VARIATION IN THE SIZE AND COMPOSITION OF EGGS OF THE EUROPEAN STARLING

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ABSTRACT.—Between one and five eggs from each of 37 clutches ($n = 88$) of the European Starling (*Sturnus vulgaris*) were analyzed to determine the relative amounts of shell, yolk and albumen, and the levels of water, lipid, and nonlipid dry matter in these components. On average, the yolk made up 17.7% of fresh egg mass. The albumen contained 89.8% water; yolks contained 55.7% water and 29.9% lipid. Amounts of ash and concentrations of cations in the yolk and albumen are reported. The mass of the shell varied in direct proportion to fresh egg mass, the amount of albumen varied in proportion to the 1.1 power of egg mass, and the yolk in proportion to the square root of egg mass. Unlike the eggs of precocial species, however, both the yolk and lipid content of the egg were poorly correlated with egg mass ($R^2 = 0.22$ and 0.14, respectively). A principal components analysis revealed that 90% of the variation in egg size and composition could be related to three factors roughly corresponding to egg size (51%), percent yolk (27%), and ratio of lipid to nonlipid dry matter in the yolk (14%). As in other passerines, between 50 and 80% of variation in most egg characteristics occurred among clutches rather than within clutches; composition of the yolk was least related to clutch. With respect to position in the laying sequence, only the percentage of water in the egg showed a significant trend, decreasing slightly from first to last. Because egg size is a poor predictor of yolk size, it may not necessarily provide a useful index to egg quality or be correlated with nestling growth and survival.

The relative size and chemical composition of the yolk of birds' eggs varies greatly among species, primarily in accordance with the precocity of the neonate (Romanoff and Romanoff 1949, Nice 1962, Ricklefs 1977a, Ar and Yom-Tov 1978, Carey et al. 1980). Less is known about intraspecific variation in egg composition. Yolk size appears to increase in direct proportion to egg size in precocial species (Romanoff and Romanoff 1949, Parsons 1970, Ricklefs et al. 1978, Ankney 1980), but it is poorly related to egg size in altricial species (Schifferli 1973, Ricklefs 1977b, Bryant 1978, Ricklefs and Montevecchi 1979). Although egg size has been shown to vary in relation to year, season, clutch size, position in laying sequence, and individual female in several studies (e.g., Parsons 1970, Väisänen et al. 1972, Howe 1978, O'Connor 1979, Ojanen et al. 1981), the relationship of these factors to egg composition has not been investigated. Growth and survival of chicks is influenced by egg size, as indicated by field studies of Parsons (1970,

1975), Schifferli (1973), Howe (1976), O'Connor (1979), and others. It seems reasonable to assume that egg composition might have a similar effect. The present study reports variation in composition of eggs of the European Starling (*Sturnus vulgaris*) in southeastern Pennsylvania with respect to egg size, individual female, and position in clutch.

METHODS

I collected 88 fresh eggs (between 1 and 5 from each of 37 clutches) from nest boxes near Kennett Square, Pennsylvania (see Ricklefs and Peters 1979), during late April and early May 1976. Sixty-eight of the eggs were from first clutches laid between 22 and 28 April; 20 were from replacement clutches laid between 3 and 12 May. Eggs collected during the two time-periods differed slightly with respect to mass of the shell and the water and nonlipid dry components of the yolk; relative amounts of yolk and albumen and the fraction of water, lipid, and nonlipid dry material did not differ

significantly between the samples (Ricklefs 1982). Eggs were stored in airtight plastic containers in a refrigerator for up to 18 days before processing. Loss of weight during this period was approximately $7 \, \text{mg} \cdot \text{day}^{-1}$, or $0.1\% \cdot \text{day}^{-1}$ (Ricklefs 1982). Variation in the content of water in eggs due to preprocessing treatment was statistically insignificant ($P > 0.05$) compared to variation among eggs receiving equal treatment.

