ART. 5. VARIATION OF THE SHAPES OF BIRDS' EGGS
WITHIN THE CLUTCH

by
F. W. PRESTON* AND E. J. PRESTON†

INTRODUCTION

In a previous paper, one of us (F. W. Preston‡) discussed a method of
describing with precision the shapes of individual eggs. The size of the egg
may be defined by its length (l or 2a), and its ellipticity by the ratio of its
(equatorial) diameter to its length (2b/l). In that paper ovateness is indi-
cated by a constant, c₁, and the biconical aspect by a second constant, c₂.
Alcids need a third constant, c₃, but very few others do.

In the present paper we are not concerned with Alcids, since they lay
only one egg to a clutch, and there is thus no comparison between the first
and second or last eggs of a clutch.

The problem of the present paper is to see whether there is any significant
difference between the eggs of a clutch, and if so, what that difference is.
A glance at almost any clutch of eggs will show that they are of different
shapes, and perhaps of somewhat different sizes. They may differ also in
degree of pigmentation, either of ground color or of spotting, or both, and
again they may differ markedly in gloss. The question, therefore, can be
formulated more precisely. Are there differences connected with the sequence
of laying, and are the differences correlated in any way?

On a visit to the Pea Island Refuge, North Carolina, in June 1951 with
L. B. Turner, the refuge manager, one of us saw a modest number of late
nests of the Laughing Gull (Larus atricilla). Most of these contained
only two eggs. Of the two, one was much more brilliantly pigmented and
more pyriform (had a higher c₁ value) than the other, which was paler,
duller, and more nearly elliptical. At the time we set down the more brilliant
egg as the first of a clutch of two, but lacked proof of it. The assumption
was based on observations of other species long antedating this occasion.

Several years ago Earl Schriver, in a conversation, said that the English
Sparrow (Passer domesticus) typically lays five eggs, of which the last is less
pigmented, more nearly elliptical (less ovate), and commonly smaller than
the others. He described it as a "runt" egg, and believed it to be the last
laid. Examination of a nest or two in the Frith (grounds of the Preston
Laboratories, Butler, Pa.) indicated a possibility that he might be right,
but an examination of 20 clutches at the Ohio State Museum, through the
courtesy of Dr. E. S. Thomas, was inconclusive. Mr. Schriver also said that
in his experience, the American Crow (Corvus brachyrhynchos) also tended
to lay one "runt" egg. Again, an examination of museum clutches, this time
at Carnegie Museum, Pittsburgh, failed to be conclusive. One of the
difficulties with museum clutches is that the sequence of laying is unknown,
and there is commonly some uncertainty as to whether the clutch is com-
plete. An appeal for clutches where the sequence was known and in which
it was certain that all eggs were present produced very little result. We had

*† Preston Laboratories, Butler, Pa.
‡ F. W. Preston. The shapes of birds' eggs. The Auk, April, 1953, v. 70, p. 160-182.
129

Issued August 15, 1953
two clutches of Turkey Vulture eggs loaned us by Homer Price of Payne, Ohio, and one clutch of Black-crowned Night Heron by Laurel Van Camp of Genoa, Ohio. The latter showed that the last two eggs had a $c_1$ value lower than the first, while $c_2$ had a higher (negative) value for the second egg. With the help of a young friend, James Glenn, we measured a number of clutches of American Robin eggs in the Frith and nearby, but the labor was great for the results achieved. Accordingly, it became clear that what was wanted was a species which (1) nested colonially in large numbers, (2) nested on the ground so that the nests could be inspected quickly, (3) laid few eggs, preferably two but not more than three, and (4) preferably laid eggs about the size of those of the domestic fowl, which would lend themselves to easy contouring and measuring by the machine described in the previous paper and by a spherometer.

After studying various possibilities, it seemed to us that the best available material would be the nests of the Laughing Gull in southern New Jersey, near Stone Harbor. We were fortunate in having the help of Herbert H. Mills of the T. C. Wheaton Company, an excellent amateur ornithologist, and of Burritt Wright and his assistant, Stanley Quickmire, of the Audubon Center of South Jersey. This paper accordingly reports primarily on that material.

