. Kreuger, Helsinki) were filled with water in order to find their real volumes. Regression coefficients were calculated using the real volume as the dependent variable and the product $EL \times EB^2$ as the independent one. In the formulae EL and EB are expressed in centimetres and EV in cubic centimetres. They are presented at the bottom of this page.

There are minor differences between the species in the proportions of variance in egg volume ($100 \times r^2$) that can be explained on the basis of these formulae.

3. Variation in egg dimensions

3.1. Laying sequence

Variation in egg dimensions in relation to the laying order of eggs within four-egg clutches was studied by a two-way analysis of variance (fixed model; interaction between female and eggs was untestable owing to lack of replications per cell).

The 23 Ringed Plover females analysed differ highly significantly in all four egg dimensions (Table 2). The differences in breadth and volume are proportionally larger than in length and shape. The fourth egg does not differ from the other eggs of the clutch.

The differences between the nine Dunlin females are most marked in egg breadth and volume (Table 3). The difference of the fourth egg from the clutch mean is +1.0 % (not signif.) in length, —1.3 % in breadth and +2.3 % in shape (both signif.), and —1.3 % (not signif.) in volume.

		number of eggs	% of explainable variance
Ringed Plover	$EV = 0.47048 \times EL \times EB^2 - 0.269$	(64)	96 %
Redshank	$EV = 0.37698 \times EL \times EB^2 + 3.283$	(50)	88 %
Temminck's Stint	$EV = 0.45369 \times EL \times EB^2 + 0.065$	(57)	92 %
Dunlin	$EV = 0.40938 \times EL \times EB^2 + 1.092$	(58)	92 %
Red-necked Phalarope	$EV = 0.44077 \times EL \times EB^2 + 0.211$	(47)	93 %

TABLE 2. Variation in the egg dimensions of Ringed Plover females in relation to laying sequence. Two-way variance analysis of 23 clutches (fixed model, interaction = 0).

				Variation between			
	First 3 eggs	Fourth egg	Total	Females		Eggs	
Egg	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	F (22,68)	Risk	F (1,68)	Risk
Length mm	34.46 ± 0.98	34.41 ± 1.15	34.45 ± 1.02	5.90	0.000	0.115	0.736
Breadth mm	25.03 ± 0.65	24.97 ± 0.68	25.02 ± 0.65	19.12	0.000	0.859	0.357
Shape	137.72 ± 4.02	137.83 ± 4.37	137.74 ± 4.09	4.91	0.000	0.026	0.873
Volume cc	9.91 ± 0.70	9.84 ± 0.77	9.89 ± 0.72	16.43	0.000	0.668	0.417

TABLE 3. Variation in the egg dimensions of Dunlin females in relation to laying sequence. Two-way variance analysis of 9 clutches (fixed model, interaction = 0).

				Variation between			
	First 3 eggs	Fourth egg	Total	Females		Eggs	
Egg	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	F(8,26)	Risk	F(1,26)	Risk
Length mm	34.29 ± 1.00	34.75 ± 0.64	34.40 ± 0.93	5.06	0.001	3.31	0.080
Breadth mm	24.41 ± 0.43	23.98 ± 0.59	24.30 ± 0.50	9.88	0.000	16.76	0.000
Shape	140.53 ± 4.70	144.93 ± 4.18	141.63 ± 4.91	5.26	0.001	12.45	0.002
Volume cc	9.45 ± 0.39	9.30 ± 0.45	9.42 ± 0.41	9.07	0.000	2.95	0.098

A sufficient number of Red-necked Phalarope and Temminck's Stint clutches were studied where the complete laying order was known. The nine Red-necked Phalarope females differ distinctly from each other with regard to all four variables (Table 4). Differences between the eggs are not significant, although the shape index almost reaches the limit of a significant value. More complete material comprising 28 clutches shows, however, that the fourth egg is highly significantly longer and larger by shape index than the other three eggs taken together (difference from the clutch mean 0.7 % in both cases, Table 5). Differences between the females are largest in egg breadth.

TABLE 5. Variation in the egg dimensions of Red-necked Phalarope females in relation to laying sequence (the fourth egg known). Two-way variance analysis of 28 clutches (fixed model, interaction = 0).

				Variation between			
	First 3 eggs	Fourth egg	Total	Females		Eggs	
Egg	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	F(19,59)	Risk	F(1,59)	Risk
Length mm	29.44 ± 0.78	29.73 ± 0.96	29.51 ± 0.83	7.72	0.000	13.32	0.001
Breadth mm	20.84 ± 0.50	20.80 ± 0.48	20.83 ± 0.49	8.74	0.000	0.01	0.941
Shape	141.32 ± 4.57	142.96 ± 5.48	141.73 ± 4.84	17.69	0.000	17.19	0.000
Volume cc	5.85 ± 0.34	5.89 ± 0.33	5.86 ± 0.33	5.81	0.000	2.51	0.118

TABLE 4. Variation in the egg dimensions of Red-necked Phalarope females in relation to laying sequence (complete laying order known). Two-way variance analysis of 9 clutches (fixed model, interaction = 0).

	1st egg	2nd egg	3rd egg	4th egg	Total	Variation between			
						Females		Eggs	
Egg	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	F(8,24)	Risk	F(3,24)	Risk
Length mm	29.70 ± 0.55	29.70 ± 0.76	29.63 ± 0.58	30.07 ± 0.89	29.78 ± 0.78	3.48	0.008	1.17	0.343
Breadth mm	20.87 ± 0.55	20.77 ± 0.46	20.90 ± 0.45	20.76 ± 0.42	20.83 ± 0.46	8.43	0.000	0.56	0.648
Shape	142.41 ± 3.12	143.02 ± 4.02	141.80 ± 3.24	144.83 ± 4.37	143.02 ± 3.74	7.53	0.000	2.93	0.054
Volume cc	5.91 ± 0.37	5.86 ± 0.35	5.91 ± 0.32	5.94 ± 0.34	5.91 ± 0.33	5.78	0.000	0.20	0.895

TABLE 6. Variation in the egg dimensions of Temminck's Stint females in relation to laying sequence. Two-way variance analysis of 20 clutches (fixed model, interaction = 0).