Fresh eggs were separated into shell, yolk, and albumen components. Inevitably, a small fraction of the albumen coated the yolk and inside surface of the shell. Components were dried to constant weight at 60°C. Lipids were extracted from the yolks using a 5:1 mixture of petroleum ether and chloroform. In this discussion, water content equals wet mass minus dry mass; lipid content equals dry mass minus nonlipid dry mass. Shells of 10 eggs were combusted in a muffle furnace for 12 h at 500°C. Combusting shells at 550°C resulted in loss of acid-soluble ash residue. The ash was dissolved in weak hydrochloric acid and filtered to remove carbon residues, which amounted to between 0.6 and 1.7% of the total ash. Samples of the yolk and albumen were treated similarly; concentrations of several cations were determined by atomic absorption spectrophotometry (Limnology Dept., Academy of Natural Sciences of Philadelphia). All samples were weighed to the nearest 0.001 g on a Sartorius analytical balance. The lengths and breadths of eggs were measured to the nearest 0.05 mm using dial calipers. Analyses were performed with the General Linear Models (GLM) and MATRIX procedures of the Statistical Analysis System (SAS; Helwig and Council 1979).

RESULTS

EGG DIMENSIONS AND WEIGHT

Averages and measures of dispersion of the lengths, breadths, and masses of 88 eggs are presented in Table 1. Fresh mass in grams (M) was related to length (L) and breadth (B) in centimeters by the equation

$$M = 0.035 + 0.530 LB^2$$

TABLE 1. Univariate statistics of the dimensions and masses of eggs ($n = 88$) of the European Starling in southeastern Pennsylvania.

Variable	Mean	SD	CV (%)
Length (mm)	30.08	1.10	3.67
Breadth (mm)	21.17	0.59	2.80
Mass (g)	7.19	0.54	7.50

($F[1,86]) = 1,724, P < 0.0001, R^2 = 0.95$). The standard deviation about the regression line was 0.118 g; the standard error of the slope was $0.013 \, \text{g} \cdot \text{cm}^{-3}$.

EGG COMPOSITION

The proportions of shell, yolk, and albumen, and the composition of each of these components (Table 2) were similar to those reported for a smaller sample of eggs by Ricklefs (1977b). The ash content of the shells of 10 eggs was 0.398 g (0.014 SE; carbon residue subtracted), or about 85% of the dry shell. Yolks and albumen of many eggs were combined and four subsamples of yolk and two of albumen were ashed and their levels of several cations determined. Yolks contained 5.8 g (0.1 SE) ash per 100 g lipid-free dry weight. Albumen contained 6.6 g (0.1 SE) ash per 100 g lipid-free dry weight. Levels of cations in two samples of yolk and two samples of albumen are presented in Table 3.

RELATIONSHIP OF EGG COMPONENTS TO FRESH EGG MASS

Regressions of the logarithm of component mass on the logarithm of fresh egg mass were calculated to determine the allometric relationships among egg components. The slope of the regression estimates the exponent (b) of the power relationship $Y = aX^b$. Values of b (Table 4) reveal that the mass of the shell component increased in direct proportion to egg mass ($b = 0.958 \pm 0.094$ SE), the albumen in proportion to the 1.1 power of egg mass ($b = 1.119 \pm 0.029$ SE), and the yolk in proportion approximately to the square root of egg mass ($b = 0.549 \pm 0.111$ SE), with considerable

TABLE 2. Percentage composition of major components and biochemical constituents of the eggs of the European Starling ($\bar{x} \pm$ SE, $n = 88$).

	Shell	Albumen	Yolk	Whole egg
Total egg	10.6 ± 0.07[a]	71.7 ± 0.17	17.7 ± 0.16	—
Egg component				
Nonlipid dry	61.4	10.2 ± 0.05	14.5 ± 0.12	16.3
Lipid		—	29.9 ± 0.19	5.3
Water		89.8 ± 0.05	55.7 ± 0.15	78.3

[a] Dried shell as percent of total egg was 6.5 ± 0.03.