**Field Work**

*Larus atricilla* nests by thousands on a vast acreage of saltings just west (inland) from Stone Harbor. The nests are often no more than two or three feet apart. It is possible to land readily in occasional coves, tie up the boat, and immediately begin operations among hundreds of nests. A rattan cane is pushed into the soft peat-muck beside a nest that contains only one egg. On that egg a large cross is marked with colored crayon, perhaps green. This is repeated until 50 nests are tagged on the first day.

The next day all tagged nests are re-examined, and if a second egg is found, it is marked with a big cross in red crayon. The third day a purple crayon is used, and so on. All 50 nests will not proceed to completion, but with luck, at least twenty complete clutches will be obtained. The complete clutch will usually contain three eggs. When the clutch is known to be complete in at least twenty nests, all of the eggs are contoured and spherometered. This can be done in the field if the weather is good.

Apart from clutches that were measured in the field, we found it necessary (because of rain) to collect about twenty for more detailed work at Butler. We had equally bad luck with weather in trying to perform the same experiment on eggs of the Common Tern and other species. Accordingly, the only species on which we have statistically significant data is the Laughing Gull. With this information worked out, we can get some further evidence from the others.

**The Statistics Available**

The sequence of laying in each nest is known. The nests are labeled A, B, C, etc., and the eggs in each nest are labeled in the sequence of their
laying as A1, A2, A3, for example. When there are only two eggs, they are called U1 and U2 (for example) though, as will be shown later, they would better be called U1 and U3, or U2 and U3.

After measuring, profiling, and computing, we have the following characteristics available for statistical analysis:

(1) length l, (2) maximum diameter, here called B, (3) equatorial diameter, here called 2b, in accordance with the previous paper, (4) the "cubage" \( lB^2 \), a figure roughly proportional to the volume of the egg, (5) the ellipticity, \( 2b/l \), (6) the radius of curvature of the big, or blunt, end, \( R_B \), (7) the radius of curvature of the small, or pointed, end, \( R_p \), (8) the ratio of these radii \( R_p/R_B \), (9) the constant, \( c_1 \), or ovateness, as defined in the previous paper, (10) the constant, \( c_2 \), the biconical term. These figures are tabulated in Table I, though in a different arrangement.

We also know, as above explained, that any egg labeled A, for instance, was laid by a particular bird (unless the birds parasitize each other) and that any egg with a different label (B, or C, for instance) was not laid by this particular bird, for all nests were contemporaneous, and we can not be dealing with the same bird on two different occasions.

The questions to be asked are as follows:

Eggs may differ from one another because they are laid by different individual birds; they may also differ according to whether they are first, second or third in the sequence of laying. They may differ for other reasons, perhaps many reasons, all lumped together in what follows, and classified as "error." In this sense, error includes any inaccuracies of measurement or computation and any variability due to any cause whatever, except the consequences of being laid by another parent or being of a different ordinal number in the clutch.

The first question, then, is this. In what respects (i.e., in respect of which of the characteristics of Table I) do eggs differ according to their order in the clutch? More briefly, is the last egg of a clutch significantly different from the first?

The second question is: In what respects do all eggs of a clutch bear the imprint of their parent and differ from eggs of another parent?

These two questions require an "analysis of variance," partitioning the actual variance among three factors — (1) the ordinal number in the clutch, (2) the variation between parents, and (3) the "error" or all other causes of variability.

As a practical matter, the problems would be these: "Here are three eggs of a clutch. Pick out the first, second, and third in their sequence of laying."

Or, a much more difficult assignment: "Here are 60 eggs, comprising 20 clutches each of three eggs, all shuffled. Pick out all the eggs that were the last in a clutch. Also sort the eggs into the 20 original clutches; i.e., identify the parentage of each egg."

There is a still more difficult problem: "Here are 60 eggs (or 600) picked at random from a large number of nests of a single species of bird. Determine the most probable clutch size of the species."
## TABLE I

(Values of $B$, $R_B$ and $R_P$ are in inches.)