	1st egg	2nd egg	3rd egg	4th egg	Total	Variation between			
						Females		Eggs	
Egg	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	F(19,57)	Risk	F(3,57)	Risk
Length mm	28.58 ± 0.75	28.48 ± 0.83	28.62 ± 0.79	28.90 ± 0.93	28.64 ± 0.83	12.58	0.000	4.09	0.011
Breadth mm	20.36 ± 0.52	20.48 ± 0.52	20.61 ± 0.44	20.53 ± 0.51	20.49 ± 0.50	11.88	0.000	4.43	0.007
Shape	140.43 ± 4.39	139.11 ± 4.68	138.89 ± 3.74	140.83 ± 5.30	139.82 ± 4.55	7.69	0.000	2.25	0.092
Volume cc	5.45 ± 0.34	5.49 ± 0.35	5.58 ± 0.32	5.60 ± 0.35	5.53 ± 0.34	16.69	0.000	6.29	0.001

In the 20 clutches of Temminck's Stint, there are highly significant differences between the females in all four egg dimension variables (Table 6). This species differs from the previous ones insofar as egg size changes with laying order. The egg volume increases from the first to the last egg. The difference from the clutch mean is 1.5 % in volume and less than 1 % in other dimensions.

3.2. Clutch sequence within the same year

Several successive clutches from the same year were compared by a two-way analysis of variance (mixed model, in which the female is the random variable and the order of the clutch the fixed one). If a clutch of a female contained only three eggs or only three of the four eggs were measured, the mean of the three was taken as the value for a fourth one. This operation naturally reduces the variance of the clutch, but the number of three-egg clutches is small (given in Tables 7—8 and 10—12).

In the Ringed Plover (Table 7), the Dunlin (Table 8) and Temminck's Stint (Table 10), most of the variance in egg dimensions is attributable to the variation between females (as a rule $P < 0.0005$).

Egg length of the Ringed Plover increases by 0.6—1.0 % from the 1st to the 2nd clutch, to decrease by 1.1 % in the 3rd clutch, but breadth decreases by approx 0.5 % from clutch to clutch (Table 7). These changes are reflected in a reduction, from the 1st clutch to the 2nd, of the shape index by 1.2 %, and of the volume of the 3rd clutch by 2.3 % from earlier clutches. One fairly significant interaction between females and clutches is observed in volume.

There are no statistically significant egg size differences between the 1st and the 2nd clutches of the Dunlin, but interactions between females and clutches are often large (Table 8). Even though differences between females account for

TABLE 7. Variation in the egg dimensions of Ringed Plover females in relation to consecutive 4-egg clutches from the same year. Two-way variance analysis (mixed model).

	Number of		1st clutch	2nd clutch	3rd clutch	Total	Risk for rejecting null hypothesis		
Egg	Fe-males	Clutches per fe-male	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Fe-males	Clutches	Inter-action
Length mm	7	3	33.93 ± 1.20	34.26 ± 1.40	33.87 ± 1.26	34.02 ± 1.28	0.000	0.143	0.393
	19	2	34.24 ± 1.10	34.46 ± 1.14		34.35 ± 1.12	0.000	0.060	0.539
Breadth mm	7	3	24.80 ± 0.48	24.68 ± 0.39	24.54 ± 0.45	24.67 ± 0.45	0.000	0.056	0.323
	19	2	24.98 ± 0.48	24.86 ± 0.51		24.92 ± 0.50	0.000	0.049	0.068
Shape	7	3	136.85 ± 4.54	138.84 ± 5.41	138.05 ± 5.69	137.92 ± 5.24	0.000	0.203	0.391
	19	2	137.09 ± 4.91	138.70 ± 5.59		137.90 ± 5.31	0.000	0.006	0.670
Volume cc	7	3	9.56 ± 0.60	9.55 ± 0.58	9.33 ± 0.57	9.48 ± 0.57	0.000	0.029	0.328
	19	2	9.79 ± 0.52	9.76 ± 0.51		9.77 ± 0.51	0.000	0.568	0.021

Note. 7 ♀♀ × 3 clutches include 8 clutches corrected for fixed egg size, 19 ♀♀ × 2 clutches include 6 corrected clutches.

TABLE 8. Variation in the egg dimensions of Dunlin females **in relation to two 4-egg clutches** from the same year. Two-way variance analysis (mixed model).

Egg	Years	Number of females	1st clutch Mean ± Sd.	2nd clutch Mean ± Sd.	Total Mean ± Sd.	Risk for rejecting null hypothesis Females	Clutches	Interaction
Length mm	1966—69	20	34.14 ± 0.99	34.33 ± 1.32	34.23 ± 1.17	0.000	0.401	0.000
	1966	6	34.90 ± 0.76	34.51 ± 0.78	34.71 ± 0.79	0.153	0.078	0.660
	1967	9	33.98 ± 0.93	34.12 ± 1.81	34.05 ± 1.43	0.000	0.691	0.076
Breadth mm	1966—69	20	24.35 ± 0.54	24.20 ± 0.60	24.28 ± 0.57	0.000	0.067	0.028
	1966	6	24.69 ± 0.59	24.50 ± 0.51	24.60 ± 0.55	0.000	0.262	0.003
	1967	9	24.08 ± 0.44	23.93 ± 0.61	24.00 ± 0.53	0.004	0.246	0.313
Shape	1966—69	20	140.24 ± 4.47	141.84 ± 4.96	141.04 ± 4.78	0.000	0.054	0.002
	1966	6	141.42 ± 3.90	140.90 ± 4.67	141.16 ± 4.26	0.000	0.168	0.991
	1967	9	141.19 ± 4.72	142.52 ± 5.76	141.85 ± 5.27	0.000	0.212	0.174
Volume cc	1966—69	20	9.39 ± 0.50	9.34 ± 0.57	9.36 ± 0.54	0.000	0.530	0.001
	1966	6	9.82 ± 0.50	9.58 ± 0.38	9.70 ± 0.46	0.000	0.158	0.002
	1967	9	9.16 ± 0.37	9.11 ± 0.70	9.14 ± 0.55	0.000	0.719	0.128