TABLE 3. Cation concentrations in yolk and albumen of eggs of the European Starling, with comparable data for the domestic fowl (*Gallus gallus* var. *domesticus*) and the Northern Gannet (*Sula bassanus*).

	Mn	Zn	Cu	Fe	Na	K	Ca	Mg
Per nonlipid dry mass (mg·g⁻¹)								
Yolk (n = 2)	0.018	0.42	<0.01[a]	0.25	0.89	1.8	1.8	0.53
Albumen (n = 2)	<0.02	<0.04	0.04	0.02	19.2	8.3	<0.01	0.32
Per wet mass (mg·g⁻¹)								
Yolk								
Starling[b]	0.003	0.061	<0.002	0.036	0.129	0.260	0.260	0.077
Gannet[c]	<0.002	0.059	0.004	0.131	1.16	1.03	0.432	0.162
Chicken[d]	—	0.045	0.009	0.11	0.70	1.12	1.44	1.28
Albumen								
Starling[e]	<0.002	<0.004	0.004	0.002	1.958	0.847	<0.001	0.033
Gannet[c]	<0.001	0.009	0.001	0.002	1.99	1.54	0.034	0.070
Chicken[d]	—	0.0002	0.0006	0.0009	1.61	1.67	0.12	0.09

[a] The < designates lower limit of resolution of analysis.
[b] Mg·g⁻¹ nonlipid dry × 0.145.
[c] From Ricklefs and Montevecchi (1979).
[d] From Romanoff and Romanoff (1949).
[e] Mg·g⁻¹ nonlipid dry × 0.102.

variation about the regression. Because albumen adhered to the shell when components were separated (Ricklefs 1982) and because shell membranes contain some moisture, the dry mass of the shell component provides a better estimate of the mass of the shell. The allometric relationship of this component to egg mass (0.856 ± 0.067 SE) was significantly less than 1, but greater than ⅔, showing that, as egg mass increased, shell mass decreased in relation to egg mass but increased in relation to egg surface. Although the albumen content, especially its water fraction, was strongly correlated with egg mass ($R^2 = 0.943$), the size of the yolk was only weakly correlated ($R^2 = 0.220$) and the lipid fraction of the yolk even less so ($R^2 = 0.137$).

PRINCIPAL COMPONENTS ANALYSIS OF EGG COMPOSITION

In order to determine relationships among the variables of egg composition, and to extract a set of new combinations of measurements to describe variation among starling eggs, I performed a principal components analysis (PCA). The PCA was based upon a covariance matrix calculated from the logarithms of the mass of each component of the egg: shell (dried), albumen water, albumen dry matter, yolk water, yolk lipid, and yolk nonlipid dry matter. Because the PCA was based on logarithms, the linear combinations of variables that define each eigenvector, or new axis, can be interpreted as products and ratios of variables. Three principal components explained over 90% of the variance in egg composition (Table 5). The first axis, which explained 51% of the variance, can be related to size because all the variable loadings on it had positive signs and similar magnitudes. The second axis (27%) can be in-

terpreted as the ratio of yolk to other components, and the third axis (14%) as the ratio of lipid to nonlipid dry matter in the yolk. The PCA suggests that variation in eggs can be described adequately by these variables: total mass, yolk fraction, and lipid : nonlipid ratio of the yolk.

VARIATION WITHIN AND AMONG BROODS

A casual inspection of egg measurements revealed considerable variation among clutches. Within clutches, eggs tended to be uniform in

TABLE 4. Allometric (log-log) regressions of egg components on fresh egg mass in the European Starling (n = 88).