| Egg | Length $I$ (inches) | Max. width $B (= B_{max.})$ | $R_B$ | $R_P$ | Ovateness $c_1$ | Biconicalism $c_2$ | Cubage $lb^3$ (cu. in.) | $R_P/R_R$ | Equatorial diam. 2b (mm.) | Ellipticity 2b/l |
|-----|---------------------|----------------------------|-------|-------|-----------------|------------------|-----------------------|-----------|--------------------------|---------------|
| A1  | 2.225               | 1.565                      | 0.612 | 0.298 | 0.193           | -0.105           | 5.454                 | 0.486     | 39.0                     | 0.688         |
| A2  | 2.110               | 1.554                      | 0.715 | 0.337 | 0.182           | -0.057           | 5.099                 | 0.471     | 38.9                     | 0.723         |
| A3  | 2.156               | 1.513                      | 0.646 | 0.301 | 0.216           | -0.083           | 4.888                 | 0.465     | 37.8                     | 0.701         |
| B1  | 2.158               | 1.507                      | 0.721 | 0.388 | 0.240           | -0.086           | 4.903                 | 0.400     | 37.5                     | 0.689         |
| B2  | 2.110               | 1.509                      | 0.647 | 0.358 | 0.164           | -0.068           | 4.807                 | 0.554     | 38.1                     | 0.712         |
| B3  | 2.102               | 1.438                      | 0.555 | 0.340 | 0.140           | -0.048           | 4.346                 | 0.612     | 36.2                     | 0.679         |
| C1  | 2.175               | 1.581                      | 0.726 | 0.373 | 0.206           | -0.083           | 5.437                 | 0.514     | 39.6                     | 0.722         |
| C2  | 2.035               | 1.557                      | 0.707 | 0.372 | 0.178           | -0.063           | 4.985                 | 0.525     | 39.0                     | 0.750         |
| C3  | 2.165               | 1.540                      | 0.628 | 0.375 | 0.143           | -0.104           | 5.192                 | 0.597     | 39.0                     | 0.711         |
| D1  | 2.230               | 1.608                      | 0.661 | 0.318 | 0.187           | -0.099           | 5.770                 | 0.482     | 40.4                     | 0.713         |
| D2  | 2.152               | 1.552                      | 0.686 | 0.386 | 0.212           | -0.102           | 5.184                 | 0.417     | 38.9                     | 0.711         |
| D3  | 2.168               | 1.538                      | 0.656 | 0.369 | 0.176           | -0.046           | 5.131                 | 0.562     | 38.6                     | 0.702         |
| E1  | 2.226               | 1.565                      | 0.721 | 0.404 | 0.159           | -0.028           | 5.452                 | 0.561     | 39.2                     | 0.696         |
| E2  | 2.203               | 1.540                      | 0.645 | 0.396 | 0.149           | -0.058           | 5.226                 | 0.614     | 38.7                     | 0.696         |
| E3  | 2.184               | 1.535                      | 0.557 | 0.369 | 0.123           | -0.115           | 5.151                 | 0.647     | 38.9                     | 0.702         |
| G1  | 2.115               | 1.606                      | 0.723 | 0.294 | 0.248           | -0.108           | 5.707                 | 0.407     | 39.8                     | 0.718         |
| G2  | 2.201               | 1.616                      | 0.709 | 0.310 | 0.214           | -0.150           | 5.749                 | 0.437     | 40.2                     | 0.724         |
| G3  | 2.065               | 1.599                      | 0.714 | 0.392 | 0.203           | -0.117           | 5.278                 | 0.465     | 40.0                     | 0.773         |
| H1  | 2.180               | 1.567                      | 0.701 | 0.399 | 0.188           | -0.020           | 5.358                 | 0.569     | 39.0                     | 0.709         |