Note. Reading from the top these 3 samples include 6, 2 and 3 clutches corrected for fixed egg size. **Four females in the first sample are represented with 2 + 2 clutches from consecutive years.**

most of the variation in Dunlin egg dimensions, other factors may contribute to the variation. Results of t-tests between the successive clutches of females reflect the complicated nature of these interactions. Cases where length or breadth has changed significantly or fairly significantly from the 1st to the 2nd clutch are listed in Table 9, which reveals some striking regularities:

— if the difference concerns egg length, the *length increases* by 0.9—3.3 % (in one exreme case by 8.5 %) from the 1st to the 2nd clutch

— if the difference concerns egg breadth, the *breadth decreases* by 2.0—2.7 % from the 1st to the 2nd clutch.

Laying dates of the last egg of the clutch (Table 9) indicate that if over 20 days have passed since the laying of

TABLE 9. Statistically significant or fairly significant differences in egg length and breadth between two 4-egg Dunlin clutches from the same year. Student's t-test.

Egg	Female No.	Age yrs.	Year	Laying Dates	Laying Range	1st clutch Mean ± Sd.	2nd clutch Mean ± Sd.	t-test
Length	1	≧ 6	1967	5.5., 4.6.	30	33.38 ± 0.15	33.67 ± 0.18	2.461*
	2	≧ 3	1967	(May)	≧ 15	34.33 ± 0.57	35.31 ± 0.11	3.376*
	3	≧ 3	1967	14.5., 3.6.	20	35.00 ± 0.51	36.15 ± 0.19	4.196**
	4	≧ 4	1968	(May)	≧ 20	32.47 ± 0.80	35.22 ± 0.58	5.589**
	5	≧ 4	1968	(May)	≧ 12	32.94 ± 0.12	34.70 ± 0.52	2.836*
Breadth	6	≧ 4	1966	11.5., 12.6.	32	24.43 ± 0.16	23.78 ± 0.19	5.144**
	7	≧ 2	1966	17.5., 13.6.	27	25.60 ± 0.17	25.09 ± 0.25	3.339*
	8	4	1967	(—18.5.), 16.6.	≧ 29	24.65 ± 0.10	24.19 ± 0.27	3.161*
	9	4	1969	11.5., 4.6.	24	24.24 ± 0.22	23.75 ± 0.31	2.589*
	10	≧ 1	1969	(—10.5.), 5.6.	≧ 26	24.78 ± 0.22	24.24 ± 0.16	3.922**

TABLE 10. Variation in the egg dimensions of Temminck's Stint females in relation to two 4-egg clutches from the same year. Two-way variance analysis of 15×2 clutches (mixed model).

Egg	1st clutch Mean ± Sd.	2nd clutch Mean ± Sd.	Total Mean ± Sd.	Risk for rejecting null hypothesis Females	 Clutches	 Interaction
Length mm	28.78 ± 0.64	28.81 ± 0.74	28.80 ± 0.69	0.000	0.813	0.767
Breadth mm	20.38 ± 0.54	20.60 ± 0.52	20.49 ± 0.54	0.000	0.000	0.931
Shape	141.39 ± 5.40	139.91 ± 4.95	140.65 ± 5.21	0.000	0.027	0.631
Volume cc	5.49 ± 0.28	5.62 ± 0.32	5.55 ± 0.30	0.000	0.000	0.958

Note. These include 2 clutches corrected for fixed egg size. Nine females are represented with two clutches and three females with four clutches from the years 1965—71.

the 1st clutch, the chances of abrupt change in the dimensions of the 2nd clutch increase considerably. Accordingly, laying date seems to be the main reason for interactions between females and successive clutches (Table 8). The age of the female is of minor importance in this connection, because only two of the 16 females listed in Table 8 were possibly breeding for their first time.

Temminck's Stint deviates again from the other species studied, because its egg breadth and volume increase (highly significantly) by 1.1 % and 2.4 % from the 1st to the 2nd clutch (Table 10). The shape index also decreases fairly significantly by 1.0 %. No interactions are found between females and clutches. The increase of egg size is remarkable, considering the ability of the female to lay eight eggs in approx. 10 days; under such stress one would rather expect a decrease in egg size. HILDÉN (1965) observed that this species lays two successive clutches, the first of which is incubated by the male, the second by the female. The egg laying interval is about 31 hours and the difference between the onset of laying of both clutches 6—9 days, averaging 7.4 days (16 cases from Kokkola 1963—71). On the basis of these data we are now able to calculate that there follows a pause in the ovulation cycle after the laying of the 1st clutch, corresponding to the laying of 1—2 eggs (about 2—3 days), followed by ovulation of the first egg of the 2nd clutch. Accordingly, Temminck's Stint can be said to lay one 8-egg clutch, within which the egg size continuously increases.

TABLE 11. Variation in the egg dimensions of Redshank females in relation to 4-egg clutches from 2 consecutive years. Two-way variance analysis of 11 × 2 clutches (mixed model).

Egg	1956 Mean ± Sd.	1957 Mean ± Sd.	Total Mean ± Sd.	Risk for rejecting null hypothesis Females	 Years	 Interaction
Length mm	45.19 ± 1.21	45.10 ± 1.43	45.15 ± 1.32	0.000	0.730	0.001
Breadth mm	31.18 ± 0.84	31.27 ± 1.00	31.23 ± 0.92	0.000	0.531	0.013
Shape	145.05 ± 6.10	144.38 ± 6.73	144.71 ± 6.39	0.000	0.637	0.000
Volume cc	19.86 ± 0.91	19.93 ± 1.17	19.89 ± 1.04	0.000	0.543	0.540

3.3. Clutch sequence effects between consecutive years

Several first clutches of the same females taken from consecutive years were compared by a two-way analysis of variance (mixed model, in which the female is the random variable and the year (= age) the fixed one). Tables 11 and 12 show that the variation in Redshank and Dunlin egg measurements is again mainly due to differences between females.