Variable	Statistics[a]			
	a	b	s_b	R^2
Shell				
Total	−0.941	0.958	0.094	0.545
Dry	−0.066	0.856	0.067	0.655
Water	−1.490	1.114	0.204	0.256
Albumen				
Total	−0.248	1.119	0.029	0.943
Dry	−1.314	1.203	0.071	0.768
Water	−0.287	1.109	0.030	0.940
Yolk				
Total	−0.370	0.549	0.111	0.220
Water	−0.611	0.532	0.121	0.183
Nonlipid dry	−1.377	0.743	0.151	0.220
Lipid	−0.864	0.512	0.139	0.137
Whole egg				
Total[b]	−0.004	1.002	0.005	0.998
Water	−0.141	1.039	0.011	0.990
Nonlipid dry	−0.782	0.992	0.046	0.845
Lipid	−0.864	0.512	0.139	0.137

[a] a and b are the intercept and slope in the equation log Y = a + b log X; s_b is the standard error of b; R^2 is the square of the correlation coefficient, the coefficient of determination.
[b] Values deviate from a perfect correlation because of losses of material especially water, during processing and errors in weighings.

TABLE 5. Principal components analysis of variation in composition of eggs of the European Starling ($n = 88$).[a]

Variable	Variance	Components		
		I	II	III
Shell: dry	0.00118	0.311	0.328	−0.226
Albumen: water	0.00138	0.381	0.367	−0.192
dry	0.00199	0.434	0.531	0.004
Yolk: water	0.00164	0.393	−0.434	−0.037
nonlipid dry	0.00265	0.547	−0.261	0.694
lipid	0.00203	0.340	−0.468	−0.656
Percent of total variance		50.8	27.4	14.2
Cumulative percent		50.8	78.2	92.4

[a] Analysis based on logarithms of original variables.

size, shape, and color compared to the population as a whole. Within-brood and between-brood variations in egg components were compared in a one-way analysis of variance (ANOVA) based on 78 eggs in 27 clutches for which two or more eggs were analyzed. The results of the ANOVA showed that most measurements of size and indices of egg composition were significantly more variable within the population as a whole than within clutches (Table 6). Variation between clutches accounted for between 50 and 80% of the total in most cases. The composition of the yolk was least associated with clutch, with only about 50% of the variation in the water and lipid fractions occurring between clutches. The non-lipid fraction of the whole yolk, and the lipid and nonlipid fractions of the dry matter of the yolk did not vary significantly between clutches, even though the lipid : nonlipid ratio of the yolk is a major component of variation among all eggs. Of the overall dimensions and mass of the egg, 71 to 72% of the variance occurred between clutches; of the yolk fraction of the whole egg, 72%; and of the water fraction of the albumen, despite its relative constancy both within and between species, 82%. Because the ANOVA presented in Table 6 is unbalanced owing to varying numbers of eggs per clutch (two to five), estimates of variance components may be difficult to interpret. But comparable results from a more balanced design involving four and five eggs per clutch are similar (Table 8) and reconfirm the conclusions concerning within- and between-clutch variation in egg components.

Some of the variables included in the ANOVA were highly correlated with the size of the egg (Table 4), and their variation between clutches may have been related fortuitously to variation in egg mass between clutches. To separate the effects of egg mass and clutch, I performed an analysis of covariance (ANCOVA), with egg mass as the covariable and with clutch as the single effect, for dry shell,

TABLE 6. Analysis of variance in composition of eggs between clutches of the European Starling ($n = 78$ eggs, 27 clutches).

Variable	Statistics[a]			
	$F_{(26,51)}$	P	R^2	Error SD
Length (mm)	4.57	<0.0001	0.712	0.0765
Breadth (mm)	4.86	<0.0001	0.724	0.0401
Mass (g)	4.56	<0.0001	0.711	0.3710
Egg (%)				
Dry shell	3.82	<0.0001	0.674	0.0021
Albumen	3.65	<0.0001	0.663	0.0112
Yolk	4.83	<0.0001	0.723	0.0125
Water	3.48	<0.0001	0.653	0.0043
Egg (% dry)				
Lipid	3.35	<0.0001	0.644	0.0249
Albumen (%)				
Water	8.24	<0.0001	0.816	0.0025
Yolk (%)				
Water	1.83	0.032	0.497	0.0113
Lipid	2.02	0.016	0.521	0.0140
Nonlipid dry	1.11	0.365	0.375	0.0109
Yolk (% dry)				
Lipid	1.49	0.110	0.446	0.0240

[a] F = ratio of between-clutches mean squares to error mean squares, calculated with 26 and 51 degrees of freedom; P = probability that F does not differ significantly from 1; R^2 = coefficient of determination; error SD = within-clutch standard deviation.

albumen, and yolk fractions of the whole egg, water fraction of the whole egg, and lipid fraction of the dried contents of the whole egg. In every case, variation between clutches was significant, and adding mass as a covariate had little effect on the F-ratio.