| H2  | 2.132               | 1.545                      | 0.689 | 0.360 | 0.188           | -0.009           | 5.090                 | 0.522     | 38.6                     | 0.721         |
| H3  | 2.149               | 1.476                      | 0.647 | 0.359 | 0.168           | -0.018           | 4.683                 | 0.555     | 37.1                     | 0.680         |
| I1  | 2.159               | 1.543                      | 0.701 | 0.417 | 0.156           | +0.008           | 5.141                 | 0.595     | 38.7                     | 0.707         |
| I2  | 2.184               | 1.563                      | 0.677 | 0.330 | 0.207           | -0.008           | 5.335                 | 0.488     | 39.1                     | 0.708         |
| I3  | 2.166               | 1.512                      | 0.594 | 0.336 | 0.161           | -0.070           | 4.952                 | 0.566     | 38.0                     | 0.691         |
| J1  | 2.226               | 1.523                      | 0.551 | 0.568 | 0.172           | -0.057           | 5.164                 | 0.668     | 38.1                     | 0.679         |
| J2  | 2.060               | 1.538                      | 0.677 | 0.373 | 0.154           | -0.034           | 4.873                 | 0.550     | 38.6                     | 0.739         |
| J3  | 2.056               | 1.493                      | 0.612 | 0.321 | 0.155           | -0.095           | 4.587                 | 0.525     | 37.6                     | 0.723         |
| K1  | K2  | K3  | L1  | L2  | L3  | M1  | M2  | M3  | N1  | N2  | N3  | O1  | O2  | O3  | P1  | P2  | P3  | Q1  | Q2  | Q3  | R1  | R2  | S1  | S2  | T1  | T2  | U1  | U2  |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 2.121 | 2.194 | 2.039 | 2.192 | 2.122 | 2.125 | 2.151 | 2.172 | 2.158 | 2.154 | 2.182 | 2.125 | 2.134 | 2.203 | 2.189 | 2.51 | 2.062 | 1.969 | 2.128 | 2.145 | 2.260 | 2.463 | 2.272 | 2.212 | 2.089 | 2.156 | 2.044 | 2.111 | 2.060 |
| 1.551 | 1.543 | 1.544 | 1.633 | 1.591 | 1.581 | 1.506 | 1.502 | 1.468 | 1.510 | 1.556 | 1.464 | 1.511 | 1.480 | 1.459 | 1.41 | 1.450 | 1.392 | 1.520 | 1.557 | 1.505 | 1.510 | 1.527 | 1.496 | 1.468 | 1.575 | 1.532 | 1.579 | 1.527 |
| 0.688 | 0.660 | 0.695 | 0.789 | 0.685 | 0.654 | 0.664 | 0.651 | 0.574 | 0.592 | 0.619 | 0.527 | 0.622 | 0.631 | 0.612 | 0.536 | 0.648 | 0.564 | 0.605 | 0.669 | 0.595 | 0.605 | 0.582 | 0.578 | 0.706 | 0.620 | 0.660 | 0.624 |
| 0.373 | 0.331 | 0.390 | 0.361 | 0.347 | 0.437 | 0.340 | 0.346 | 0.360 | 0.325 | 0.275 | 0.312 | 0.410 | 0.365 | 0.387 | 0.238 | 0.290 | 0.342 | 0.338 | 0.331 | 0.301 | 0.316 | 0.309 | 0.316 | 0.380 | 0.386 | 0.431 | 0.408 |
| 0.177 | 0.203 | 0.197 | 0.215 | 0.190 | 0.116 | 0.174 | 0.182 | 0.125 | 0.195 | 0.196 | 0.161 | 0.148 | 0.169 | 0.139 | 0.238 | 0.216 | 0.146 | 0.177 | 0.210 | 0.201 | 0.166 | 0.192 | 0.151 | 0.164 | 0.110 | 0.147 |
| -0.058 | -0.059 | -0.056 | -0.071 | -0.107 | -0.064 | -0.008 | -0.058 | -0.040 | -0.049 | -0.134 | -0.093 | 4.559 | 4.871 | 4.828 | 4.603 | +0.015 | -0.073 | -0.037 | -0.084 | -0.068 | -0.053 | +0.043 | 5.621 | 5.301 | 4.952 | 4.504 | -0.018 | -0.067 | 4.295 | 4.807 |
| 5.106 | 5.227 | 4.858 | 5.845 | 5.374 | 5.315 | 4.882 | 4.900 | 4.652 | 4.912 | 5.287 | 5.591 | 5.619 | 5.678 | 4.663 | 4.999 | 4.339 | 3.815 | 4.916 | 5.199 | 5.123 | 5.621 | 5.301 | 4.952 | 4.504 | 5.852 | 4.795 | 5.266 | 4.807 |
| 0.543 | 0.501 | 0.560 | 0.457 | 0.506 | 0.669 | 0.512 | 0.531 | 0.627 | 0.567 | 0.445 | 0.591 | 0.619 | 0.578 | 0.632 | 0.68 | 0.447 | 0.607 | 0.558 | 0.495 | 0.506 | 0.637 | 0.572 | 0.532 | 0.547 | 0.538 | 0.623 | 0.653 | 0.653 |
| 38.8 | 38.5 | 39.0 | 40.7 | 39.7 | 39.8 | 37.8 | 37.6 | 36.8 | 37.6 | 39.0 | 36.7 | 38.0 | 36.8 | 36.9 | 34.8 | 36.1 | 35.0 | 38.2 | 38.8 | 37.6 | 37.6 | 38.2 | 37.3 | 37.0 | 39.4 | 38.6 | 39.5 | 38.2 | 0.720 | 0.738 | 0.730 |
| 0.725 | 0.690 | 0.760 | 0.741 | 0.740 | 0.739 | 0.692 | 0.686 | 0.677 | 0.686 | 0.702 | 0.663 | 0.701 | 0.659 | 0.668 | 0.545 | 0.691 | 0.716 | 0.655 | 0.712 | 0.716 | 0.655 | 0.663 | 0.671 | 0.696 | 0.720 | 0.738 | 0.730 |
Results