No yearly differences were found between the Redshank clutches taken in two consecutive years (1956—57) from the Frisian Islands (Table 11). Exceptions to this exist, however, because there are marked interactions between females and years in egg length, breadth and shape (but not in volume).

In the Dunlin, there were significant or fairly significant yearly differences in egg length, breadth and volume (not in shape) between the four years 1966—69 at Pori (Table 12). The eggs were about 1.7 % larger in 1966 and 1968 than in 1967 and 1969 (it is assumed that the causes of these differences were climatic, but the matter will not be discussed in this study). Although the mean egg volumes changed from year to year, their standard deviations remained almost unchanged. In general, this yearly variation concerned all females, but there were exceptions, since several interactions between females and years are fairly significant. However, the P-values for these interactions generally do not reach as high levels of significance as those between the years, not even the P-values for the interactions between Dunlin females and two clutches from the same year.

One reason for the interactions between females and years in the Redshank and the Dunlin is supposedly the proportion of females breeding for their first time. Young individuals often start laying late compared with older ones (see literature in VÄISÄNEN 1969, p. 40). The measured clutches of females of known age were too few to allow a three-factor analysis of females, ages and years. Indirect conclusions may, however, be drawn from the effect of age on egg size. Table 12 shows the values for the first clutches of seven Dunlin females from four successive years. In the first year, only one of these birds laid for the first time (ages in years 2, ≥ 2, ≥ 2, ≥ 2, 3, ≥ 4 and ≥ 9). No clear age-bound trend appears in the egg size of these birds, but it may be concealed by the much stronger effect of the years. Because about 75 % of the Dunlin females have bred on at least one earlier occasion (SOIKKELI 1970b), their egg size has greater effect on the variance of a population than the egg size of young birds.

3.4. Components of population variance

A hierarchical (nested) analysis of variance was performed separately for each of the five wader species. Females with more than one measured clutch from one or several years were included in the analysis of three factors, female, clutches of each female, and eggs in each clutch.

It was assumed, in using the hierarchial model, that the effects of the factors are independent. It is true that there may sometimes appear to be interactions between females and clutches (Paragraphs 3.2.—3.3.) in the Redshank and the Dunlin, which partly invalidate the analysis (principles in e.g. SIMPSON *et al.* 1960, p. 298—304, SNEDECOR & COCHRAN 1967, p. 291—294). The analysis was programmed for unequal numbers of observations at various levels, and the program also gave the estimated percentages of variance components. They are listed in Table 13, which also gives the variance ratios and their significances. (Because the variance percentages are estimates, they may be negative if true

TABLE 12. Variation in the egg dimensions of Dunlin females in relation to 4-egg clutches from 2—4 successive years (the first clutches). Two-way variance analysis (mixed model).

Egg	Number of		1966	1967	1968	1969	Total		Risk for rejecting null hypothesis		
	Years	Females	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Mean ± Sd.	Number of eggs	Females	Years	Interaction
Length mm	4	7	34.61 ± 0.88	34.38 ± 0.75	34.38 ± 0.69	34.44 ± 0.88	34.41 ± 0.72	112	0.000	0.544	0.115
	3	8	34.55 ± 0.61	34.27 ± 0.69	34.27 ± 0.73	—	34.30 ± 0.71	96	0.000	0.128	0.604
	2	18	34.46 ± 0.67	34.16 ± 0.75	—	—	34.50 ± 0.82	144	0.000	0.029	0.660
	2	12	—	34.15 ± 0.88	34.36 ± 1.05	—	34.26 ± 0.97	96	0.000	0.322	0.056
	2	13	—	—	34.57 ± 0.93	34.54 ± 0.93	34.55 ± 0.93	104	0.000	0.866	0.043
Breadth mm	4	7	24.48 ± 0.44	24.30 ± 0.52	24.50 ± 0.48	24.30 ± 0.50	24.40 ± 0.49	112	0.000	0.045	0.242
	3	8	24.44 ± 0.43	24.23 ± 0.54	24.41 ± 0.50	—	24.36 ± 0.49	96	0.000	0.044	0.161
	2	18	24.56 ± 0.54	24.40 ± 0.64	—	—	24.48 ± 0.59	144	0.000	0.012	0.030
	2	12	—	24.23 ± 0.54	24.42 ± 0.50	—	24.32 ± 0.53	96	0.000	0.045	0.106
	2	13	—	—	24.51 ± 0.45	24.32 ± 0.43	24.41 ± 0.45	104	0.000	0.005	0.710
Shape	4	7	141.16 ± 2.81	141.06 ± 4.25	140.38 ± 4.30	141.78 ± 4.45	141.10 ± 3.99	112	0.000	0.613	0.062
	3	8	141.03 ± 2.95	141.03 ± 4.00	140.43 ± 4.12	—	140.83 ± 3.70	96	0.000	0.690	0.424
	2	18	140.95 ± 4.34	141.05 ± 4.20	—	—	141.00 ± 4.26	144	0.000	0.846	0.451
	2	12	—	141.02 ± 3.87	140.70 ± 4.68	—	140.86 ± 4.27	96	0.000	0.649	0.583
	2	13	—	—	141.08 ± 4.69	142.08 ± 4.55	141.58 ± 4.63	104	0.000	0.176	0.474
Volume cc	4	7	9.58 ± 0.39	9.38 ± 0.39	9.54 ± 0.34	9.42 ± 0.42	9.48 ± 0.39	112	0.000	0.027	0.418
	3	8	9.53 ± 0.39	9.30 ± 0.42	9.47 ± 0.38	—	9.43 ± 0.41	96	0.000	0.008	0.377
	2	18	9.65 ± 0.46	9.47 ± 0.51	—	—	9.56 ± 0.50	144	0.000	0.003	0.055
	2	12	—	9.30 ± 0.48	9.50 ± 0.47	—	9.40 ± 0.48	96	0.000	0.065	0.004
	2	13	—	—	9.60 ± 0.38	9.46 ± 0.38	9.53 ± 0.39	104	0.000	0.056	0.042

Note. From the top down these 5 samples include 2, 1, 1, 2 and 3 clutches corrected for fixed egg size.