The ANOVAs summarized in Table 6 suggest that variation in scores on principal components I and II should have a strong between-clutch component, but that scores on component III should not. This was verified directly by ANOVA, in which 60% of the variation in component I and 73% in component II occurred between clutches; there was no significant variation between clutches in scores on component III.

POSITION WITHIN THE CLUTCH

I collected enough eggs from 11 nests to test the effect of position in the laying sequence on

TABLE 7. Analysis of covariance relating egg composition to mass, clutch, and position in laying sequence.

Percent	Effects[a]		
	Mass $F_{(1,25)}$[b]	Clutch $F_{(10,25)}$[b]	Position $F_{(14,25)}$
Dry shell	16.2	8.0	0.6
Albumen	53.5	7.0	2.9[c]
Yolk	50.7	5.9	1.4
Water	21.3	5.1	2.9[c]
Lipid in dry	18.8	4.7	1.2

[a] F = ratio of mean squares due to effect divided by error mean square.
[b] All F-ratios significant, $P < 0.0001$.
[c] $P < 0.05$.

TABLE 8. Analysis of variance relating egg composition to clutch and position in laying sequence.

Variable	Effect[a]	
	Clutch $F(10,26)$	Position $F(4,26)$
Albumen (%)		
Water	14.0[b]	2.64[c]
Yolk (%)		
Water	3.3[d]	1.26
Lipid	2.6[e]	0.28
Nonlipid dry	1.1	2.02
Yolk (% dry)		
Lipid	1.5	1.29

[a] F = ratio of effect mean square divided by error mean square.
[b] $P < 0.0001$.
[c] $P = 0.057$.
[d] $P < 0.01$.
[e] $P < 0.05$.

egg composition. Of the 11 clutches, 1 was of six eggs, 7 of five eggs, and 3 of four eggs. Of the 42 eggs processed of the 53 possible, 9, 9, 10, 6, 7, and 1 were from positions 1 through 6, respectively. The single egg of position 6 was deleted from the analysis. The effect of position was determined in three separate ANOVAs or ANCOVAs.

In the first ANOVA, egg mass was related to clutch and position. As found in previous analyses, the effect of clutch was highly significant ($F[10,26] = 7.34$, $P < 0.0001$); the effect of position was, however, not significant ($F[4,26] = 0.93$, $P = 0.46$). The error standard deviation, 0.39 g, was large compared to the variation among positions in mass (averages 7.49, 7.23, 7.25, 7.10, 7.33 for positions 1 to 5).

In the second ANCOVA, five variables that are correlated with egg mass (dry shell, albumen, yolk, and water fractions of the whole egg, and lipid fraction of the dried egg contents) were related to egg mass, clutch, and position (Table 7). The albumen and water fractions of the egg varied significantly with respect to position. The mean values for albumen fraction, adjusted for egg mass and clutch, were 0.725, 0.716, 0.717, 0.727, and 0.717 for positions 1 to 5 (error SD = 0.0080). Eggs 1 and 4 had significantly higher values than eggs 2, 3, and 5, indicating no trend with respect to position. The water fraction of the whole egg decreased from 0.787 to 0.786, 0.784, 0.783, and 0.781 over positions 1 to 5 (error SD = 0.0035). To determine whether this trend was significant or not, I tested contrasts for two models. The linear contrast was significant ($F[1,25] = 10.75$, $P = 0.0003$). Adding a quadratic contrast did not increase the explained sum of squares appreciably, indicating that the trend was not significantly different from linear.