It is not necessary to go through all the intricate computations that were made. We can simplify matters by reporting the outcome of most of them very briefly. There were available 16* clutches of three eggs each, and four clutches of two eggs each. On the basis of these clutches, we find:

1. The most striking thing is that eggs fall into two categories, “normal” eggs and “terminal” eggs. The first and second eggs of a clutch of three are not safely distinguishable from one another by any of our statistical “characteristics,” but the third egg can be picked out from the others. When a clutch consists of only two eggs, one egg is “normal” and the other terminal. This confirms the impressions of Mr. Schriver and our own suspicions at Pea Island.

2. The length \( l \) of the egg does not differ significantly either between the eggs of a clutch or between the eggs of different parents. It is therefore of no statistical use for our present questions. On the other hand, the maximum width \( B \) is very significantly different between the third egg of a clutch and the others. It is less for the third egg, and given that three eggs come from a single clutch, the third may be picked out with almost mathematical precision by choosing the one with lowest maximum diameter.

3. The curvature of the small end of an egg is without significance, but the curvature of the blunt end is highly significant, the third egg of a clutch having a low value of \( R_B \). The ratio \( R_p/R_B \), somewhat surprisingly, is almost without significance.

4. The ellipticity \( (2b/l) \), like \( l \) itself, is of no significance in attempting to sort out clutches from one another, or in sorting out the sequence of a clutch. Also, we find no use for the cubage since the significant element is \( B \) itself.

5. The constant, \( c_p \), does not differ significantly within a clutch, and between different clutches it differs hardly consistently enough to be useful in practice. The other constant, \( c_t \), on the other hand, differs very significantly within clutches, though between different clutches it is not so significant in this respect as \( B \). It is, therefore, likely to prove most useful in separating out terminal eggs from a large batch of assorted eggs.

It follows that, of the various statistics, only three are useful, or “significant,” for our purposes, \( B, R_B \) and \( c_t \). These, however, are not all useful for the same purposes, and the precise question that is asked will determine which characteristic should be analyzed.

If we are given three eggs of a clutch and are told to pick out the third egg, we use \( B \).

If we are given 60 eggs and told to pick out the 20 “last” eggs, we use \( c_t \).

If we are given six eggs and are told that they comprise two clutches, and are told to separate them into those two clutches, our best plan would be to operate with \( B \).

* There were 16 for profile work, but only 15 for end curvature determinations (because of an accident).
It seems that $R_B$ tends to parallel $c_i$, but it is, theoretically, only partially dependent on $c_i$, and is partly independent. Its field of utility is perhaps a little less than that of $c_i$, but it must be remembered that it is more easily measured, if a spherometer of the right kind is on hand.

In Table II are listed our findings as to the "significance," and hence the utility, of the various characteristics. The percentage of the variance assignable to the three categories (ordinal number in the clutch, different parentage, and "error") is also given. The method of computation is as follows.

The total variance of each characteristic is first partitioned into that due to sequence in a clutch, that due to different parentage, and the "error." Estimates of each of these, isolated from the other two, are computed. If there were $m$ clutches of $n$ eggs each, the mean value of the characteristic for the $L$th clutch was $x_L$, and the mean for all $l$th eggs was $x_l$, the mean of the total being $\bar{x}$, we should have:

$$\text{Variance due to sequence} = m \sum_{l} \frac{(x_l - \bar{x})^2}{n(n-1)} = V_s$$

$$\text{Variance due to parentage} = n \sum_{L} \frac{(x_L - \bar{x})^2}{m(m-1)} = V_p$$

$$\text{Variance due to "error"} = \sum \frac{(x - \bar{x})^2 - m \sum_{L} \frac{(x_L - \bar{x})^2}{m} - n \sum_{l} \frac{(x_l - \bar{x})^2}{n}}{(m-1)(n-1)} = V_e$$