TABLE 13. Variation in the egg dimensions of five wader species at female, clutch and egg levels, computed separately on each of the species. Hierarchical analysis of variance.

Species	Number of			Estimated percentages of variance and the significance of corresponding F-tests											
				Length			Breadth			Shape			Volume		
	♀♀	Clutches	Eggs	♀♀	Clutches	Eggs	♀♀	Clutches	Eggs	♀♀	Clutches	Eggs	♀♀	Clutches	Eggs
Ringed Plover	27	78	299	53.6***	3.1	43.4	54.2***	15.2***	30.6	47.8***	0.4	51.8	58.2***	15.6***	26.2
Redshank	11	22	85	(62.0***	12.8**	25.2)	(76.0***	5.6*	18.4)	(64.9**	17.7***	17.4)	76.6***	—1.5	24.9
Temminck's Stint	17	58	223	35.5***	6.9	57.5	52.6***	15.9***	31.5	47.7***	10.2**	42.2	44.5***	15.0***	40.5
Dunlin	35	111	427	41.5***	11.4***	47.1	55.9***	8.9***	35.2	40.4***	10.9***	48.7	55.8***	10.6***	33.6
Red-necked Phalarope	7	20	78	20.9	36.5***	42.5	79.0***	7.4**	13.6	63.3***	9.9*	26.8	59.2**	21.3***	19.5

variance is close to zero — there is a case of this kind in the table.)

As a common rule, the major fraction of variance in egg dimensions is due to differences between the females (Table 13). Variation between clutches plays a lesser role, whereas variation between eggs is quite considerable. In four of the wader species studied, about 60 % of the variance of volume (biologically the most important of the four egg dimension variables) was caused by the females, but not more than about 20 % by clutches. The effect of females is great on the breadth of eggs, too.

The following phenomena are typical of the separate species:

The *Ringed Plover.* Differences between females are approximately equal in all four variables. Minor differences may appear between the clutches of a female (see also Table 7). Variation within the clutch is greatest in egg shape and smallest in volume.

The *Redshank.* By comparing the analysis of the same materials in Table 11 (two-way analysis of variance) and 13 (hierarchical analysis of variance) we observe how interactions have caused biases in the analysis of egg length, breadth and shape. There are no statistically significant differences between the Redshank clutches from two years, although such seem to appear in the hierarchical analysis. Because no interactions between females and clutches were found in egg volume, this variable is apparently the most suitable for a statistical analysis of Redshank clutches, especially if we bear in mind that the variation in egg volume between females is great and that between clutches small. The data for this species are rather scanty, however.

In *Temminck's Stint,* egg size increases both within the clutch from the first egg to the last one, and from the first to the second clutch (Tables 6 and 10), although the effect of females is much greater than that of clutches in the hierarchical analysis (Table 13). However, the variation between clutches is significant in breadth, shape and volume, but not in length. Between females, too, egg length varies less than other variables.

Variations in the *Dunlin* parallel those in the Ringed Plover, since the relative role of females is great in each variable (c. 50 % of variance) compared with minor differences between clutches (c. 10 % of variance). Significant interactions between females and clutches from the same year (Table 8) and from several years (Table 12) were rather few. They seem mainly to appear in very late replacement clutches, the number of which is disproportionately low in the data subjected to hierarchical analysis. Accordingly, the results for this species in Table 13 cannot be badly biased. The variation between females is greatest in egg breadth and volume.

The data for seven *Red-necked Phalarope* females can give only preliminary results. Possible interactions (no data for this species) between females and clutches may also reduce the validity of the hierarchical analysis. Egg length seems to vary in a very peculiar way, for variation between females is low and that between clutches high. The effect of females on the variance of the other three variables is very great.

3.5. Relations between female body size and egg size

Correlations between female body size variables (weight, wing length, in two species also bill length) for each of the five wader species and egg dimensions were computed. One female was taken as one observation in the analysis. If there were several measurements for some variable of a female, their mean was used.

Some of the correlation coefficients between female size and egg size variables are significant or fairly significant in the Ringed Plover, the Redshank and the Dunlin (Table 14). In the two former species egg length, in the Dunlin egg breadth, has a higher correlation with body size. In Temminck's Stint there are no significant correlations. This is partly because of the low number of observations, but negative correlations are remarkably common in this species. In the Red-necked Phalarope, wing length correlates with egg length in a peculiar way: the longer the wing of a female, the longer and narrower the eggs it lays.

If we estimate those fractions of variances that are explainable by the highest correlation coefficients in the Ringed Plover, the Redshank and the Dunlin ($100 \times r^2$), we find that they are rather low. The highest coefficients in the Ringed Plower show that about 20 % of variation in egg size could be explained by the weight of female. One must remember, however, that marked and regular changes occur in the weight of wader species during laying and incubation (HOLMES 1966, MERCER 1968), and that our weight measurements were taken only once during incubation. This source of error has most probably reduced our correlations between female body size and egg size.

That more exact measurements of females are necessary is shown by the different correlation between weight and wing length in both sexes. In the Redshank females this was low ($r = 0.139$, $N = 70$, Table 14), but in males highly significant ($r = 0.472$, $N = 72$, $P < 0.001$). In the Red-necked Phalarope, the respective value for females was 0.436 (not significant, however, because $N = 11$) and for males 0.136 ($N = 29$). One possible explanation for these differences is that the low coefficient for female Redshanks reflects the effect of stress caused by laying and

TABLE 14. Correlation coefficients between female body size and egg dimensions.