In the third ANOVA, five variables that were not significantly correlated with egg mass were related to clutch and position (Table 8). Although the water fraction of the yolk did not vary significantly among positions, the linear contrast was just significant ($F[1,26] = 4.30$, $P = 0.048$). The adjusted means (0.559, 0.558, 0.557, 0.549, 0.550, error SD = 0.010) indicated a decrease with laying sequence. Of the remaining variables, position bordered on being a significant effect only for the water fraction of the albumen ($P = 0.057$). For this variable, however, the linear contrast was highly significant ($F[1,26] = 9.13$, $P = 0.0056$). The adjusted means (0.8998, 0.8997, 0.8990, 0.8965, 0.8969, error SD = 0.0024) suggested a decreasing trend, with eggs 4 and 5 having about 0.3% less water in the albumen than eggs 1, 2, and 3. Linear and quadratic contrasts for the other variables were not significant. As one might have expected, egg position did not contribute significantly to variation in scores on principal components I, II, or III.

DISCUSSION

The principal results of my analysis may be summarized as follows: (1) The major components of variation in egg composition were related to the overall size of the egg, the relative size of the yolk, and the fraction of lipid in the dry content of the yolk. (2) The size of the yolk was only weakly correlated with the overall size of the egg; the lipid fraction of the dried yolk not at all. (3) Most indices of egg composition varied significantly between clutches, with clutch explaining 50 to 80% of the total variance, in agreement with the findings of Ojanen et al. (1979) on egg size in several passerines. Lipid fraction of the dried yolk did not vary among clutches. (4) With respect to position in the laying sequence, only the water fraction showed a significant trend, decreasing slightly from first to last.

Because variation in egg composition has not been reported in such detail in the past, there is no basis for comparing the eggs of the European Starling with other species. The eggs of the starling are similar to those of other altricial species in having small yolk and lipid fractions (Ricklefs 1977a). Although few species have been investigated, it appears that yolk size is poorly correlated with egg weight in altricial birds (see Ricklefs and Montevecchi 1979), whereas, the two are strongly correlated in precocial species (Romanoff and Romanoff 1949, Ricklefs et al. 1978).

Egg size in the starling appears to be unrelated to position in the laying sequence, in contrast to Howe's (1976, 1978) findings on the Common Grackle (*Quiscalus quiscula*). Ojanen et al. (1981) surveyed several studies on

passerines and found that egg size increased with position in the clutch in 14 species, decreased in 4 species, and showed no regular trend in 4 species, including the European Starling. Howe (1976) and O'Connor (1978) interpreted patterns in intraclutch variation in egg size in terms of the relationship of relative egg size to sibling competition. Although the mass of passerine neonates is directly related to egg size within species (Schifferli 1973, Howe 1976, Nolan and Thompson 1978), and a further effect of egg size on nestling growth is plausible (Schifferli 1973, O'Connor 1975), the potential influence of egg size on intrabrood relationships must be small compared to the manipulation of the time of hatching by the parent. Further information concerning the influence of egg size and composition on neonate quality and subsequent growth in experimentally controlled competitive environments would seem necessary before intraclutch patterns in egg size can be interpreted.

Although most indices of egg composition also were unrelated to position, the water fraction of the egg decreased significantly, suggesting a change in the secretory function of the oviduct during the laying sequence. The water fraction of the albumen also varied significantly among clutches, and perhaps may provide a useful index to some aspect of the physiological state of the female.

Data on the composition of starling eggs should give caution to the use of egg size or mass as a measure of egg "quality." Large eggs provide more albumen and more water, but egg size is a poor predictor of yolk size and provides even less information concerning the lipid content of the egg. Samples of one or two eggs from within a clutch can provide information on the size of the yolk of the remaining eggs but not of the lipid fraction of the dried yolk. As yet, no information is available concerning the relationship of egg composition to the size or nutritional and hormonal status of the female, or to the size and quality of the neonate and its subsequent development.

ACKNOWLEDGMENTS

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