The ratios $\frac{V_s}{V_e}$ = Sequence variance Error and $\frac{V_p}{V_e}$ = Parentage variance Error are then found. These ratios are measures of the significance of the variances due to sequence and parentage. If there were in reality no variance other than error (i.e., the true value of the computed ratio were zero), the ratio computed from a small sample, although not zero (owing to sampling errors) would generally be small. In fact, in 99% of computations on similar small samples, its value would not exceed a certain limit, called the 1% point, and in 19 such trials out of 20, its value would not exceed a certain (smaller) limit, called the 5% point. G. W. Snedecor’s tables* of these 1% and 5% points, or F values, for different sized samples, were used in the present investigation as the criterion of significance of variance. Thus, if the computed ratio exceeded the 1% point, the variance was considered "significant"; if it was less than the 5% point, the variance was "not significant"; while if the value of the ratio was between the 1% and 5% points, the variance was called "barely significant."

The computed ratios, F values, and significances relating to the variances of the different characteristics are tabulated in Table II.

* G. W. Snedecor. Statistical methods, applied to experiments in agriculture and biology. Ed. 4, 1946. Collegiate Press, Inc., Ames, Iowa.
| No. clutches analyzed | l (inches) | B (inches) | lB² (cu. in.) | R₉ (inches) | R₉(1) (inches) | R₉/R₉(1) | c₁ | c₂ | 2b/l |
|----------------------|-----------|-----------|---------------|-------------|---------------|-----------|-----|-----|------|
|                      | 15        | 15        | 15            | 15          | 15            | 15        | 15  | 16  | 16   |
| Computed variance    |           |           |               |             |               |           |     |     |      |
|                      | (Sequence:| 2.35      | 21.84         | 17.60       | 8.73          | 0.85      | 5.25 | 10.81 | 2.58 | 1.09 |
|                      | (Parentage:| 0.74      | 11.83         | 6.55        | 2.34          | 2.77      | 2.18 | 2.12 | 3.19 | 1.90 |
|                      | F value for 1% level |          |               |             |               |           |     |     |      |
|                      | (Sequence:| 5.45      | 5.45          | 5.45        | 5.45          | 5.45      | 5.45 | 5.39 | 5.39 | 5.39 |
|                      | (Parentage:| 2.80      | 2.80          | 2.80        | 2.80          | 2.80      | 2.80 | 2.70 | 2.70 | 2.70 |
|                      | F value for 5% level |          |               |             |               |           |     |     |      |
|                      | (Sequence:| 3.34      | 3.34          | 3.34        | 3.34          | 3.34      | 3.34 | 3.32 | 3.32 | 3.32 |
|                      | (Parentage:| 2.06      | 2.06          | 2.06        | 2.06          | 2.06      | 2.06 | 2.02 | 2.02 | 2.02 |
| Significance         |           |           |               |             |               |           |     |     |      |
|                      | (Sequence:| no        | yes           | yes         | yes           | no        | barely | yes | no   | no   |
|                      | (Parentage:| no        | yes           | yes         | barely        | barely | yes | no   | no   |
| Variability          |           |           |               |             |               |           |     |     |      |
|                      | (Sequence:| 0.000118  | 0.00246       | 0.1719      | 0.00448       | 0.00000  | 0.00419 | 0.00180 | 0.00044 | 0.00011 |
|                      | (Parentage:| 0.00000   | 0.00026       | 0.0115      | 0.00015       | 0.00011  | 0.00023 | 0.00004 | 0.00012 | 0.00020 |
|                      | Error:    | 0.00259   | 0.00335       | 0.0311      | 0.00174       | 0.00090  | 0.00235 | 0.00055 | 0.00085 | 0.00354 |
|                      | Total:    | 0.00377   | 0.00337       | 0.2145      | 0.00637       | 0.00101  | 0.00737 | 0.00239 | 0.00141 | 0.00385 |
| Partition of variability (%) |       |           |               |             |               |           |     |     |      |
|                      | (Sequence:| 31.3      | 80.1          | 80.1        | 70.3          | 0.0      | 56.9  | 75.3  | 31.2  | 26.2 |
|                      | (Parentage:| 0.0       | 8.5           | 5.4         | 2.4           | 2.4      | 10.9  | 3.1   | 1.7   | 8.5  |
|                      | Error:    | 68.7      | 11.4          | 14.5        | 27.3          | 89.1     | 40.0  | 23.0  | 60.3  | 91.9 |
| Coefficient of variation (%) |       |           |               |             |               |           |     |     |      |
|                      | (Sequence:| 1.6       | 3.2           | 8.0         | 10.2          | 0.0      | 12.1  | 23.7  | 34.1  | 0.8  |
|                      | (Parentage:| 0.0       | 1.0           | 3.3         | 1.9           | 2.9      | 3.5   | 17.5  | 1.0   | 1.0  |
|                      | Error:    | 2.4       | 1.2           | 3.4         | 6.4           | 8.6      | 10.1  | 13.1  | 47.1  | 4.2  |
| Mean value of characteristic for |       |           |               |             |               |           |     |     |      |
|                      | 1st egg:  | 2.178     | 1.553         | 5.26        | 0.674         | 0.354    | 0.526 | 0.192 | -0.0489 | 1.390 |
|                      | 2nd egg:  | 2.148     | 1.547         | 5.14        | 0.671         | 0.341    | 0.558 | 0.188 | -0.0715 | 1.421 |
|                      | 3rd egg:  | 2.139     | 1.511         | 4.89        | 0.618         | 0.352    | 0.570 | 0.157 | -0.0650 | 1.406 |
|                      | All eggs: | 2.155     | 1.537         | 5.10        | 0.654         | 0.349    | 0.534 | 0.179 | -0.0618 | 1.406 |
Next, the relative importance of the different causes of variance is determined by computing the variability, $\sigma^2$, as follows:

- Variability due to sequence $= \sigma_s^2 = \frac{V_s - V_e}{n}$
- Variability due to parentage $= \sigma_p^2 = \frac{V_p - V_e}{m}$
- Variability due to error $= \sigma_e^2 = V_e$

The percentage partition of variability among the three categories is then found, the total being 100%, and by extracting square roots, the coefficient of variability, $\sigma$, expressed as a percentage of the mean value of the characteristic may be computed. All these quantities are tabulated in Table II.

Analyses of variance carried out for the various characteristics on the first two eggs of each clutch alone showed no significant difference for any characteristic. Results of this are not given in Table II.

It will be obvious that there is no real prospect of identifying the parentage of an egg by any criterion listed. The question whether an egg is a normal egg or a terminal one is all that can be decided. For this purpose, $B$ is the best statistic when a single clutch is offered, and $c_1$, when a random collection is offered. This is because $c_1$ varies but little from bird to bird, but greatly between normal and terminal eggs.

Examination of the mean values of each characteristic for the first, second, and third eggs of a clutch respectively (Table II) shows that for $B$, $c_1$, and $R_B$ (the characteristics in which we are primarily interested) the third egg tends to have a value lower than the first two, which barely differ from one another, while $c_2$ tends to have a higher (negative) value for the second egg than for either of the others, though this does not occur consistently enough to be significant. It is therefore evident that the first two eggs of clutches can not be accurately distinguished from each other, but the third egg may be separated from the others with some considerable accuracy by examining their characteristics.

Accordingly, two experiments were performed on the available sample. First, the experimenter was given the $c_1$ values of 48 eggs, and the $R_B$ and $B$ values of 45 eggs, and told to identify the 16 "last" eggs of the 48-egg sample, and the 15 "last" eggs of the 45-egg sample. By choosing those eggs with the least $c_1$, $R_B$ and $B$ values in each case, and comparing with the known data, the following results were obtained.

| Characteristic used | No. of “last” eggs chosen | Fraction correct | Accuracy (%) | Random expectation of accuracy (%) |
|---------------------|---------------------------|------------------|--------------|-----------------------------------|
| $c_1$               | 11                        | 11/16            | 68.75        | 31.25*                            |
| $R_B$               | 8                         | 8/15             | 53.3         | 33.3                              |
| $B$                 | 8                         | 8/15             | 53.3         | 33.3                              |