			Female		Egg			
Species	Female	N	Wing	Bill	Length	Breadth	Shape	Volume
Ringed	Weight	35	0.623**	—	0.434**	0.233	0.302	0.378*
Plover	Wing	15	—	—	0.003	—0.225	0.180	—0.131
Redshank	Weight	70	0.139	—	0.254*	0.166	0.091	0.265*
	Wing	71	—	—	0.250*	0.058	0.155	0.177
Temminck's	Weight	21	—	—	—0.088	—0.266	0.112	—0.316
Stint	Wing	20	—	—	—0.370	—0.204	—0.157	—0.343
	Bill	11	0.114	—	—0.126	0.302	—0.268	0.150
Dunlin	Weight	66	0.199	0.328**	0.279	0.181	0.143	0.276*
	Wing	64	—	0.254*	0.044	0.352**	—0.198	0.281*
	Bill	67	0.252*	—	0.209	0.348**	—0.029	0.357**
Red-necked	Weight	11	0.436	—	0.488	—0.367	0.500	—0.100
Phalarope	Wing	11	—	—	0.619*	—0.652*	0.742**	—0.312

incubation (the male also incubates), and that for the male Red-necked Phalarope the stress of incubation (the female does not incubate).

As sources of error also arise from annual variations in weight and environmental variations in egg measurements, one may assume that correlations between female size and egg size are in reality larger and can be explained more satisfactorily than would appear from Table 14.

4. Discussion

4.1. Effect of heredity and body size on the egg size of waders

The size and shape of the eggs of a wader female may vary with the laying sequence within a clutch. There may also be differences between the clutches of the same year or consecutive years, but even the largest of the differences from the clutch mean were only of the order of 1 to 2.5 per cent. The effect of females was great in all cases. The mean value for the female component in the phenotypic variation in egg volume was 0.59 (range 0.44—0.77). In nine studies of the Domestic Fowl, the mean heritability of egg weight was 0.51 (0.30—0.63, summarized in HILL *et al.* 1966). Egg weight and volume are equivalent indices of egg size, owing to their almost absolute positive correlation in the Domestic Fowl (r = 0.989, N = 94) as well as in the Black-headed Gull *Larus ridibundus* (r = 0.972, N = 94), according to unpublished data. Thus the variance component in egg size attributable to females was of the same order in waders (phenotypic variation partitioned by the hierarchical analysis of variance) and in the Domestic Fowl (the ratio of the additive genetic variance, e.g. FALCONER 1964, p. 134, to phenotypic variance). Accordingly the role of heredity in determination of egg size is as great in waders as in the Domestic Fowl.

In the Ringed Plover, the Redshank and the Dunlin the highest phenotypic correlations between female body size and egg size range from 0.265—0.378. Most probably these values are too low, because of the method by which the body size of the female was measured. Negative (not significant, however) coefficients for Temminck's Stint (r = —0.316) and Red-necked Phalarope ($r = -0.100$) indicate that the female body size of these two species may correlate in some exceptional way with egg size. (The effect of the male genome on egg size could not be treated in this study.)

Few interactions occur between females and clutches in the egg dimensions, but some of them are statistically significant. In the Dunlin, very late laying seems to be the most important cause of these interactions, as abrupt changes in egg dimensions occurred more often in late-laid replacement clutches. Dunlin, breeding for the first time, usually lay later than older females (SOIKKELI 1967), and in the Redshank, the laying date becomes annually 2.5 days earlier during the first four breeding seasons, whereafter the shift becomes less marked (GROSSKOPF 1970). The younger a female is, the more disposed it is to lay eggs of abnormal size, the primary reason for this being late breeding.

4.2. Selection and variability in egg dimensions

Heritability of March body weight in the Domestic Fowl is, according to many studies, 0.60—0.70. Phenotypic and genotypic correlations between body weight and egg weight are usually about equal, e.g. in HILL *et al.* (1966) 0.46 and 0.69 ± 0.14 ($r \pm S_r$), respectively. These correlations may, however, differ from each other in response to selection. According to FESTING & NORDSKOG (1967) the observed genetic correlations of four Leghorn lines, selected for a single quantitative trait (named in parenthesis) over seven generations were: 0.60 (high body weight), 0.57 (low body weight), 0.10 (high egg weight) and 0.78 (low egg weight). The basis for the differences is that body weight and egg weight are evidently controlled by both independent and pleiotropic genes. (See also VERGHESE & NORDSKOG 1968, HASSAN & NORDSKOG 1971, NORDSKOG & HASSAN 1971).

The Herring Gull *Larus argentatus* is the only bird species in which the relationship between egg size and post-hatching chick mortality has been studied under natural conditions (PARSONS 1970). Most of the mortality took place in the first week after hatching, subsequent mortality being independent of the size of the egg from which the chick hatched. On the basis of 1400 observations, a highly significant positive correlation between egg size and chick survival was established, corresponding to approximately 80 per cent survival in the largest eggs against 10 per cent in the smallest eggs.

If generalisations may be made on the basis of the results of the Herring Gull studies, the selection of large egg size is really effective. Consequently, it could cause a low genetic correlation between female size and egg size, as directional selection of large egg size of the Domestic Fowl (FESTING & NORDSKOG 1967) caused a decrease in this correlation to the value 0.10 (the phenotypic correlation 0.39 remained on a rather high level). If this also holds true for species breeding in the wild, it severely decreases the usability of egg dimensions as indices of female body size.

The variation in egg dimensions within a three-egg gull clutch is greater than in other bird groups studied up to date, since the third egg is regularly smaller than the other two. The mean percentual difference in the volume of the third egg from the clutch mean averages 4.4 % in nine gull species. In the following weighed mean values are listed with the studies from which the egg measurements have been taken: *Rissa tridactyla* 4.1 % (33 clutches), COULSON 1963; *Larus marinus* 2.8 % (218), *L. argentatus* 6.2 % (310), *L. fuscus* 5.3 % (241), PALUDAN 1951, Harris 1964, Barth 1967/68; *L. canus* 4.4 % (138), Barth 1967/68; *L. californicus* 4.8 % (151), Behle & Goates 1957, Vermeer 1969; *L. delawarensis* 4.4. % (43), Vermeer 1969; *L. atricilla* 4.1 % (15), Preston & Preston 1953; *L. ridibundus* 3.5 % (105), Ytreberg 1956. The value for a tern species *Sterna hirundo* is only 1.2 % (22), Gemperle & Preston 1955.

The effect of laying sequence on egg size has been established e.g. in the following species belonging to other groups: (a) the first egg is smaller than the other eggs in *Phalacrocorax aristotelis,* Coulson *et al.* 1969, and in *Parus major* and *P. caeruleus,* Winkel 1970; (b) the last egg is smaller than the other eggs in *Melanitta fusca,* Koskimies 1957, and in several Anatids, Bezzel & Schwarzenbach 1968; (c) the last egg is larger than the other eggs in *Troglodytes aedon,* Kendeigh *et al.* 1956; and (d) egg size increases with laying sequence in *Alauda arvensis,* Delius 1965, and in *Turdus philomelos,* Pikula 1971. In these species, however, as in this study of waders, the greatest differences between one egg and the clutch mean (volume) are 1—2 %. The Great Tit is an exception, since the volume of the first egg of the clutch differs 4.9 % from the clutch mean (Winkel 1970), but one egg contributes little to the variance of a clutch in this species, owing to its large clutch size.

In the Domestic Fowl egg size increases during the first 3—4 months of egg production. On the longer time scale of successive breeding seasons the same is true for several sea birds (*Megadyptes antipodes,* Richdale 1955, 1957; *Rissa tridactyla,* Coulson 1963; *Sula bassana,* Nelson 1966; *Puffinus tenuirostris,* Serventy 1967). There are especially striking egg size increases in the Shag, the difference between the mean volume of eggs laid by first-breeding 2-year-old females and birds over 8 years being 13 % (Coulson *et al.* 1969). The fact that older birds bred earlier than younger ones caused egg volume to decrease with the advance of the breeding season, but within an age class the early breeding birds laid larger eggs. Similar conditions were found in the Kittiwake. According to Bayes *et al.* (1964) the egg size of the Great Skua *Catharacta skua* likewise decreases as the breeding season advances.

The effect of age on egg size has not been studied in the *Larus*-species, but apparently, as in the Kittiwake, it is influenced by both age and breeding season, since Barth (1967/68) has observed the egg size of *Larus marinus, L. argentatus, L. fuscus* and *L. canus* to decrease towards the end of the breeding season. Further yearly changes take place in the egg size of *L. fuscus* and *L. argentatus* populations. Barth (1967/68) seems to underestimate their importance. His Table 3 lists 14 between-years comparisons of egg volume in Norwegian populations of these two species. A t-test revealed the difference found in four cases to be significant or highly significant (changes in mean volumes: *L. fuscus* Troms 1961—64, —7.2 % and Kristianstad 1942—43, +4.5 %; *L. argentatus* Troms 1960—64, +3.9 % and Tarva 1953—55, —4.3 %). This fits well with the fact that, of nine gull species, egg size variation within the clutch was proportionally greatest in these two.

Variation in the egg size of a female gull is great within the clutch, between the clutches laid at the beginning and the end of the breeding season and between years. Non-genetic factors apparently have a marked effect on egg dimensions. Accordingly, female body size and egg size need not necessarily be correlated, if population means from separate geographical areas are compared. Egg size does not parallel the body size cline of the Herring Gull on the western coast of Scandinavia (BARTH 1967, 1967/68, 1968). In Troms (in the north) body size and egg size are large, and in the Kristianstad—Bornholm area (in the south) small. Birds inhabiting Tarva (in central Norway) are of medium size, but their egg size is smaller than in the south. (It must be mentioned, as a warning example, that if we select from the four-year data from Tarva the clutches of the first study year (Table 3 in BARTH 1967/68), egg size does, however, agree with the cline of body size).

That selection of large egg size leads to low genetic correlation between female body size and egg size and low heritability of the latter seems to be valid for gulls. The trend towards increased egg size in gulls is, however, opposed by another selection pressure i.e. a tendency to fixed clutch size. The relative egg size evolved by each species and family is presumably a compromise between conflicting advantages, resulting in e.g. clutches of a large number of small eggs, or a small number of large eggs. LACK (1968) discusses these questions, referring (p. 261) e.g. to the studies made of a gull species *Creagus furcatus* from the Galapagos Islands. This species has a clutch of one egg and two brood-patches, which suggests that it descends from a form which laid two eggs.

In contrast, egg size variation within waders differs greatly from that of gulls. Variations within the clutch are small and the egg dimensions of a female remain almost the same in repeated clutches during the same breeding season and from year to year. (Of the egg size of females breeding for their first time we had no direct data, but RITTINGHAUS (1956) mentions, without giving exact data, however, that the egg size of young Kentish Plovers *Charadrius alexandrinus* does not differ from that of older breeders.) The heritability of egg size is high and the body size and the egg size of a wader female are in most species positively correlated. This was evident, when regional mean values for wing length and egg volume in the Ringed Plover were compared. In the circumpolar cline of this species these two variables were in near-perfect positive correlation (VÄISÄNEN 1969: Fig. 7). Very probably the heritability of wader body size is high and genetic correlation between body size and egg size also high.