*This value, 31.25%, or 5 out of 16, is the most probable accuracy that would be obtained in one random choice of 16 eggs from the 48. If a larger number of similar random trials were performed, the expectation would of course be 33.3%.
Secondly, the experimenter was given the information used in the first experiment, but was also told which eggs were in the same clutch. By choosing the egg from each clutch with the lowest value of \( c_i \), \( R_B \), or \( B \), the fractions of "last" eggs selected were as follows:

| Characteristic used | No. of "last" eggs chosen | Fraction correct | Accuracy (%) |
|---------------------|----------------------------|------------------|--------------|
| \( c_i \)           | 12                         | 12/16            | 75.0         |
| \( R_B \)           | 11                         | 11/15            | 73.3         |
| \( B \)             | 14                         | 14/15            | 93.3         |

The random expectations of accuracy were the same as in the first experiment. Actually, in the last case, 100% accuracy was very nearly obtained, the difference in width of the second and third eggs of the only "wrong" clutch being only 0.001 inch!

Since \( Lb^2 \) depends for its significance on \( B \), from which it is derived, it serves no useful purpose that \( B \) alone can not serve in differentiating between eggs. To make sure that \( c_i \) and \( R_B \) are not similarly related, the following formulas may be considered.

\[
R_B = \frac{2b^2}{l}(1 + c_i + c_2)^2
\]

\[
R_p = \frac{2b^2}{l}(1 - c_i + c_2)^2
\]

\[
B = b(2 + c_2^2) \text{ approx., when } 2b = \text{equatorial diameter}
\]

The connection between \( R_p \) and \( c_i \) is obviously not simple, and their significances for our purpose are not identical.

In an attempt to account, in some measure, for the different variances due to error (Table I), the experimental errors were roughly estimated. This showed that the difference in error found between \( B \) and \( c_i \) (coefficients 1.2 and 13.1, Table I) is due largely to experimental error (probable relative errors 0.19% and 9.35%); \( R_B \) also has a large relative error (1.54%).

Finally, the four two-egg clutches available were examined, and the two eggs appeared to be most similar to the first and third eggs of three-egg clutches, although the sample was much too small for any significance to be attached to this result. The two eggs differed most in \( c_i \) and \( c_2 \).

**Summary**

In general, the analysis may be said to show that the terminal egg of a clutch of the Laughing Gull differs significantly from the earlier, "normal," eggs in several particulars. It is probable that this is also true for many other birds, and if so, our results may lead to several useful applications.

Only quantitative characteristics are used in this paper. Other properties,
such as pigmentation of background or of spotting, not here reduced to
quantitative measurements, may be as useful or more so.

The fact that the terminal egg is different is here proved. The reason for
its being different is not discussed. This is presumably a matter of the
physiological condition of the parent, and this may lead to further under-
standing of the subject.

Although this paper establishes the fact that, for this particular collection
of eggs of this particular species, there is a significant difference between
terminal eggs and the other eggs of a clutch, and although the investigation
was undertaken in the hope that it might develop results applicable to birds
in general, it should be understood that no claim is made that this has been
accomplished. It may be that other species, or even the same species under
different conditions, do not show the same phenomena. However, qualitative
observations suggest that this is probably not the only collection of eggs for
which some such results would be valid.

Kendeigh* (1941) found that the weight of eggs of the House Wren
(Troglodytes aedon), near Cleveland, Ohio, varied with the temperature of
the days immediately preceding laying, and that there was an optimum
temperature (about 20 deg. C.) at which weight was greatest for May and
June clutches. The effect of temperature upon the size of eggs of the
domestic fowl had been noticed by others (See Kendeigh's bibliography). The
possibility that temperature variations may have affected the size and shape
of the eggs of the Laughing Gull herein discussed is not disproved in the
present paper, but in view of later observations is believed not to be a
major factor.

*S. Charles Kendeigh. Length of day and energy requirements for gonad develop-
ment and egg-laying in birds. Ecology, July 1941, v. 22, p. 237-248.
Preston, F. W. and Preston, E. J. 1953. "Variation of the shapes of birds’ eggs within the clutch." Annals of the Carnegie Museum 33, 129–139.

View This Item Online: https://www.biodiversitylibrary.org/item/216821
Permalink: https://www.biodiversitylibrary.org/partpdf/330888

Holding Institution
Smithsonian Libraries

Sponsored by
Biodiversity Heritage Library

Copyright & Reuse
Copyright Status: In Copyright. Digitized with the permission of the rights holder
Rights Holder: Carnegie Museum of Natural History
License: https://creativecommons.org/licenses/by-nc-sa/4.0/
Rights: https://www.biodiversitylibrary.org/permissions/

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.