4.3. Usefulness of variability in egg dimensions for studies

Variability in egg dimensions has already proved useful in studies made at the species level (HEINROTH 1922, LACK 1967, 1968, v. HAARTMAN 1971), but we know relatively little about the biological importance of their variation within populations and individual females. At the population level, egg dimensions may be useful in taxonomic and evolutionary studies based on correlations between female body size and egg size (*Charadrius hiaticula,* VÄISÄNEN 1969; *Pelecanus occidentalis,* ANDERSON & HICKEY 1970; *Gavia immer,* ANDERSON *et al.* 1970). Variation at the individual female level may give indices for the age structure of a population (*Rissa tridactyla,* COULSON 1963; *Phalacrocorax aristotelis,* COULSON *et al.* 1969) and reproductive success (*Larus argentatus,* PARSONS 1970). The results of JENKINS *et al.* (1967) on the Red Grouse *Lagopus scoticus* indicate that small egg size in a population is correlated in certain years with low reproductive success, but on the other hand, the egg size of the Pheasant *Phasianus colchinus* is under effective genetic control since, though female weight and clutch-size increased notably from yearlings to two-year-old females, egg size did not change (Labinsky & Jackson 1969). Of passerine birds we know that the egg size and body weight of the Great Tit are positively correlated (Jones 1970), but that there are probable age- and habitat-bound variations in the egg length of the Song Thrush (Gromazki 1966; on the effect of age on egg size see also Nice 1937, p. 115, for *Melospiza melodia*; Kendeigh *et al.* 1956, p. 57, for *Troglodytes aedon*; Winkel 1970, for *Parus major* and *P. caeruleus*), and that the egg dimensions of the Pied Flycatcher *Ficedula hypoleuca* are directly influenced by environmental factors (Sternberg & Winkel 1970). In several Anatids, the egg size of which seems to have a strong hereditary basis (*Melanitta fusca,* Koskimies (1957), minor intraspecific differences occur between the egg length of females in relation to clutch-size (Bezzel & Schwarzenbach 1968).

Summing up we suggest that, the more precocial a species, the more suitable indices egg dimensions are for taxonomic and evolutionary studies, and the more altricial a species, the more egg dimensions depend upon the age of the female and possibly influence the young's chance of surviving.

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Selostus: **Perimän vaikutuksesta kahlaajalintujen munamittavaihteluun**

Epäsuorin menetelmin (siis ei risteytyskokein) tutkittiin, kuinka suuri vaikutus perimällä on kahlaajien munamittavaihteluun. Aineisto koostui 7—35 värirengastetun naaraan pesyeiden munien pituuksista ja leveyksistä Pohjanlahden rannikolta (tylli, lapinsirri, suosirri ja vesipääsky) sekä Friisien saarilta (punajalkaviklo), pääasiassa yhdestä paikallisesta populaatiosta kutakin lajia. Naarailta mitattiin useita pesyeitä samalta vuodelta tai peräkkäisiltä vuosilta. Varianssianalyysillä tutkittiin 4-munaisen pesyeen munien pituuden, leveyden, muodon ja tilavuuden vaihtelun osatekijöitä sekä korrelaatioanalyysillä suhdetta naaraan ruumiinkokoon.

Lajista riippuen esiintyy pesyeen sisällä (munien välillä munintajärjestyksessä) tai naaraan pesyeiden välillä (saman vuoden useammat pesyeet tai eri vuosien pesyeet) tilastollisesti merkitseviä eroja. Tämä vaihtelu on kuitenkin suhteellisen pientä, koska suurimmillaan erot ovat 1—2 % pesyeen keskiarvosta laskettuna. Munamittavaihtelun pääosa on naaraiden välistä vaihtelua. Kukin naaras siis munii kooltaan ja muodoltaan sille yksilöllisiä munia.

Pesyeisiin, joiden munankoko selvästi poikkesi naaraan yksilöllisestä munankoosta, kiinnitettiin erityistä huomiota (tilastollisesti ilmaistuna: tutkittiin vuorovaikutusta naaraiden ja pesyeiden välillä). Munamitoiltaan poikkeavia pesyeitä esiintyi suhteellisen harvoin. Naaraan iällä ei nähtävästi ole suurtakaan vaikutusta munien mittasuhteisiin. Hyvin myöhään munituissa pesyeissä munankoko voi vaihdella äkillisesti. Täten uusintapesyeet ja ensi kertaa pesivien naaraiden pesyeet (normaalisti myöhäisiä) ovat erityisen alttiita munien mittasuhteiden muutoksille.

Naaraan koolle ja munan koolle saatiin kolmella lajilla merkitsevät, mutta pienehköt positiiviset korrelaatiot. Todelliset korrelaatiot lienevät suurempia, koska naaraiden painomittauksia ei ajoitettu niiden syklisiin painonvaihteluihin.

Kun munamittojen kokonaisvaihtelu ositettiin hierarkkisen varianssianalyysin avulla, osoittautui neljällä lajilla n. 60 % kokonaisvaihtelusta naaraiden väliseksi vaihteluksi, kun naaraan eri pesyeiden väliseksi vaihteluksi tuli korkeintaan n. 20 % kokonaisvaihtelusta. Lapinsirrillä, joka poikkeaa muista kahlaajalajeista siinä, että sen munankoko kasvaa sekä pesyeen sisällä munasta toiseen että ensimmäisestä toiseen pesyeeseen saman pesimäkauden aikana (naaras munii kaksi pesyettä 10 vrk:n sisällä), vastaavat arvot olivat 45 % ja 15 %.

Vertaamalla kahlaajanaaraiden välisen fenotyyppisen vaihtelun arvoja kanalla suoritettuihin munankoon periytyvyystutkimuksiin voidaan päätellä, että kahlaajanaaraan munankoko on suurelta osin periytyvä kuten kanankin munankoko. Tulosten vertailu muiden lajien munamittavaihteluun, munankokoon kohdistuvaan valintapaineeseen ja naaraan ja munan koon suhteisiin viittaa siihen, että mitä pesäpakoisempi laji on, sitä selvemmin perimän vaikutus tulee esiin sen munien mittasuhteissa. Mitä kehittyneemmässä tilassa lajin poikaset kuoriutuvat, sitä käyttökelpoisempia indeksejä munamitoista nähtävästi saadaan tätä (prekokiaalista) lajia koskeviin taksonomisiin ja evoluutiotutkimuksiin, ja mitä vähemmän kehittyneinä poikaset kuoriutuvat, sitä enemmän munamittoja voi tarkastella tämän (altrikiaalisen) lajin naaraskohtaisina iän ja poikastuoton mahdollisina indikaattoreina.

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